ACTA AGROBOTANICA
Vol. 60 (2): 31–37
2007

“SWEET BUT DANGEROUS”: NECTARIES IN CARNIVOROUS PLANTS

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Received: 24.09.2007

Summary

In carnivorous plants, two types of nectaries occur: extra-floral nectaries, generally associated with prey luring, and floral ones associated with pollination. Nectar produced by extra-floral nectaries not only attracts prey but may also be involved in trapping prey and plays a role in myrmecophily. The diversity of nectary structure in carnivorous plants reflects complicated evolutionary routes in this unique ecological group.

Key words: nectaries, nectar, carnivorous plants, carnivorous syndrome, osmophores, pollination

INTRODUCTION

Carnivorous plants are common both in the education and science. They are useful material in children education; see several books for kids e.g.: Batten 2000 “Hungry plants”, but also for academic students. The scientific interest in carnivorous plants is still increasing (Porembski and Barthlott, 2006). Carnivorous plants are important as a model system in ecological and biological cell research (e.g. Ellison et al. 2003; Adlassnig et al. 2005; Płachno et al. 2007). They are also used as ornamental plants. Several international retailers sell carnivorous plants which are reproduced using *in vitro* cultures. Many carnivorous plants are very easily grown as home plants; others are suitable and attractive for outdoor cultivation. Especially *Sarracenia* are favorite plants for garden bogs and fens in temperate countries. Pitchers of *Sarracenia* are used by floriculturists as cut “flowers”. For this purpose, species and hybrids which produce tall and upright pitchers are preferred. It is worth mentioning that only in the USA several millions of pitchers of *S. leucophylla* are sold every year (Romanowski, 2002).

In carnivorous plants two types of nectaries occur: extra-floral nectaries which are generally associated with prey attraction and floral ones associated with pollination. The anatomy of extra-floral nectaries of carnivorous plants was summarized by Lloyd (1942), later by Juniper et al. (1989). Recently, new and important pieces of information on both extra- and floral nectaries in carnivorous plants were added by Vogel (1998). In the last years, interactions between nectaries and animals were deeply studied in *Nepenthes*. In some species of this genus, extra-floral nectaries play a role in myrmecophily (Merbach et al. 1999; Merbach et al. 2000; Merbach et al. 2007). Nectar produced by the extra-floral nectaries not only attracts prey but is also involved in trapping prey alone. The presence of a nectar film on the surface of the *Nepenthes* peristome disrupts an attachment for adhesive insect pads (Bohn and Federle, 2004). Some of nectaries in carnivorous plants may have similar role as osmophores e.g. in *Heliamphora*, nectary cells have features of cells producing monoterpenes (Płachno et al. 2007a). Also, progress in cultivation of “difficult”, rare and endangered carnivorous plants and in exploration of their unique habitats such as: tepuis, ghats, and tropical forest, improves our knowledge on both prey attraction and pollination in this special ecological group of plants.

The aim of this paper is to shortly summarize recent knowledge on nectaries in selected genera of carnivorous plants.

