

REVIEW

Quite a few reasons for calling carnivores ‘the most wonderful plants in the world’

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Received: 30 May 2011 Returned for revision: 28 June 2011 Accepted: 8 August 2011 Published electronically: 21 September 2011

- **Background** A plant is considered carnivorous if it receives any noticeable benefit from catching small animals. The morphological and physiological adaptations to carnivorous existence is most complex in plants, thanks to which carnivorous plants have been cited by Darwin as ‘the most wonderful plants in the world’. When considering the range of these adaptations, one realizes that the carnivory is a result of a multitude of different features.
- **Scope** This review discusses a selection of relevant articles, culled from a wide array of research topics on plant carnivory, and focuses in particular on physiological processes associated with active trapping and digestion of prey. Carnivory offers the plants special advantages in habitats where nutrient supply is scarce. Counterbalancing costs are the investments in synthesis and the maintenance of trapping organs and hydrolysing enzymes. With the progress in genetic, molecular and microscopic techniques, we are well on the way to a full appreciation of various aspects of plant carnivory.
- **Conclusions** Sufficiently complex to be of scientific interest and finite enough to allow conclusive appraisal, carnivorous plants can be viewed as unique models for the examination of rapid organ movements, plant excitability, enzyme secretion, nutrient absorption, food-web relationships, phylogenetic and intergeneric relationships or structural and mineral investment in carnivory.

Key words: Carnivorous plants, model plants, traps, rapid organ movements, gland functioning, nutrient absorption, action potentials, plant excitability, plant indicators.

INTRODUCTION

We are accustomed to thinking of plants as being immobile and harmless, and this may be a reason for our fascination with carnivorous plants and especially about those that move while trapping. Such interest began in Victorian England and spread with the popularization of *Insectivorous Plants* by Darwin (1875) (Chase *et al.*, 2009). Leading to the emergence of the so-called carnivorous syndrome, a carnivorous lifestyle has resulted in significant adaptive and functional implications (Laakkonen *et al.*, 2006). The most obvious manifestation of the syndrome is the emergence of traps. They originate from leaves that have become specialized in trapping, prey digestion and nutrient absorption, thereby decreasing their photosynthetic rates (to zero in case of the colourless traps of *Genlisea* and terrestrial *Utricularia*, Adamec, 2006). The compact anatomy of traps (reminiscent of roots), which is to restrict apoplastic conductivity (Pavlovič *et al.*, 2007), serves the selective symplastic transport of nutrients gained from carnivory. Investments in the following cause considerable maintenance costs: attractants such as nectars and odours (Juniper *et al.*, 1989; Moran, 1996; Bohn and Federle, 2004; Bennett and Ellison, 2009; Bhattarai and Horner, 2009; Jürgens *et al.*, 2009); edible trichomes (Merbach *et al.*, 2002); colourful projections (Schaefer and

Ruxton, 2008) and UV patterns (Moran *et al.*, 1999); resinous droplets (Voigt and Gorb, 2010) or slime that in *Drosophyllum* has a scent of honey, which may mimic nectar (Jürgens *et al.*, 2009); glands excreting mucilage (*Drosera*, *Pinguicula*, *Byblis*) or a hydrophobic resin (*Roridula*) to catch prey (Juniper *et al.*, 1989); glands excreting digestive enzymes – these digestive glands, with their attendant mechanisms for simultaneous enzyme secretion and nutrient absorption are an anatomical birthmark of the carnivorous syndrome (Lüttge, 1971; Benzing *et al.*, 1976); exudation of organic compounds to support the microbial community associated with the traps (Sirová *et al.*, 2009, 2010); and nutrient uptake machinery (An *et al.*, 2001) required for functioning of each single trap (Knight, 1992; Adamec, 2006, 2010a; Pavlovič *et al.*, 2007; Hájek and Adamec, 2010). Therefore, it is not surprising that the dual use of leaves for photosynthesis and nutrient uptake has deeply reduced the net photosynthetic rate of terrestrial carnivorous plants, leading ultimately to reduction of the relative growth rate (Ellison, 2006; Farnsworth and Ellison, 2008); giant carnivorous species are the exception rather than the rule: *Triphyphyllum peltatum*, *Nepenthes rajah*, *N. edwardsiana*, *N. ampullaria*, *N. rafflesiana* and *N. rafflesiana* var. *gigantea*, *N. palawanensis*, *N. attenboroughii* (newly discovered by Robinson *et al.*, 2009), *Sarracenia leucophylla*, *Drosera*

gigantea and *D. regia*. For the reasons given above (i.e. high maintenance costs), some carnivorous plants are only carnivorous when favoured by environmental conditions, e.g. *Pinguicula* and pygmy *Drosera* spp. (Rice, 2007), or during periods of extended growth, when extra nutrient supply is needed (*Triphyophyllum peltatum*) (Bringmann et al., 2002). To assess the expenditures and gains of carnivory, an ecological cost–benefit model was created (Givnish et al., 1984). The model assumes that the cost of capturing animals is offset by the nutrient uptake in nutrient-poor environments. This is the case when the most photosynthetically productive leaves are supplied with macroelements gained from carnivory, otherwise being unable to conduct photosynthesis efficiently (Ellison, 2006; Farnsworth and Ellison, 2008; Ellison and Gotelli, 2009). Accordingly, as evaluated for non-carnivorous plants, the positive correlation between CO₂ fixation and N-availability (foliar tissue N content) has long been known (Field and Mooney, 1986). Recently, the mineral cost of carnivory (i.e. the proportion of minerals contained in traps) has been defined and quantified in aquatic carnivorous species (Adamec, 2010b).

Because carnivory is largely a substitute for environmentally limited macroelements, carnivorous plants are able to cope with extreme habitats such as oligotrophic waters, dystrophic pools, peat bogs, fens, swamps, marshes, heaths,

mountain slopes, dripping rocks, clayish sands, fire-impooverished soils and heavily leached areas (Juniper et al., 1989). The distribution pattern points, however, to the predominant co-occurrence of carnivorous plants with both sunny and wet habitats (Table 1), where neither light nor water are limiting factors (Givnish et al., 1984; Brewer et al., 2011). Under such conditions, these plants use their prey mostly as an alternative source of nitrogen, phosphorus and sulphur (Juniper et al., 1989; Butler and Ellison, 2007), but also as a source of ions, which though not necessarily environment-limited are easily taken up from prey bodies, e.g. potassium (Green et al., 1979; Karlsson, 1988; Płachno et al., 2009; Adamec et al., 2010a), magnesium (Adamec, 2002, 2010a; Płachno et al., 2009), manganese (Steinhauser et al., 2007) and even carbon (Fabian-Galan and Salageanu, 1968; Lüttge, 1983; Adamec, 1997; Rischer et al., 2002). The direct uptake of prey-derived organic carbon was shown to be of crucial importance when CO₂ and light were limited (Adamec, 1997). There are over 700 carnivorous plant species recognized today (Table 2) and these species are constantly growing in number (Fleischmann et al., 2007, 2008; Cheek and Jebb, 2009; Fleischmann and Rivadavia, 2009; Lee et al., 2009; Robinson et al., 2009; Zamudio and Olvera, 2009; Suksathan and Parnell, 2010; Souza and Bove, 2011). On the other hand, the conservation status of some

TABLE 1. Division of traps and distribution of habitats of carnivorous plants

Trap	Genus/species	Common name	Natural habitat	Region
Pitfall	<i>Sarracenia</i>	pitcher plants	fens, swamps, coastal plains, grassy plains	north, east and south of North America
	<i>Darlingtonia californica</i>	cobra lily	boggy areas and near streams in mountain	Sierra Nevada mountains in south Oregon and north California (elevation up to 2500 m)
	<i>Heliamphora</i>	sun pitchers	highland meadows	endemic to Guiana highlands
	<i>Nepenthes</i>	tropical pitcher plants	'Lowlanders' – humid lowland forests; 'Highlanders' – tropical montane forests	subtropical regions of Asia (China, Singapore, India, Thailand, Vietnam, Cambodia, Philippines, Malay Peninsula), Australia, Seychelles and Madagascar
	<i>Cephalotus follicularis</i>	Albany pitcher, fly-catcher, moccasin plant	coastal plains	endemic to south-west Australia
	<i>Brocchinia</i>	bromeliads	<i>B. tatei</i> and <i>B. micrantha</i> – sunny, open areas with sandstone; others – epiphyte of unshaded trees	endemic to Guyana, Venezuela and Columbia (elevation 500–2900 m)
	<i>Catopsis berteroniana</i>		epiphyte of unshaded trees	southern USA, Latin America, Brazil
Eel-trap	<i>Genlisea</i>	corkscrew plants	wetlands up to 2500 m	endemic to Guiana highlands, Angola, Zambia, Tanzania, Madagascar
Fly-paper	<i>Sarracenia psittacina</i>	parrot pitcher plant	wetter parts of boggy areas	south-eastern USA (Georgia, Florida)
	<i>Drosera</i>	sundews	marshes, fens, wet stands, boggy shorelines	all continents but Antarctica
	<i>Drosophyllum lusitanicum</i>	Portuguese dewy pine	slightly basic soils of narrow coastal or maritime regions	endemic to Portugal, southern Spain and northern Morocco
	<i>Triphyophyllum peltatum</i>	West African liana	tropical rain forests	Sierra Leone, Liberia, Ivory Coast
	<i>Pinguicula</i>	butterworts	highly humid, wet areas and montane regions (elevation up to 1900 m)	Europe, North America, northern Asia, West Africa, west coast of South America
	<i>Byblis</i>	rainbow plants	acid sands and desert areas	native to Australia and New Guinea
	<i>Roridula gorgonias</i> , <i>Roridula dentata</i>	flycatcher bushes or bug plants	fynbos area, coastal mountain and slopes at elevation 900–1200 m	endemic to south Africa
Snap-trap	<i>Dionaea muscipula</i>	Venus flytrap	bogs, swamps, wet savannahs	North and South Carolina (USA)
	<i>Aldrovanda vesiculosa</i>	waterwheel plant	shallow and warm standing waters	central Europe, east Asia, Africa, Australia
Suction-trap	<i>Utricularia</i>	bladderworts	all kinds of still waters and water films, wet soils, sands, rocks	all continents but Antarctica

