



## Carnivorous Plants: Physiology, ecology, and evolution

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### CHAPTER

## 1 Introduction: what is a carnivorous plant?

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### Abstract

The approximately 800 species of carnivorous plant together provide a classic example of convergent evolution. The known carnivorous species and genera represent nine independent angiosperm lineages. They are united by a suite of five essential traits that together make up the ‘carnivorous syndrome’: (1) capturing or trapping prey in specialized, usually attractive, traps; (2) killing the captured prey; (3) digesting the prey; (4) absorption of metabolites (nutrients) from the killed and digested prey; and (5) use of these metabolites for plant growth and development. Although many other ‘paracarnivorous’ plants have one or two of these traits, only plants that have all five of them that function in a coordinated way can be considered true carnivorous plants.

**Keywords:** Carnivorous plants, carnivorous syndrome, traits

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We perceive the relationship between plants and animals asymmetrically. As a rule, plants are producers and animals are consumers—of both plants and other animals. Most animals actively move freely through their environment, whereas plants are rooted in place and comparatively immobile. And while animals are on the offensive, searching for and eating plants, the plants are on the defensive, warding off animals physically and chemically. This asymmetry has resulted in a coevolutionary arms race between plants and animals that has, at least in part, spurred their diversification (Ehrlich and Raven 1964).

There are, however, at least 800 species of plants (Appendix) that have turned the tables on animals and become predators of animals. These carnivorous plants, which literally swallow (Latin: *vorare*) flesh (*carnis*), have evolved independently in at least ten evolutionarily separate lineages (Chapter 3). Despite their relative rarity among the > 350,000 species of flowering plants, carnivorous plants have attracted the attention of many scientists in a wide range of disciplines, from botany to zoology, anatomy and physiology to ecology and evolution, and biophysics to bioengineering.

As with much of contemporary biology, serious study of carnivorous plants began with Darwin (1875, Chase et al. 2009). In *Insectivorous Plants*, Darwin (1875) raised several fundamental questions: How do carnivorous

plants capture and kill insects, do they obtain nutrients from the captured prey that increase the fitness of carnivorous plants, and what is the evolutionary origin (i.e., homology) of the specialized organs (e.g., glands, hairs, “tentacles” of the sundews [*Drosera* spp.] and other taxa then placed in the Droseraceae, and active traps of *Dionaea*, *Aldrovanda*, and *Utricularia*). These questions have been revisited in synthetic reviews at roughly 50-year intervals (Lloyd 1942, Juniper et al. 1989, and this present volume).

## 1.1 The carnivorous syndrome

Answering any of Darwin’s questions, and others that have arisen in the last 140 years, depends on accurate identification of carnivorous plants and delimitation of them from noncarnivorous ones. Identifying and delimiting carnivorous plants requires understanding their evolutionary histories (Chapters 3–10); identification of their essential morphological and physiological traits (Chapters 12–19); and parsing of the details of their interactions with their prey, pollinators, and symbionts (Chapters 21–26). Like many plants, carnivorous ones are sparsely distributed and restricted to particular habitats (Chapter 2), many of which are continually altered by human activities and are vulnerable to climatic change (Chapters 27–28). As the knowledge of carnivorous plants has expanded, so too has their relevance for understanding noncarnivorous ones (and *vice versa*), and, after more than a century of detailed study, carnivorous plants no longer are seen simply as botanical monstrosities.

The 19 genera of carnivorous plants represent at least ten evolutionarily different lineages that are united by a group of shared, functional traits that enable the plants to obtain most of their nutrients from animal prey: rapid movements of traps that are regulated electrophysiologically; secretion of hydrolytic enzymes that digest proteins, chitins, and other organic compounds; foliar uptake of nutrients; stimulation by foliar nutrient uptake of uptake of nutrients by roots; and stimulation of plant growth by foliar nutrient uptake (Adamec 2011c). Although each of these functional traits or physiological processes also can occur—usually singly—in noncarnivorous plants, they normally co-occur in carnivorous plants where they are coupled in series firmly to another. Together, they form a coordinated cluster of characters referred to as the “carnivorous syndrome” (Juniper et al. 1989; Adamec 1997a).