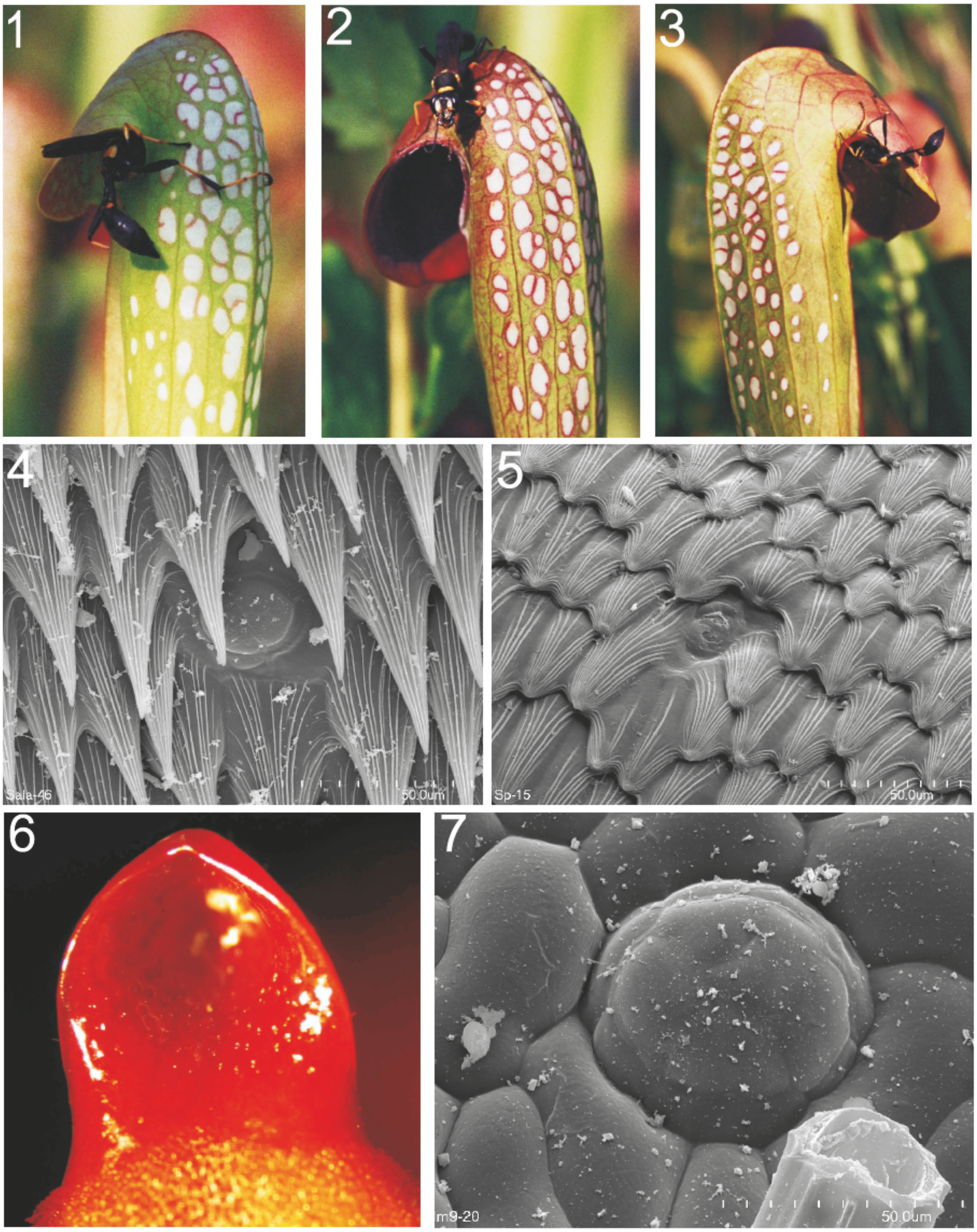
Survey of the genera

Extrafloral nectaries

Extra-floral nectaries occur in carnivorous plants, forming pitfall traps (*Darlingtonia*, *Heliamphora*, *Sarracenia, Cephalotus*, *Nepenthes*), and in *Dionaea* forming snap-trap (Juniper et al. 1989).

Sarracenia

Nectaries occur in the attractive zone of the pitcher, including the inside of the lid, and are especially abundant on the peristome surface (Figs 1-3). Nectaries form nectar guides on the outer pitcher surface (Juniper et al. 1989; Vogel, 1998). The nectary