TABLE 2. Phylogenetic position of carnivorous plants

Division	Class	Order	Family	Genus/species	No. of species	
Anthophyta (angiosperms)	Monocotyledones	Poales	Bromeliaceae	<i>Brocchinia</i>	2	
				<i>Catopsis berteroniana</i>	1	
	Dicotyledones	Caryophyllales	Dioncophyllaceae	<i>Triphyophyllum peltatum</i>	1	
				Droseraceae	<i>Aldrovanda vesiculosa</i>	1
					<i>Dionaea muscipula</i>	1
			Drosophyllaceae	<i>Drosera</i>	>184	
				<i>Drosophyllum lusitanicum</i>	1	
				Nepenthaceae	<i>Nepenthes</i>	>110
					Oxalidales	Cephalotaceae
			Ericales	Roridulaceae		<i>Roridula</i>
				Sarraceniaceae	<i>Heliophora</i>	18
					<i>Sarracenia</i>	9
			<i>Darlingtonia californica</i>		1	
			Lamiales	Lentibulariaceae	<i>Pinguicula</i>	>96
					<i>Genlisea</i>	>22
<i>Utricularia</i>	>250					
Byblidaceae	<i>Byblis</i>	>7				

endemic carnivores growing in areas with intense human activity (e.g. *Drosophyllum lusitanicum*) present an alarming picture of ongoing declines (Gonçalves and Romano, 2005). *In vitro* propagation, especially in combination with conventional practices (seed banks or habitat conservation) could be a remedy for endangered species, providing an alternative to replenish wild stocks (Jang et al., 2003; Gonçalves and Romano, 2007; Grevenstuk et al., 2010)

PASSIVE TRAPS

In passive traps there is no motion while trapping and enzyme secretion is constitutive, i.e. independent of the presence of a prey (Heslop-Harrison, 1975; Płachno et al., 2005a, b, 2006). In the presence of prey, however, the basal level of secretion increases (Gallie and Chang, 1997; McNally et al., 1988; Eilenberg et al., 2006). Moreover, the amount of enzymes released seems to be correlated to the size of the prey (Darwin, 1875; Heslop-Harrison, 1975; Owen et al., 1999; An et al., 2002). In other words, the expression/secretion of digestive enzymes is regulated by a signal transduction mechanism. This lets the plant respond to the availability of food resources and thus adjust the cost–benefit ratio efficiently (Gallie and Chang, 1997). Nevertheless, passive traps can be viewed as the containers of digestive fluid: pitfalls (*Sarracenia*, *Darlingtonia*, *Heliophora*, *Cephalotus*, *Nepenthes*), tanks (*Brocchinia*, *Catopsis*), vesicles (eel-traps of *Genlisea*) and fly-papers (*Drosophyllum*, *Triphyophyllum*, *Byblis*, *Roridula*, majority of *Pinguicula* spp.).

The pitfalls of dicots have the shape of pitchers (Fig. 1A, C, D, E), in which at least three distinctive zones can be recognized (Juniper et al., 1989). A rim of slick surface covered with nectaries and trichomes both lures and deceives; when wet, the rim is especially slippery (Bohn and Federle, 2004; Gorb and Gorb, 2006; Bennett and Ellison, 2009); moreover *Sarracenia flava* nectar contains coniine (an alkaloid anaesthetic to insects) to increase prey-capture efficiency. The waxy zone directly beneath the rim prevents escape; for this, its walls may be covered with waxy scales (*Nepenthes*), protruding aldehyde crystals (*Sarracenia*, *Darlingtonia*), cuticular

foldings (*Nepenthes*, *Cephalotus*, *Heliophora*), downward-pointing hairs (*Heliophora*, *Sarracenia*, *Darlingtonia*) or guard-cell-originating lunate cells (*Nepenthes*) (Juniper et al., 1989; Jaffe et al., 1992; Owen and Lennon, 1999; McPherson, 2009; Poppinga et al., 2010; Moran and Clarke, 2010). In *Nepenthes*, alkaloid fumes promote successful capture (Ratsirarson and Silander, 1996), while fluid viscosity increases its retentive properties (Giusto et al., 2008; Moran and Clarke, 2010; Bonhomme et al., 2011b). The lowest part of the pitcher, the digestive zone, harbours numerous digestive glands (Fig. 2A–D) or a glandular epithelium (*Sarracenia*). *Nepenthes*, *Sarracenia* and *Cephalotus follicularis* protect their enzymes (proteases, peptidases, phosphatases, esterases, chitinases, nucleases) from rainfall dilution by covering the pitchers with lids. As most *Heliophora* species do not produce enzymes (Jaffe et al., 1992), its lid has reduced in size to become a small ‘nectar spoon’ while excess rainwater is drained off through a slit. Deprived of its own enzymes, too, *Darlingtonia californica* is unique in that it regulates the pitcher water level by pumping it up through its roots. As low pH promotes the action of proteolytic enzymes (Amagase, 1972; Heslop-Harrison, 1976) and the uptake of organic substances (Heslop-Harrison, 1976; Schulze et al., 1999), the pitcher fluid is highly acidic (An et al., 2001). Additionally, oxygen free radicals produced by the pitcher plants aid in the digestion of prey bodies (Chia et al., 2004).

Although among Bromeliaceae (monocots), only *Brocchinia reducta* (Fig. 1B) has been shown to secrete phosphatase (Płachno and Jankun, 2005; this needs to be confirmed with other methods) and neither *B. hechtiioides* nor *Catopsis berteroniana* produces proteases, these three species are established plant carnivores. Depending on a food-web to acquire nutrients, these plants provide habitats for frogs, insects (e.g. ants), other carnivorous plants (e.g. *Utricularia humboldtii*) and bacteria (including nitrogen-fixing bacteria), themselves exploiting whatever is left over: faeces, animal or vegetable debris. Absorption of N-compounds is carried out by specialized trichomes (Benzing et al., 1976).

Small soil-borne organisms (bacteria, algae, nematodes, rotifers, annelids, crustaceans and mites) are found in the