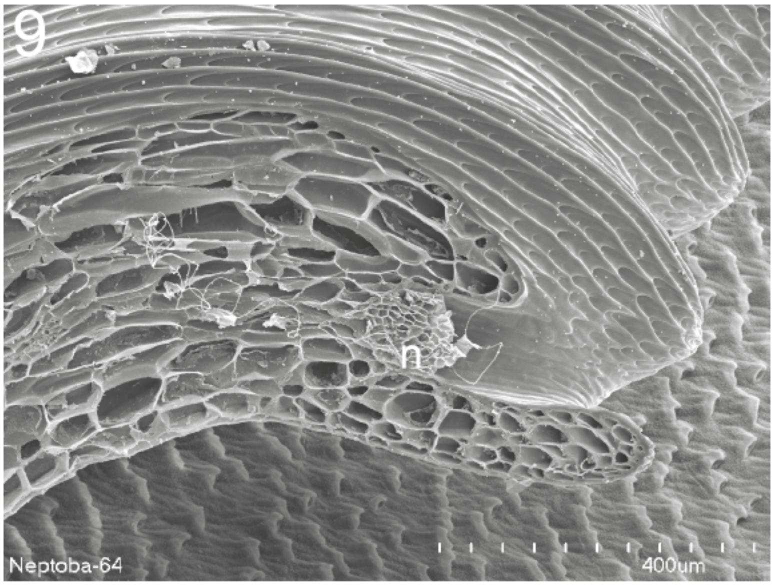
Figs 1–3. Wasps looking for nectar on the pitchers of *Sarracenia minor*, Meadowview Biological Research Station, Virginia, USA.

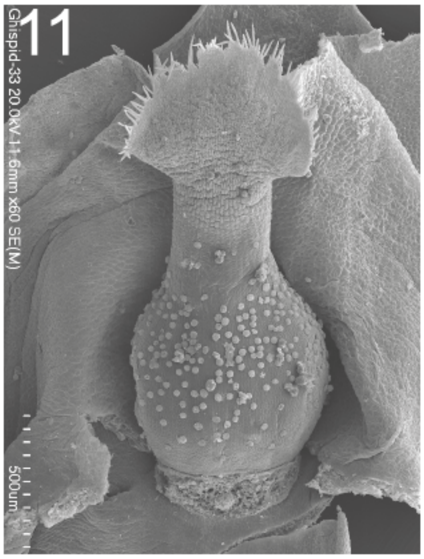
Fig. 4. Nectary fom the attractive zone of the pitcher of *S. alabamensis*.

Fig. 5. Nectary fom the attractive zone of the pitcher of *S. purpurea*.

Fig. 6. The nectar spoon of *Heliamphora heterodoxa* pitcher, note nectar drop.

Fig. 7. Small nectary fom the attractive zone of the pitcher of *Heliamphora minor*.





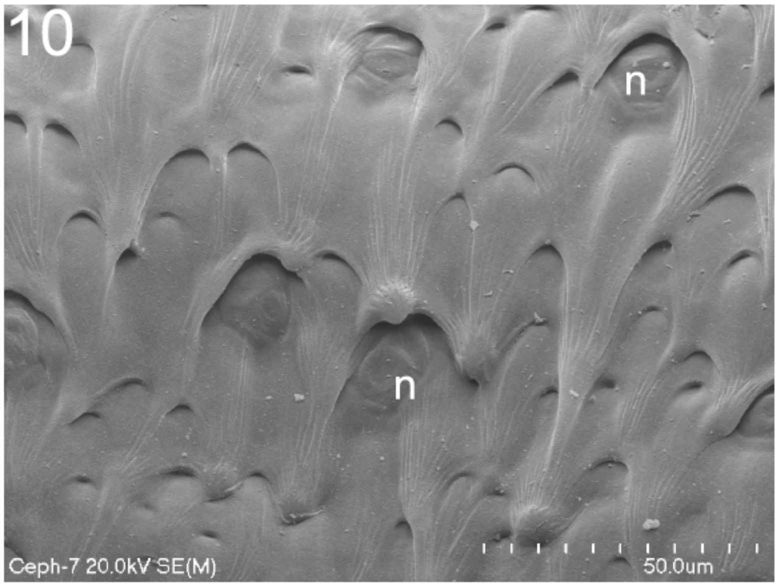


Fig. 8. Pitcher of *Nepenthes* hybride with magnificent peristome.

Fig. 9. Peristome nectary (n) of *Nepenthes tobaica*.

Fig. 10. Nectaries (n) from the pitcher of *Cephalotus follicularis*.

Fig. 11. Style of *Utricularia australis* with numerous small nectaries.

from the attractive zone of the pitcher has similar architecture across the genus ("*Sarracenia*-type" Figs 4-5) and consists of 10–12 cells. Its base has a contact with two to five cells with reticulate or spirally thickened cell walls (Lloyd, 1942). The density is 30–50 nectaries per mm^2 in the attractive zone of the pitcher (Vogel, 1998).

Darlingtonia

Darlingtonia californica Torrey, endemic to southern Oregon and northern California, USA, forms tall pitchers with a characteristic fishtail appendage, which directs a potential prey towards the trap entrance, hence the common name of this plant is "cobra lily". Insects are attracted by the sweet fragrance, nectar, and also by appendage coloration (e.g., Schnell, 2002; Rice, 2006). The nectar is secreted by the extrafloral nectaries which occur on the fishtail appendage, mouth, and hood of the pitcher. They are small, few-celled, and completely sunken in parenchyma (Lloyd, 1942). Nectar lures many insects, e.g., wasps, however, the trap is very ineffective because only about 2% of visiting insects are caught (Dixon et al. 2005).

Heliamphora

In *Heliamphora* there are two kinds of nectaries: giant ones restricted to the nectar spoon (Fig. 6) and small ones (Fig. 7) which occur on the outer and partly on the inner pitcher surface. The latter type of nectaries has a basic structure very similar to the extra-floral nectaries of *Sarracenia*; "*Sarracenia*-type" (Lloyd, 1942; Vogel, 1998). The giant nectaries are the major source of nectar, their anatomy was perfectly described using light microscopy by Lloyd (1942). However, their ultrastructure has just recently been studied (Płachno et al. 2007a). It is worth mentioning *Heliamphora folliculata*, a species which forms a chamber to store nectar (Wistuba et al. 2001). However, nectaries of this species have similar architecture as other species in this genus (Płachno et al. 2007a). In some species, nectar production is very large, and nectar trickles from nectar spoon to the interior of the pitcher (McPherson, 2007). *H. neblinae* has mutual interactions with ants which protect traps. It produces nectar collected by ants which, what is more interesting, use the old, dead traps as nests (McPherson, 2007). *Heliamphora* traps produce not only nectar but also several volatile compounds, e.g. enol diacetal monoterpene (sarracenin), erucamide, phenol, cinerone, phenylacetaldehyde and methyl esters for prey attraction (Jaffé et al. 1995).

Nepenthes

Extrafloral nectaries occur in the whole *Nepenthes* plant (stem, leaves, and inflorescence), excluding petals where the floral nectaries occur (Macfarlane, 1908; Merbach, 2001). There are differences in distribution, quantity, and size of nectaries among species (Merbach et al. 2001). After Merbach (2001), there are the three main types of extrafloral nectaries in this genus: spherical hollow nectaries, disc-like nectaries, and peristome nectaries (Figs 8-9). From an anatomical and morphological point of view, disc-like nectaries resemble digestive glands from pitchers (Parkes, 1980). In some species as in *N. maxima*, nectaries in the pitcher rim may form a ring of the secretory tissue (Parkes, 1980). It is to underline that there are especially large nectaries which occur on the pair of sharp thorns under the pitcher lid of *N. bicalcarata* (Merbach, 1999). The nectary anatomy in this genus was described in detail by several authors, e.g., Lloyd (1942) and Parkes (1980). However, their ultrastructure was examined only by Vassilyev (1977) who studied peristomal nectaries; later his results were repeated by Juniper at al. (1989), thus they are not mentioned here in my paper. Generally, extrafloral nectaries on the pitcher surface are associated with prey attraction. For example in *N. ampularia*, a species which uses leaf litter as a source of nitrogen and rarely catches prey (Moran et al. 2003), nectaries from the pitcher lid are rare or event absent, moreover nectaries from the peristome are small as compared to other species (Clarke, 2001). However, some *Nepenthes* species may produce nectar for a different purpose. Sunbirds feed on nectar from pitcher lids e.g. in *N. faizaliana* (see Fig. 25 in Clarke, 1997). *N. lowii* has upper pitchers with a unique shape which produce a white sugar-rich substance at the tips of the bristles under the lid. This substance, which is different than nectar in other *Nepenthes* species, allures birds. It was suggested that this species more benefits from trapping of birds and mammalian excrements than from catching insects (Clarke, 1997).