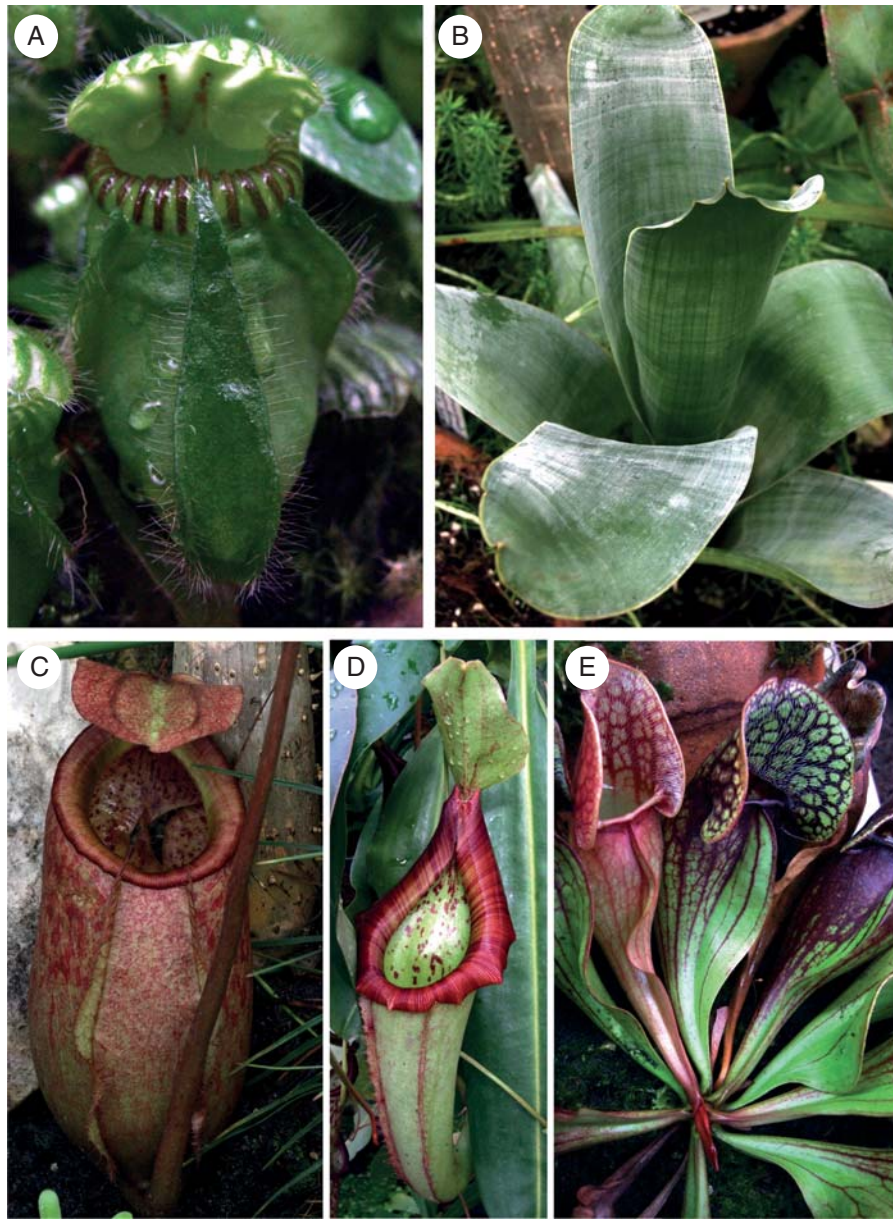


FIG. 1. Diversity of pitfalls: (A) pitcher of an Albany pitcher plant *Cephalotus follicularis*; (B) *Brocchinia reducta* as an example of carnivorous bromeliads; (C) *Nepenthes merrilliana*; (D) *Nepenthes* hybrid 'Miranda'; (E) North American pitcher plant *Sarracenia purpurea*.

subterranean eel-traps of rootless *Genlisea* (Płachno *et al.*, 2005a) (Fig. 3A, B). The Y-shaped eel-traps consist of two arms joined to a long (3–15 cm) thin (0.5–0.8 mm) neck, whose other end forms a digestive chamber known as a vesicle. Arranged along the arms and the long neck, the vesicle-pointing hairs prevent escape of prey. Digestion takes place in the vesicle, where there are numerous digestive glands, which in some species (*Genlisea margaretae*) are concentrated along vascular bundles (Płachno *et al.*, 2007). Juniper *et al.* (1989) found that *Genlisea*'s digestive glands morphologically resemble the sessile digestive glands of *Pinguicula*, which seems to be well corroborated by the common origin of both genera (Ellison and Gotelli, 2009). Although some organisms are chemotactically attracted in

order to be digested by *Genlisea* (Barthlott *et al.*, 1998), others grow inside the traps as symbionts or commensals, arguing for the prevalence of trophic microsystems in all genera equipped with passive traps (Studnička, 1996).

In general, trophic plant–commensal relationships are multi-level and complex, with the microbial component being of crucial importance (Barrera *et al.*, 1989; Steinhauser *et al.*, 2007; Butler *et al.*, 2008; Peterson *et al.*, 2008; Koopman *et al.*, 2010; Adlassnig *et al.*, 2011). The strategy of taking advantage of commensal organisms is especially critical for carnivores deprived of digestive enzymes such as bromeliads (Frank and O'Meara, 1984), *Darlingtonia californica* (Ellison and Farnsworth, 2005), the majority of *Heliamphora* spp. except *H. tatei* (Barrera

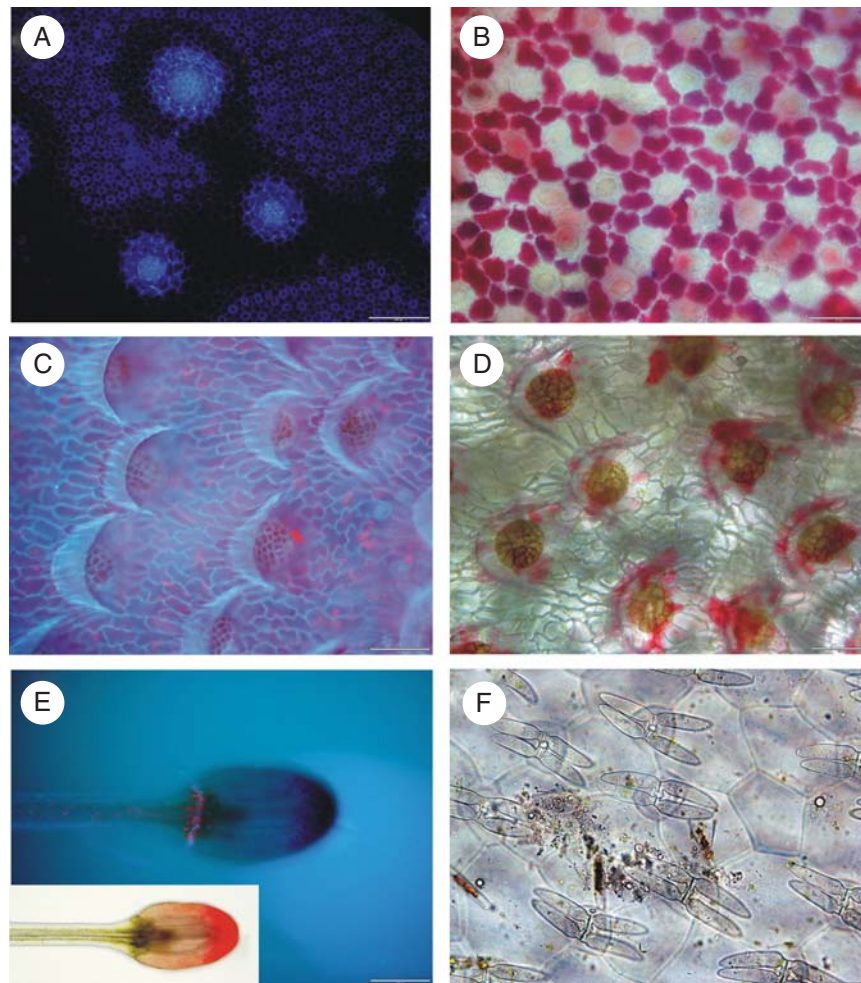


FIG. 2. Digestive glands of carnivorous plants. (A) Three large and numerous small digestive glands of the pitfall type of the *Cephalotus follicularis* trap – note strong auto-fluorescence of the apical part of the large glands under UV light; scale bar = 200 μm . (B) Numerous small glands from the pitcher of *Cephalotus follicularis* – note red anthocyanine in the epidermal cells, which surround glands; scale bar = 50 μm . (C,D) Digestive glands from the pitcher of *Nepenthes ampullaria*; scale bar = 100 μm . (E) Emergence of *Drosera filiformis* – note auto-fluorescence under UV light: blue – cutinized walls of barrier cells and red – chlorophyll; scale bar = 100 μm . Inset: the same emergence under light microscopy. (F) Quadrifid hairs from the trap of *Utricularia volubilis*; scale bar = 50 μm .

et al., 1989; Jaffe *et al.*, 1992; Adlassnig *et al.*, 2011), *Nepenthes ampullaria* (Moran *et al.*, 2003) and *N. lowii* (Clarke *et al.*, 2009). *Nepenthes lowii* has a mutualistic relationship with treeshrews *Tupaia montana* and its pitchers act as faeces repositories for these small mammals native to tropical forests (Clarke *et al.*, 2009, 2010). The small woolly bat *Kerivoula hardwickii* uses a different type of pitcher in Borneo, *Nepenthes rafflesiana elongata*, as a lavatory and home as well (Grafe *et al.*, 2011). *Nepenthes rajah* utilizes faeces of both the diurnal *Tupaia montana* and the nocturnal rat *Rattus baluensis* (Greenwood *et al.*, 2011; Wells *et al.*, 2011). Additionally, *Nepenthes rajah* hosts mosquito larvae (*Culex rajah*, *Toxorhynchites rajah*), while *N. bicalcarata* shelters ants (*Camponotus schmitzi*). Although both latter named species secrete digestive enzymes, they benefit from their commensals in such a way that the crushing of ‘prey’ by larvae or ants speeds up the digestive breakdown of prey, which more than compensates for the partial loss of prey supply (Bonhomme *et al.*, 2011a). *Sarracenia purpurea*,

which is capable of producing some hydrolytic enzymes, also prefers mutual commensalism with bacteria, protozoa, algae and dipteran larvae (Atwater *et al.*, 2006; Gebühr *et al.*, 2006; Gray *et al.*, 2006; Plachno *et al.*, 2006; Peterson *et al.*, 2008; Plachno and Wołowski, 2008; Buckley *et al.*, 2010). Among ‘fly-papers’, *Pinguicula vulgaris* and *P. lusitanica*, which utilize nutrients from pollen-, seed- or canopy-leaching, need assistant microorganisms which support them by disposing of detritus (Darwin, 1875; Lavarack, 1979; Juniper *et al.*, 1989; Moran *et al.*, 2003). *Byblis* and *Roridula* both benefit from commensalism with Capsid bugs: *Setocornis*, *Cyrtopeltis*, *Pameridea roridulae* and *Pameridea marlothii* (Ellis and Midgley, 1996; Hartmeyer, 1998; Midgley and Stock, 1998; Anderson and Midgley, 2002, 2003, 2007). Thus, our understanding of carnivory may be broadened today by recognition of the fact that carnivorous plants are able to lure and capture a prey and then utilize (absorb) prey-derived compounds, regardless of whether these compounds are provided directly or by

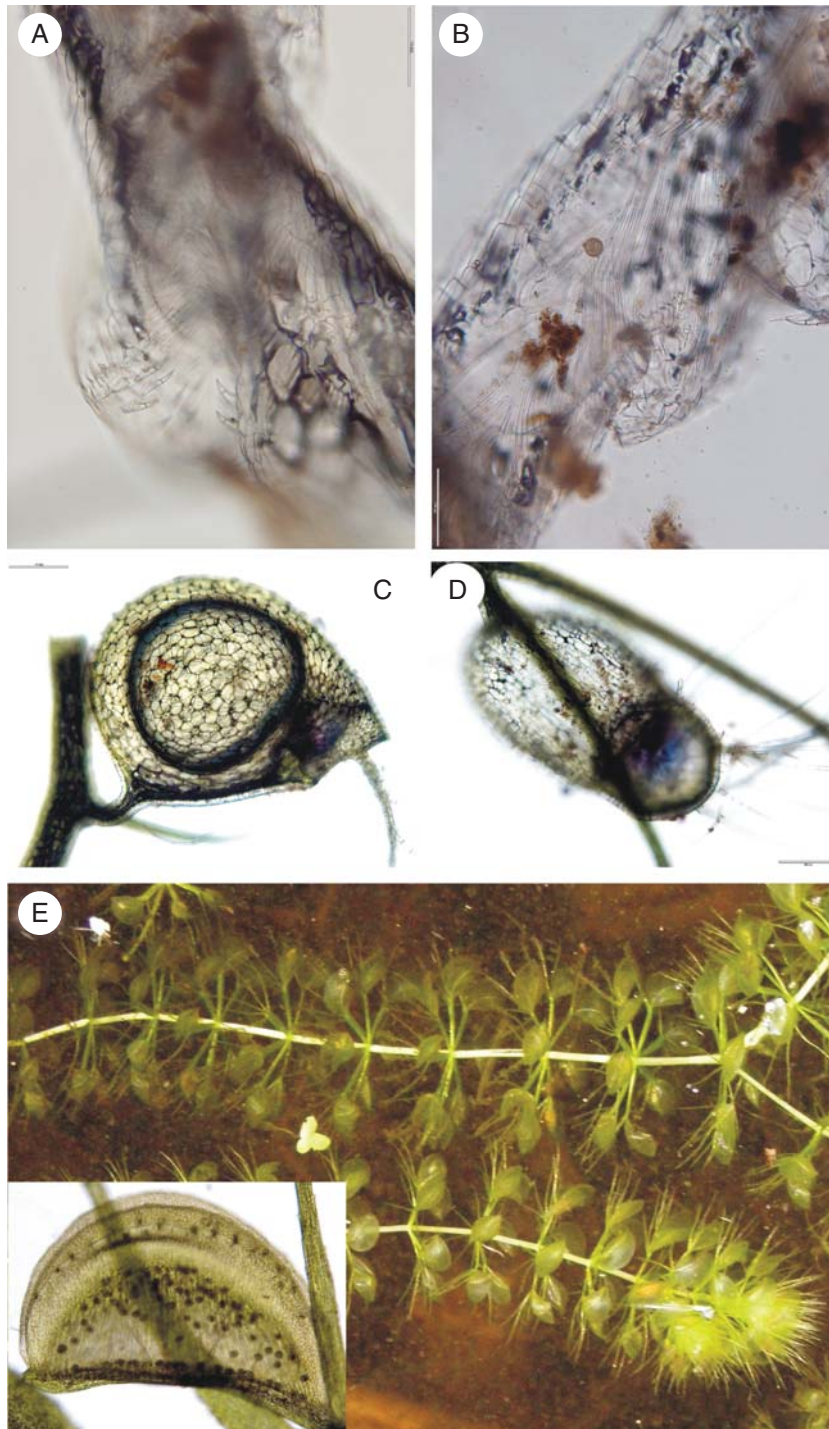


FIG. 3. Subterranean and aquatic traps. (A,B) Part of the eel trap of *Genlisea margaretae*: (A) external view opening in the arm of the trap; (B) the same but from internal view; scale bars = 100 μm . (C,D) Bladders of *Utricularia gibba*; scale bars = 200 μm . (E) The waterwheel plant *Aldrovanda vesiculosa* in the Velký Londýn sand-pit near Třeboň (South Bohemia, Czech Republic); inset: magnification of the tropical clone *Aldrovanda* trap – dark points depict digestive glands; scale bar = 200 μm .

commensal or symbiotic organisms. In other words, the ability to efficiently absorb nutrients has become the real clincher of carnivory (Jolivet, 1998; Bringmann *et al.*, 2001; Darnowski *et al.*, 2007; Płachno *et al.*, 2009), while the presence of commensal or symbiotic associations may

be viewed as additional evidence (Hess *et al.*, 2005). It can be argued that the production of enzymes by the plant itself, when commensals are already doing it, would be an unnecessary cost for the plant that is still able to absorb nutrients (Hartmeyer, 1998).

ACTIVE TRAPS

Active traps move while trapping. To synchronize their movements action potentials (APs) are generated (see below). Adhesive fly-papers, and snap- and suction-traps may be counted as active traps. Adhesive traps (either active, Fig. 4A, C; or passive, Fig. 4B) are evenly covered with mucilage-producing glands which, when stalk-shaped, are designated tentacles (Fig. 2E). In active adhesive traps, the tentacles bend when stimulated. *Drosera burmannii* and *D. glanduligera* bend their tentacles quickly, i.e. in seconds (5–15 s) or even less (0–15 s), respectively (Gibson and Waller, 2009); it is to the latter we owe the term ‘snap-tentacle’ (Hartmeyer and Hartmeyer, 2005). Apart from tentacle bending, in most *Drosera* and some *Pinguicula* spp., the ‘stimulated’ leaf curves around the prey to maximize contact with it and extend the area of digestion/absorption around it (Legendre, 2002b). Although leaf movement takes on average a couple of hours, re-furling the unravelled position takes a whole day. An exception is *D. capensis*, which enwraps a prey in 30 min (http://en.wikipedia.org/wiki/Drosera_capensis).

The tentacles of *Drosera* have direct connections with the vascular system, due to the increased water consumption during mucilage production (Williams and Pickard, 1974). On prey capture, mucilage production is intensified. First,

formic acid initiates the digestive process of the insect body, and the excretion of digestive enzymes (proteases, phosphatases, peroxidases, nucleases, carbohydrases and amylases) then facilitates the break-down process (Heslop-Harrison and Knox, 1971; Marburger, 1979; Juniper *et al.*, 1989). The chitin skeleton usually remains undigested, although chitinase activity may be present in the digestive exudation of *Drosera* (Matusíková *et al.*, 2005). Chitinous remnants may also be disposed of by associated mites (Antor and García, 1995).