In some *Nepenthes* species, extra-floral nectaries fulfill also an important role in the mutual interactions between the plant host and ants. Ants protect the host against herbivores, e.g., from weevils which destroy pitchers (Merbach et al. 2007). Myrmecophily is documented the best in *N. bicalcarata*, which is the host for *Campanotus schmitzi* that makes its nest in the pitcher hollow tendrils. These ants "swim" in the pitcher fluid, retrieve a part of prey caught by the plant (Clarke and Kitching, 1995), and also exploit nectar produced by the host plant (Merbach et al. 1999).

Pitchers of *Nepenthes* usually do not produce a strongly sweet odour, thus their nectaries are not osmophores, though *N. rafflesiana* has fragrant pitchers with a strong sweet scent (Philips and Lamb, 1996). Commonly, pitchers, which are full of carcasses of prey, emit a special odour which may attract insects like calliphorid and muscid flies (Clarke, 2001).

Cephalotus

Nectaries occur on the outer pitcher surface but mostly on the lid surface and teeth (Fig. 10). The nectary has a very simple architecture, it consists of 6 secretory cells and several endodermal cells with lignified transverse walls (Parkes, 1980).

Floral nectaries

Some carnivorous plants lack flower nectaries. For example, *Drosera anglica* produces the fragrance--lacking, nectarless flowers, which are rarely pollinated by insects. Self-pollination in this species is responsible for the main seeds production (Murza and Davis, 2005). Similar observations were done on *D. rotundifolia* and *D. linearis* (Murza and Davis, 2003). In other *Drosera* species, especially tropical and subtropical, the pollination mechanism may be different. For example, flowers of some *Drosera* species are visited by birds. Future research on pollination mechanism in this genus is needed (Murza and Davis, 2005). Within *Sarraceniaceae* family, the genus *Heliamphora* produces nectarless, pollen-flowers, and is pollinated by bumblebees (Renner, 1989; Vogel, 1998).

Utricularia

Some *Utricularia* species produce cleistogamous flowers which do not need insects, but probably all *Utricularia* species produce chasmogamous flowers which are attractive for animals. Species vary both in flower colors and size (Taylor, 1989). Many types of hairs occur on the flower surface (Farooq and Siddiqui, 1966) and some of them are secretory. Several *Utricularia* species classed with different sections have the same type of nectaries. The nectary has a very simple architecture and consists of a basal cell, a middle cell with a Casparian-like lateral cell wall, and a multicellular head which produces nectar (Płachno in preparation). This kind of glandular hairs occurs commonly in the spur but may also occur in different parts of flower, e.g., style (Fig. 11) (Farooq and Siddiqui, 1966; Taylor, 1989). Nectar is produced inside the spur (e.g., Hobbhahn et al. 2006) but in some species, e.g. *U. dichotoma*, droplets of nectar were observed on the external spur surface (Płachno unpub.). However, Jérémie (1989) suggested that in autogamous *Utricularia alpina* nectar was not produced. In some *Utricularia*, e.g., in *U. purpurascens*, the same population of both flowers with and without nectar occur (Anand et al. 2007). For long time, only sparse information on pollination biology of this genus was available, however, a detailed study on pollination of some terrestrial *Utricularia* species in the Indian Western Ghats has recently been published (Hobbhahn et al. 2006). These authors found that more than 50 species of various insects (bees, butterflies, moths, hawk month, dipterans) had visited flowers. Though the nectar of this terrestrial *Utricularia* species is rich in sugar, it is produced in extremely small volumes (Hobbhahn et al. 2006). Some species (*U. campbelliana, U. quelchii*) are visited and probably pollinated by hummingbirds (Taylor, 1989).