Dionaea muscipula with snap-traps (Fig. 4D) is the most splendid example of the prey capture among land plants (Darwin, 1875), while its closest descendent *Aldrovanda vesiculosa* (Fig. 3E), which displays a similar catching-technique, has adapted an aquatic lifestyle in dystrophic waters (Arber, 1920). Both species snap their bi-lobe-traps whenever the multicellular trigger hairs (20 in *Aldrovanda*, three in *Dionaea*) of epidermal origin are touched (Hodick and Sievers, 1986). In *Aldrovanda*, ten trigger hairs stand along the hinge (midrib), eight along the trap border line and two somewhere in the middle. In *Dionaea*, there are three in the centre. Around the rims of each trap there are four-armed glands in *Aldrovanda* and star-like sessile glands in *Dionaea*, which secrete sweet mucilage to attract prey and to seal the lobes hermetically during digestion (Juniper *et al.*, 1989). The central zone of the lobes is richly covered with numerous sessile digestive



FIG. 4. Diversity of fly paper traps and numerous snap traps of the Venus flytrap *Dionaea muscipula* (D). (A) An example of the sundew *Drosera* – an active fly sticky trap type; note numerous emergences with mucilage droplets, which both attract and catch prey. (B) Portuguese sundew *Drosophyllum lusitanicum* – a passive fly sticky trap type. (C) *Pinguicula gigantea* from Mexico – an active fly sticky trap.

glands both in *Aldrovanda* and in *Dionaea*. The two genera share a similar morphology of the digestive glands which, scattered over the inner epidermis, are without vascular connection (Hodick and Sievers, 1986). Digestion may take from one to several days, depending on the size of the prey. The secreted H^+ ions speed up amino acid uptake (Rea and Whatley, 1983). When the trap eventually re-opens: (1) it is usually not capable of further functioning and starts to decay (*Aldrovanda*) – to prevent loss of valuable mineral nutrients, highly efficient re-utilization takes place in *Aldrovanda*; (2) it is ready to capture another insect (*Dionaea*), but the process may be less effective if the trigger hairs are partially damaged – the average trap of *Dionaea* is able to digest 2–4 prey items in its life span, reducing prey bodies to a husk of chitin (Darwin, 1875).

Suction-traps (bladders) are ranked among the most complex leaf structures ever to have been examined in plants (Juniper *et al.*, 1989). They are found exclusively in *Utricularia* – all members of the genus are rootless, having bladders instead of roots (Fig. 3C, D). Charles Darwin thought that *Utricularia* traps were passive and it was Mary Treat who first called them active (Treat, 1876; Sanders, 2009/2010). The walls of the bladder are thin, consisting of two layers of cells. Various types of hairs cover the inside and outside of the bladder (Thurston and Seabury, 1975). The so-called trigger hairs (surrounding the entrance and the door of the bladder), button-like glands (absorbing or excreting salt depending on the developmental stage) and stalked trichomes (with mucilage-secretory functions) are found on the outer side (Lüttge, 1983). The quadrifids (four-armed trichomes; Fig. 2F) and the bifids (two-armed trichomes) – both names coined by Darwin (1875) – appear on the internal wall (Lüttge, 1983; Płachno and Jankun, 2004). Quadrifid trichomes play a substantial role in enzyme secretion/nutrient absorption as glands of this type are of a large surface, and thus provide an important means of increasing secretion/absorption area without extending the size of the trap (Fineran and Lee, 1975). Esterases, glucosidases, chitinase, aminopeptidases (proteases) and acid phosphatases have been identified in the trap fluid (Juniper *et al.*, 1989; Sirová *et al.*, 2003, 2009; Adamec *et al.*, 2010b). The latter enzymes have also been found in the bifid hairs (Płachno *et al.*, 2006). For most *Utricularia* species, phosphatases exhibit the highest activity, while the activities of other enzymes are usually lower by one or two orders of magnitude; very low or even zero activity was found for aminopeptidase (Sirová *et al.*, 2003; Płachno *et al.*, 2006; Adamec *et al.*, 2010b). All studies show that phosphatase secretion is constitutive, independent of prey capture or N or P addition to the ambient culture water, but dependent on trap age. The fluid pH is usually 4.8–5.1 (but between 5.7 and 7.3 in *U. foliosa*) and seems to be regulated by the traps (Sirová *et al.*, 2003).

The bifid hairs are indispensable for water removal (Sasago and Sibaoka, 1985a). Water moves from the bladder interior, crossing the bifid trichomes, bladder-wall cells and threshold cells (an additional layer of cells located directly below the entrance of a bladder) to reach the outer environment (Sasago and Sibaoka, 1985b). For this, the bifid arms inside as well as the button-like glands on the external side of the

bladder are covered with an ‘open structure’ cuticle (cuticular gaps) (Lüttge, 1983; Płachno and Jankun, 2004). Along with the threshold cells, the bifid arms are presumed to function like a salt-excreting gland facilitating water extrusion (Sasago and Sibaoka, 1985a). More precisely, water moves passively after chlorides, while the energy-dependent transport of Cl^- ions against an electrochemical gradient needs a continuous supply of ATP (Sydenham and Findlay, 1975). It was experimentally shown that the water outflow sufficient for the next trap firing lasts 20–30 min and requires energy from respiration only (Lloyd, 1929; Sasago and Sibaoka, 1985b). It was also hypothesized that *Utricularia* is able to reset the traps so quickly thanks to the irreversible mutation in cytochrome *c* oxidase in the respiratory chain (Jobson *et al.*, 2004), which causes a 20% reduction in the overall energy efficiency of the respiratory chain (Laakkonen *et al.*, 2006). However, as the intact trap lumen is permanently anoxic, it is not clear which respiratory mechanism is used by the *Utricularia* trap to obtain the ATP energy for their exacting functions (Adamec, 2007).

Finally, when negative pressure is generated, elastic energy is stored (Skotheim and Mahadevan, 2005; Marmottant *et al.*, 2009). Thereafter, the negative pressure equilibrium seems to ‘lean on’ the trigger hairs. Each trigger hair acts as a lever, breaking the seal and releasing the energy whenever something (living creature or strong current) disturbs it (Sydenham and Findlay, 1973). However, the existence of trigger hairs is not indispensable to bladder suction (Lloyd, 1942). This, in turn, is consistent with the recent finding that, after an extended lag period, the traps suck in water spontaneously without hair triggering (Marmottant *et al.*, 2009; Adamec, 2011a; Vincent *et al.*, 2011). During firing, the pressure difference between the inside and outside of the bladder decreases from -17 kPa to 0 (Sydenham and Findlay, 1973; Sasago and Sibaoka, 1985a, b).

Terrestrial bladderworts have tiny traps that mostly feed on protozoa and rotifers, while aquatic species can hold more substantial prey, such as crustacean zooplankton (e.g. water fleas), nematodes, mosquito larvae, insects, tadpoles and even small fish (Darwin, 1875). Still, for *Utricularia* living in nutrient-poor waters, algae constitute up to 80% of their diet (Peroutka *et al.*, 2008). Moreover, inside the traps, the living algae and microbial commensals make up trophic communities (food-webs) rather than submitting to predator–prey interaction, delivering hydrolytic enzymes in return for food supply (Richards, 2001; Sirová *et al.*, 2003, 2009, 2010). To support those microbial commensal communities, aquatic *Utricularia* species secrete great amounts of organic substances into the trap fluid (Sirová *et al.*, 2009, 2010).

The shunting of carbon into bladders results on the one hand in the decline of phototrophic organs in *Utricularia macro-rhiza* (Knight, 1992). On the other hand, the same *Utricularia* is also in a position to decrease the number of traps when the macroelements are superfluous (Knight and Frost, 1991; Friday, 1992; Bern, 1997; Guisande *et al.*, 2004; Kibriya and Jones, 2007; Adamec, 2008). The decrease in the number or biomass of trapping organs under nutrient excess resembles the behaviours of *Drosera rotundifolia* (Thorén *et al.*, 2003), *D. binata* (Stewart and Nilsen, 1993), *Triphyophyllum peltatum* (Bringmann *et al.*, 2002),

Nepenthes talangensis (Pavlovič *et al.*, 2010b) or *Sarracenia* (Ellison and Gotelli, 2002; Farnsworth and Ellison, 2008), while the decrease in the number of phototrophic leaves seems to resemble a dwelling strategy of *Aldrovanda vesiculosa* (Fabian-Galan and Salageanu, 1968). Thus, the adaptive capacity of aquatic *Utricularia* spp. in particular and of the majority of carnivorous plants in general is truly outstanding (Laakkonen *et al.*, 2006).

ECOLOGICAL IMPLICATIONS

It appears that a significant majority of carnivorous plant species can survive without prey availability, especially under favourable conditions, e.g. if they are deprived of plant competitors and/or grow on fertilized soils (Bruzzese *et al.*, 2010). Under such circumstances, the development of carnivory might even be partly blocked (Knight and Frost, 1991; Adamec, 1997; Ellison, 2006; Farnsworth and Ellison, 2008). In extreme cases, all metabolic investments in carnivory become invalid; for example, no pitchers are produced (Ellison and Gotelli, 2002) or no glandular leaves appear (Bringmann *et al.*, 2002). However, under conditions of nutrient abundance, although they should benefit from a metabolic boost (Adamec, 1997, 2002; Hanslin and Karlsson, 1996), the majority of carnivores cannot compete with non-carnivorous plants in their natural habitats (Juniper *et al.*, 1989; Schulze *et al.*, 2001; Gaertner *et al.*, 2010). Sacrificing photosynthesis and growth rate for the sake of the carnivorous syndrome, they cannot gain mass as quickly as non-carnivores. Their goal of survival, therefore, is to thrive in extreme habitats, where carnivory is the lesser of two evils (Chase *et al.*, 2009).

The carnivorous habit may also be abandoned under conditions of low light, as is the case with *Heliamphora* (Jaffe *et al.*, 1992), *Pinguicula* (Zamora *et al.*, 1998), *Utricularia* (Bern, 1997) and *Nepenthes* (Pavlovič *et al.*, 2007). This argues that investments in carnivory are not feasible under such circumstances. Alternatively, additional nutrient supply is indispensable only during increased demands such as fast growth (Jaffe *et al.*, 1992), maturation (Bringmann *et al.*, 2002) or reproduction (Darnowski *et al.*, 2006). Irrespective of the reasons, the reported adaptations enable the plants to optimize the carnivory trade-off. The strategy of *Cephalotus follicularis*, *Genlisea*, *Triphyophyllum peltatum*, *Utricularia* and some *Pinguicula* of segregating into the photosynthetic and insectivorous leaves/organs serves the same function (Pavlovič *et al.*, 2007). It can be concluded that such a variety of adaptive plasticity among carnivores is one of reasons for regarding them as ‘the real wonders’ like Darwin (1875) did. However, for Charles Darwin and his good friend Sir John Scott Burdon-Sanderson, fast movement while trapping and the attendant electrical responses were the biggest delight to discover (Burdon-Sanderson, 1873).

ELECTRICAL SIGNALLING IN CARNIVORES

The APs in the snap-traps of *Dionaea muscipula* and *Aldrovanda vesiculosa* are the fastest self-propagating electrical signals reported in plants to date (Trębacz *et al.*, 2006; Fromm and Lautner, 2007). In *Aldrovanda*, they were shown to propagate at 80 mm s⁻¹ (Iijima and Sibaoka, 1982), while

average rates of AP transmission in non-carnivorous plants range from few up to 30 mm s⁻¹ (Trębacz *et al.*, 2006; Fromm and Lautner, 2007). In *Dionaea*, APs reach up to 250 mm s⁻¹ in midrib-forward direction, and ‘only’ 60–170 mm s⁻¹ when running towards the trap margins. Also, AP durations of 1 s in *A. vesiculosa* (Iijima and Sibaoka, 1981) and of 2 s in *D. muscipula* (Hodick and Sievers, 1988) are unique among plants. By comparison, APs in the closely related *Drosera* have an average duration of 10–20 s (Williams and Spanswick, 1976), whereas in lower plants a single AP can even last dozens of minutes (Koselski *et al.*, 2008).

One AP for *Aldrovanda vesiculosa* and at least two for *Dionaea muscipula* are necessary to cause a trap to shut (Brown, 1916). Like a tightened spring, elastic energy, accumulated through an active process which is still imperfectly understood, is passively released within 100 ms to bring about a change in lobe position (Forterre *et al.*, 2005). However, the trap is not yet completely closed and will reopen relatively quickly (within several hours), if not stimulated repeatedly (Lüttge, 1983). Incomplete closure produces gaps between interlocking tines, which gives a sufficiently small prey a chance to escape. This could be an adaptive trait of energy saving, because a small prey does not provide sufficient amounts of nutrients to benefit the plant (Pavlovič *et al.*, 2010a). If the prey is too large to break out, it begins to scramble, touching the hairs repeatedly. The series of APs thus generated triggers a complete closure. Within 0.5–2 h the two lobes of the trap become tightly pressed to each other (Affolter and Olivo, 1975; Lichtner and Williams, 1977). This second closure step relies on a loss of turgor of the upper epidermis and adjacent mesophyll cells (Sibaoka, 1991) and simultaneous extension of the lower epidermis (Hodick and Sievers, 1989). The loss of turgor is associated with passive K⁺ release. The K⁺-channels that might be involved have already been identified in *Dionaea* (Iijima and Hagiwara, 1987). Accordingly, midrib-located K⁺ uptake is responsible for active trap re-opening in *Aldrovanda* (Iijima and Sibaoka, 1983). An entrapped animal stimulates digestive glands to produce enzymes either by triggering of successive APs or through urea excretion, or both (Lüttge, 1971, 1983; Robins and Juniper, 1980d). Needless to say, there are many more chemical substances other than urea which can stimulate gland exudation (e.g. amino acids, ammonium, methyl jasmonate, coronatin; Robins, 1976; Šlesak, 2002) and many of them also act as AP elicitors (Lüttge, 1983; Ueda *et al.*, 2010). Once evoked, the AP spreads, without a fall of amplitude, through numerous plasmodesmata from one cell to another throughout the entire traps of *Aldrovanda* (Iijima and Sibaoka, 1982) and *Dionaea* (Hodick and Sievers, 1988). As almost all cells of the trap are electrically coupled, they exhibit comparable resting membrane potentials (from -80 to -160 mV, depending on experimental conditions), are equally excitable and their APs display similar amplitudes (about 130 mV, when the concentration of Ca²⁺ in the bath is around 1 mM) (Sibaoka, 1966; Iijima and Sibaoka, 1981; Hodick and Sievers, 1986, 1988). The AP amplitudes depend heavily on Ca²⁺-influx, which has been elegantly shown by observing the corresponding growth of their values with an increase in [Ca²⁺]_{ext} (Iijima and Sibaoka, 1985; Hodick and Sievers, 1986, 1988;

Sibaoka, 1991). The peak AP value increased by 26–28 mV with a tenfold increase in $[Ca^{2+}]_{ext}$. Inversely, Ca-ionophores or chemicals disturbing Ca-homeostasis hamper AP amplitudes, prolong repolarization (Fig. 5; Trębacz *et al.*, 1996; Król *et al.*, 2006) and slow down trap closure (Volkov *et al.*, 2008). Apart from Ca^{2+} , Cl^- ions may also be considered part of the depolarization phase, which was indirectly revealed by the use of a Cl^- -channel blocker (A9C) (Król *et al.*, 2006).

In *Drosera*, APs are generated in the head of tentacles in response to chemical (Na^+ , chitin or prey defecation) or mechanical (touch) stimulation (Williams and Pickard, 1974). As little weight as that of a human hair (0.822 mg) is sufficient to initiate the response; among various chemicals, NaCl, NH_4Cl , urea, amino acids and phosphate are capable of triggering APs in this genus (Lüttge, 1983). The APs move down the stalk of the tentacle at 5 mm s^{-1} , while upward propagation is twice as fast (Williams and Pickard, 1972a, b; Williams and Spanswick, 1976). The inner stalk cells (reminiscent of the phloem parenchyma) and the outer cells (epidermis), both electrically coupled by numerous plasmodesmata, are responsible for the rapid transmission of APs (Williams and Pickard, 1974; Williams and Spanswick, 1976). Two succeeding APs within 1 min are necessary for tentacle movement and just 1 min later the tentacle has completely curled (Williams and Pickard, 1972b).

It seems that the first AP facilitates the spread of another (Sibaoka, 1966; Fromm and Lautner, 2007). The requirement for two successive APs serves to protect the trap against any accidental and undesirable stimulation [e.g. by rain, temperature drops (Król *et al.*, 2006) or light (Trębacz and Sievers, 1998)], and points to the interesting proposition that the plants (here, *Dionaea* and *Drosera*) may possess a kind of memory which allows them to take action only in response to the second AP (plant memory; Trewavas, 2005a, b; Baluška and Mancuso, 2007; Volkov *et al.*, 2009a). As the membrane potential returns to its resting value directly after the passage of the AP, the resting potential cannot act as an

'accumulator' in the memory process. There is also no indication that the memory is associated in any way with a receptor potential (RP – membrane potential change that precedes AP but is too small to evoke it) (Jacobson, 1965). Instead, by analogy to animal nerve systems, a stepwise accumulation of bioactive substances during successive stimulations of the trap was suggested (Ueda and Nakamura, 2006; Ueda *et al.*, 2010).

There is no consensus that APs are involved in movement of *Utricularia* bladders (Juniper *et al.*, 1989). Although Diannelidis and Umrath (1953) reported that electrical stimulation causes the trap to 'fire', other researchers have been unable to repeat their results; even though single AP-like changes were noted, the traps did not fire (Sydenham and Findlay, 1973, 1975). Although recent findings indirectly support the mechanical concept of trap triggering (Joyeux *et al.*, 2011; Vincent *et al.*, 2011), it is tempting to speculate that APs must be evoked repeatedly – by analogy to snapping species (Brown, 1916) – to trigger trap movement.