Sarracenia* and *Darlingtonia

Sarracenia flowers produce nectar at the glabrous ovary. Nectar in the flowers was reported in *S. flava*, *S. minor* and *S. purpurea*, but floral nectaries were studied in detail only in *S. purpurea* by Vogel (1998). They are a larger version (60–100 cells) of nectaries from the pitcher attractive zone and occur in the basis of ovary tubercles. There are about 50 nectaries per mm^2. The floral nectar has a similar composition as the nectar produced by extra-floral nectaries (Vogel, 1998).

Sarracenia flowers emit a fragrance which, in the same way as nectar, attracts pollinators, but there are differences between species or groups of species: e.g., *S. oreophila, S. flava* – flowers have feline fragrance, *S. minor* – watermelon fragrance, *S. rubra* – sweet, *S. jonesii* and *S. alabamensis* – strawberry fragrance (Schnell, 2002; Rice, 2006). The primary pollinator of *S. purpurea* are queen bumblebees, but pollination of other species of *Sarracenia* still needs further study (Schnell, 2002).

In contrast to *Sarracenia*, the occurrence of the floral nectaries in *Darlingtonia* is under debate. For instance, according to DeBuhr (1973, after Vogel, 1998) nectar is totally absent. However, Schnell (2002) pg. 234 wrote shortly that in *Darlingtonia* flower “nectar from the basal glands” occurred.

Nepenthes

Nepenthes is a dioecious genus. Both female and male flowers possess nectaries, however, the females produce a more concentrated nectar (Frazier, 2001). Floral nectaries have similar architecture as disc nectaries from vegetative parts.

Several insects visit *Nepenthes* flowers, but most effective pollinators are moths, flies, wasps, and butterflies (Frazier, 2001).

Cephalotus

In contrast to the showy pitchers, *Cephalotus* produces inconspicuous, small entomophilous flowers. The flower produces honey-like scent and has a nectar disk with around 135 emergences (pillars). The disc has features of a mesenchymatic nectary. The pillars are filled with glandular tissue. On the top of the each pillar, there is an immobile, open stoma through which nectar is secreted. The nectar is rich in glucose and fructose (Vogel, 1998).

CONCLUSION

The diversity of nectary structure in carnivorous plants reflects complicated evolutionary routes of this ecological group.

Acknowledgements

Major part of this paper was written during my stay at Indiana University Southeast (USA). The author is greateful to Douglas Darnowski (Indiana University Southeast) and Philip M. Sheridan (Meadowview Biological Research Station, Virginia, USA) for their hospitality. Sincere thanks are due to Lubomir Adamec and Douglas Darnowski for reading the manuscript and correction of the language.

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„Słodkie ale niebezpieczne”: nektarniki u roślin mięsożernych

Streszczenie

U roślin mięsożernych występują dwa typy nektarników: kwiatowe oraz pozakwiatowe. Pierwsze odpowiadają za wabienie zapylaczy, natomiast drugie za przywabienie zdobyczy. Nektar wytwarzany przez nektarniki pozakwiatowe jest produkowany przede wszystkim w celu zwabienia zdobyczy, ale może także uczestniczyć w mutualistycznych interakcjach pomiędzy rośliną mięsożerną a mrówkami. Zróżnicowana architektura nektarników u roślin mięsożernych jest skorelowana ze skomplikowaną ewolucją tej specyficznej grupy ekologicznej roślin.