A quite different role is played by APs in the protocarnivorous *Stylidium* (Darnowski *et al.*, 2006, 2007), in that they are a part of its pollination strategy (Findlay, 1978; Findlay and Findlay, 1975, 1981, 1984; Findlay and Pallaghy, 1978). As they have little to do with its carnivorous lifestyle, we need not discuss them further at this point.

SECRETION AND ABSORPTION

Darwin (1875) was the first to show that carnivorous plants secrete their digestive fluid in response to nitrogenous substances. Among these substances, uric acid (the principal constituent of insect faeces) and glutamine (the major amino acid of insect haemolymph) turned out to be the most effective elicitors of secretion (Robins, 1976). In *Dionaea*, repetitive electrical or mechanical stimulation evokes enzyme secretion, too (K. Trębacz and E. Król, unpubl. res.). Thus, APs can also be considered as elicitors of secretion. Once stimulated, the gland cells undergo a cycle of ultrastructural changes generally divided into two phases, the secretory and the resorptive (Heslop-Harrison and Heslop-Harrison, 1981). During the secretory phase, cell wall erodes, plasmalemma becomes less invaginated and vacuoles shrink (pointing to their involvement in enzyme storage and release), but *de novo* protein synthesis also takes place (Robins and Juniper, 1980b; McNally *et al.*, 1988). In general, mucilage-secreting cells discharge the Golgi-originated bodies [*Drosera* (Outenreath and Dauwalder, 1982a)], while the exocytosis of digestive enzymes involves a membrane fusion with storage vesicles of endoplasmic reticulum (ER) origin [*Pinguicula* (Vassilyev and Muravnik, 1988a, b), *Genlisea* (Płachno *et al.*, 2007), *Drosera* (Heslop-Harrison, 1976), *Dionaea* (Robins and Juniper, 1980c)]. A split between mucilage- and enzyme-secreting glands has been reported for Lamiales (*Pinguicula*, *Utricularia*, *Byblis*) and for some Droseraceae *sensu lato* [*Drosophyllum* (Heslop-Harrison and Knox, 1971; Juniper *et al.*, 1989; Legendre, 2002a, Płachno *et al.*, 2006)]. On the other hand, there are reports of glands secreting polysaccharides and proteolytic enzymes at the same time, for example *Pinguicula* (Lüttge, 1971) and *Dionaea* (Robins and Juniper, 1980c). Although *Pinguicula*'s sessile glands were presumed

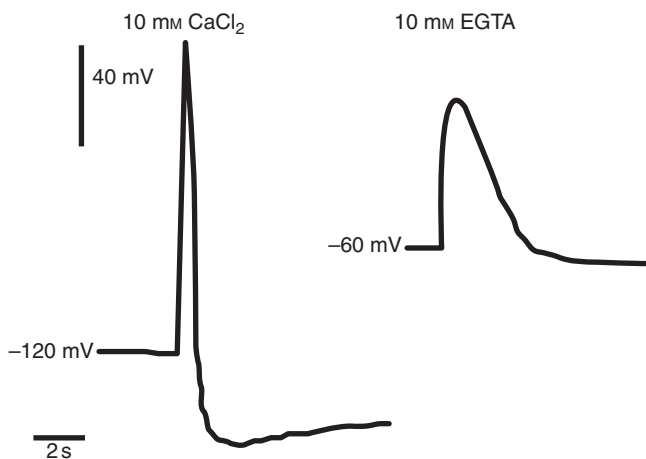


FIG. 5. Action potentials recorded in terminal gland cells after touching a trigger hair and in the presence of 10 mM $CaCl_2$ (left) or of a calcium chelator [10 mM EGTA (right)] in the external solution. Note that in the absence of free calcium ions, not only is the amplitude of the action potential but also the membrane resting potential are drastically affected.

to undergo holocrine secretion (Heslop-Harrison, 1975, 1976; Heslop-Harrison and Heslop-Harrison, 1980, 1981), other reports clearly showed that these cells display a granulocyte mode of secretion (Vassilyev and Muravnik, 1988a, b), as in the case of the other carnivores. By analogy to enzyme secretion, absorption of nutrients is either constitutive or needs to be triggered (Rea and Whatley, 1983). Absorption of nutrients is executed by all gland types (Outenreath and Dauwalder, 1982b) as well as through any available apertures in the protecting cuticle (Juniper et al., 1989; Anderson, 2005). Within any one gland, these two processes may be temporally (Heslop-Harrison and Heslop-Harrison, 1981) or developmentally (Owen et al., 1999) separated. In *Dionaea*, secretion precedes absorption only slightly, and during several-day-long digestion, both processes happen at the same time (Robins and Juniper, 1980e). In *Nepenthes*, too, both processes coincide after the first successful capture, and a bi-directional transport of various compounds takes place (Owen et al., 1999). Because for *Pinguicula* each sessile gland is used only once, the absorption starts only when the secretion ends. The absorbed substances migrate through the apoplast and symplast of the terminal cells (Owen et al., 1999). In the endodermal layer, they must enter the symplast, which is an active and selective process. The previously secreted H^+ ions now play a direct role in the symport uptake of nitrogenous compounds (Rea and Whatley, 1983). Among these (ammonium, amino acids, peptides, uric acid) ammonium is preferred, and ammonium transporters have long been shown to be highly expressed in the glands (Schulze et al., 1999). The absorbed material is stored in the small vacuoles, which persist in an increased number through the whole absorption phase (Robins and Juniper, 1980e). At the end of the phase, the cell walls are rebuilt and the glands return to their state prior to stimulation.

GLAND MORPHOLOGY

The secretory (slime and digestive) glands may be described as stalk- [*Drosera* (Fig. 2E), *Drosophyllum*, *Triphyophyllum*, *Pinguicula*, *Byblis*, *Roridula*, *Utricularia* (Fig. 2F)], sessile- [*Cephalotus* (Fig. 2A, B), *Drosophyllum*, *Drosera*, *Dionaea*, *Aldrovanda*, *Pinguicula*, *Genlisea* and *Utricularia*] or sunken-glands [*Nepenthes* (Fig. 2C, D), *Brochinia*, *Catopsis*], (Juniper et al., 1989). The main role of digestive glands is to secrete digestive fluids and to absorb nutrients. The special

pitcher epithelium has developed as an alternative in *Sarracenia* to perform both these functions (Hepburn et al., 1920; Joel and Heide-Jørgensen, 1985; Gallie and Chang, 1997). Nevertheless, in *Sarracenia purpurea* only a small amount of the fluid is produced by the epithelium and most of the enzymes come from the pitcher inhabitants (Hepburn and St. John, 1927; Hepburn et al., 1927; Plummer and Jackson, 1963); in another member of this family, *Darlingtonia*, the fluid is rarely secreted (Treat, 1875) or is produced in very small amounts (Adlassnig et al., 2011; our pers. obs.).

The stalk glands may resemble tentacles, trichomes, arms, emergences, projections, papillae, bristles or hairs. As for the sessile or sunken glands, their anatomical structures are less distinctive as they look like pinheads more or less embedded into the epidermis (Owen and Lennon, 1999). In all the types, however, at least three functional compartments are always present: terminal (secretory), middle (endodermal) and basal (reservoir) cells (Fig. 6). The terminals of secretory cells make up the outermost layer of cells, forming a visible swelling. Within a gland, the number of secretory layers as well the number of secretory cells in each layer varies: one (rarely) to four (typically) and up to eight secretory cells forming one-layered heads in *Utricularia* and *Genlisea*, respectively; two layers of secretory cells in *Dionaea* and *Aldrovanda*; and more than two layers in the large glands of *Nepenthes*. The cuticular coat covering the outermost cells is extremely thin and discontinuous, enabling secretion as well as absorption (Williams and Pickard, 1974; Joel et al., 1983). The presence of cuticular material is, nevertheless, indispensable for the protection of the inside of the traps from self-digestion and microbial infection. A markedly protruding plasmalemma is a distinct feature of terminal cells. Thanks to numerous cell-wall ingrowths, the plasma membrane of terminal cells is deeply invaginated. A labyrinthine structure of the plasmalemma considerably extends the surface which faces the outer environment. Some secretory cells are further characterized by abundant pit-fields with numerous plasmodesmata [*Nepenthes* (Owen et al., 1999)], which facilitate fast symplastic connection between terminal and middle cells [*Genlisea* (Płachno et al., 2007)]. The plasmodesmata as well as the labyrinthine ingrowths are laid down non-randomly, indicating that their distribution and orientation are precisely controlled (Robins and Juniper, 1980a). The plasmalemma is assisted by many mitochondria, extended ER and Golgi vesicles, all of which are reminiscent

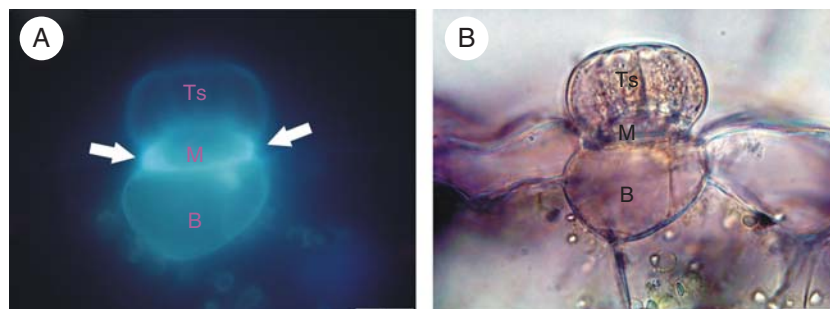


FIG. 6. Digestive gland anatomy. (A,B) Section through the *Pinguicula* digestive gland: TS, terminal (secretory) cells; M, middle (stalk) cell with Casparian-like lateral wall (arrows), auto-fluorescence under UV light; B, basal cell; scale bars = 20 μ m.

of transfer cells (Offler *et al.*, 2003). The large vacuole of terminal cells (Płachno *et al.*, 2007) usually houses storage substances which may be used as energy supplies during intensive secretion (Robins and Juniper, 1980b). It may also serve as a reservoir for digestive enzymes (Schwab *et al.*, 1969) and osmotically active salts (Heslop-Harrison and Heslop-Harrison, 1981). Like plasmalemma morphology, the dynamic status of the vacuoles during secretion/absorption cycles is carefully monitored (Robins and Juniper, 1980a; Robins and Juniper, 1980e).

In *Utricularia*, bifids and quadrifids (Fig. 2F) are unique examples of terminal cells, in which a highly specialized regional separation of function occurs (Fineran and Lee, 1975; Płachno and Jankun, 2004). The arms execute absorption and secretion in the upper section, while the bottom regions (stalks) discharge supportive and conductive functions typical of the middle cells (Fineran and Lee, 1975). In the glandular organs of the other carnivores, the secretory cells lie over the highly specialized endodermal middle cells. In these endodermal cells, heavily suberized cell walls create a barrier for apoplastic transport (and also for external solutions) in such a way that the hydrophobic suberin-like endodermal deposits form a continuity with epidermal cuticle (Robins and Juniper, 1980a; Owen and Lennon, 1999). The middle cells are simply 'a bottleneck' for apoplastic–symplastic exchange. They play a pivotal role in nutrient uptake as they prevent uncontrolled leakage between the apoplast and symplast (Fineran and Lee, 1975).

Numerous plasmodesmata between the middle and basal cells are of vital importance. Their distribution within the gland is not random, but shows a strong polarity, increasing toward the inside [*Dionaea* (Robins and Juniper, 1980a)]. Storing K^+ and Cl^- in their central vacuole, the basal cells are sometimes called reservoir cells [*Pinguicula* (Heslop-Harrison and Heslop-Harrison, 1980)]. The high K^+ content in basal cells points to their osmoregulatory functions linked to the transfer of different solutes into and out of the traps [*Nepenthes* (Osunkoya *et al.*, 2007)]. Beside the large vacuole, the other cytoplasmic features reflecting the activities of basal cells include abundant ribosomes, rudimentary plastids and numerous electron-dense vesicles in close proximity to the nucleus and plasmalemma. The basal layer is either in direct contact with the conductive vessels (*Nepenthes*, *Pinguicula*, *Drosera*) or separated from plant vasculature by 2–3 layers of mesophyll or parenchymal cells (*Dionaea*, *Aldrovanda*, *Genlisea*).

The activity of digestive glands varies depending on trap type and conditions. In pitfalls, eel-traps, suction-traps and fly-papers of *Pinguicula*, *Drosophyllum* and *Drosera* they are characterized by a low constitutive expression of hydrolysing enzymes, intensified after prey capture (McNally *et al.*, 1988). The terrestrial *Dionaea* and aquatic *Aldrovanda* are two 'extreme' examples, where secretion of digestive enzymes commences only after induction (Juniper *et al.*, 1989).

CONCLUSIONS

Despite being of little economic importance, carnivorous plants have long held a fascination, being among the most popular plants in cultivation. They still draw the attention of many scientists as convenient model plants for such topics

as: fast movements (Joyeux *et al.*, 2011), excitability (Król *et al.*, 2006; Volkov *et al.*, 2009a, b, 2011), negative excitability–photosynthesis coupling (Pavlovič *et al.*, 2011), enzyme secretion (Vassilyev, 2005; Rottloff *et al.*, 2009), nutrient absorption (Płachno *et al.*, 2009), heavy metal phytotoxicity (Moody and Green, 2010), food–web relationships (Butler *et al.*, 2008; Mouquet *et al.*, 2008; Sirová *et al.*, 2009, 2010, 2011; Gotelli *et al.*, 2011), plasticity and genetic radiation (Greilhuber *et al.*, 2006; Albert *et al.*, 2010), phylogenetic and intergeneric relationships (Rogers *et al.*, 2010; Rahman, 2010), trade-off assessments (Pavlovič *et al.*, 2010a), and structural and mineral investment in carnivory (Guisande *et al.*, 2004, 2007; Adamec, 2008, 2009, 2010b). Carnivorous species (namely *Utricularia*) can nowadays be used as plant indicators for qualifying the degree of surface water eutrophication (Jennings and Rohr, 2011); such an approach meets the requirements of the Water Framework Directive of the European Commission 2000 (Kopeć *et al.*, 2008). *Sarracenia* spp. are suggested to be the best indicators of threats from agriculture, over-collection and invasive species, while *Drosera* spp. are particularly sensitive to agriculture (Jennings and Rohr, 2011). The biological appliance of carnivore secondary metabolites has also gained in popularity (Gonçalves *et al.*, 2008; Krollicka *et al.*, 2008; Eilenberg *et al.*, 2010; Putalun *et al.*, 2010; Mithöfer, 2011). The more that is learnt about the different taxa, the clearer it becomes that carnivory is far more common than previously thought. Because morphological and physiological adaptations to carnivorous lifestyles are quite complex (the concurrence of such abilities as prey attraction and capture, digestion, absorption, enzyme secretion and nutrient re-utilization), there are a considerable number of plants carrying on 'subtle' forms of carnivory (Chase *et al.*, 2009; Shaw and Shackleton, 2011). Thus, plant carnivory still requires a great deal of study, in terms of both its basic features and its co-evolution with non-carnivorous traits.

With the use of state-of-the-art approaches such as large-scale analysis of genes (genomic) and their products (transcriptomic, proteomic, metabolomic) we have just begun the journey to a full appreciation of the carnivorous syndrome. For example, by the means of forward genetics based on a recognizable phenotypic characteristic, one can search for genes involved in a trap movement. With the use of reverse genetics it may be possible to unmask channels involved in excitation-triggered trapping or AP spread; one can think of creating a plant line with altered activity of an ion channel by transgenic methods (over-expressor, knock-out, antisense or RNA interference). Additionally, certain expression systems afford one the opportunity of working out the channel functions in detail (Geiger *et al.*, 2009). Another approach would be to focus on nutrient transporters, following their gene expression patterns which vary under distinct nutritive stresses. One could also utilize proteome profiling or metabolic fingerprinting to trace cellular processes under nutrient limits. The very recent study by Gotelli *et al.* (2011) suggests the use of proteomic signatures of *Sarracenia purpurea* inhabitants for monitoring pitcher ecosystem biomass, health and state. As an entire aquatic food web is harboured within the traps of this carnivorous plant, the *S. purpurea* pitcher ecosystem can be used to model macro ecosystems

such as lakes or dystrophic waters (Gotelli and Ellison, 2006; Gotelli *et al.*, 2011). The biggest challenge, however, is to combine all of these approaches to obtain a more complete picture of carnivorous plants. Finally, any substantial progress made in our understanding of carnivores must surely lead to better apprehension of plant biology as a whole.

Note added in proof

The authors encourage the reader to refer to the last chapter of the recently published book *All Flesh is Grass. Plant–Animal Interrelationships* (Adamec, 2011b; Rice, 2011).

ACKNOWLEDGEMENTS

We cordially thank the referees, whose helpful and valuable comments have greatly improved the manuscript, the director of the Botanic Garden of the Jagiellonian University Prof. Bogdan Zemanek for permission to use plants from the Garden collections, and the gardener Lucyna Kurleto. Financial support by the Polish Ministry of Education to K.T. (grant no. N301 464534) and to B.J.P. (grant nos. N304 002536 and N304 220135) is gratefully acknowledged. B.J.P. acknowledges the support of an award from the Foundation for Polish Sciences (Start Programme). L.A. was partially supported by the Research Programme of the Academy of Sciences of the Czech Republic, AV0Z60050516.

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