The expression of each of these traits varies among carnivorous plants (Chapters 12–16). The main benefit of carnivory is the uptake of growth-limiting mineral nutrients from prey (Adamec 1997a; Chapters 16–19), and so we consider there to be five essential traits of the carnivorous syndrome (cf. Lloyd 1942, Givnish 1989, Juniper et al. 1989, Adamec 1997a, 2011c, Rice 2011c, Pavlovič and Saganová 2015):

1. capturing or trapping prey in specialized, usually attractive, traps;
2. killing the captured prey;
3. digesting the prey;
4. absorption of metabolites (nutrients) from the killed and digested prey;
5. use of these metabolites for plant growth and development.

Only plants that possess all five of these traits should be considered as “carnivorous” plants.

Many researchers also have considered attraction and retention of prey to be two other essential traits within the carnivorous syndrome (Juniper et al. 1989; Chapters 12, 13, 16, 21). Although these traits may improve the efficiency of carnivory, they do not appear to be required. For example, attraction has been studied and confirmed only for some carnivorous plants and does not occur in others (Givnish 1989, Guisande et al. 2007; Chapter 12). Prey retention close to the trap entrance following attraction (i.e.,

transiently before prey capture itself) occurs only in *Dionaea* and pitcher plants (Juniper et al. 1989), but most prey attracted to the latter leave unscathed (Newell and Nastase 1998, Dixon et al. 2005).

As all plants can absorb organic substances from soil by roots (e.g., from dead animals), the criterion of actively killing prey captured in traps (Chapters 13–15) separates carnivorous from mycoparasitic (a.k.a. saprophytic) plants. Digestion of prey can occur by a variety of means. Most carnivorous plants secrete hydrolytic enzymes (Chapter 16), but some rely on trap commensals (digestive mutualists: Chapters 23, 24, 26) to digest prey and mineralize the organic nutrients (e.g., Givnish 1989, Jaffe et al. 1992, Butler et al. 2008). The role of autolysis in digestion of prey carcasses has been underestimated and understudied (Chapter 16), but may play a significant role in carnivorous plants that do not secrete digestive enzymes. Many carnivorous plants can also acquire organic and mineral nutrients from detritus, pollen, algae, or microorganisms (Chapters 17, 19, 25).

## 1.2 Subsets of carnivorous plants

By analogy with parasitic plants, in which holoparasitic plants are differentiated from hemiparasitic ones, Joel (2002) distinguished holocarnivorous plants (e.g., *Aldrovanda*, *Dionaea*, *Drosera*, *Drosophyllum*, *Pinguicula*, *Utricularia*, *Nepenthes*), that secrete their own digestive enzymes, from hemicarnivorous ones (e.g., *Darlingtonia*, *Heliophora*, *Brocchinia*, *Roridula*), that do not. Rice (2011c) referred to the latter as paracarnivorous plants.

Alternatively, carnivorous plants can be subdivided based on how they obtain nutrients from prey, whether or not they secrete digestive enzymes. All genera of carnivorous plants except for *Roridula* obtain nutrients directly from their prey (Adamec 2011c). The two *Roridula* species capture prolific prey but they do not digest it. Rather, their captured prey is consumed by hemipteran bugs (*Pameridea* spp.) that live only on *Roridula* and which defecate on its leaves; the plants absorb the bug-processed nutrients through specialized cuticular gaps (Ellis and Midgley 1996, Anderson 2005; Chapters 10, 26). In *Roridula*, as in *Sarracenia purpurea* (Chapter 24) mineral nutrients from prey are gained indirectly, through excrement of digestive mutualists. A handful of species in a few other lineages of carnivorous plants also appear to have lost the carnivorous habit (Chapter 3), and at least four species of *Nepenthes*—*N. lowii*, *N. macrophylla*, *N. rajah*, and *N. hemsleyana*—obtain some or all of their nutrients from excrement of tree shrews or bats that, respectively, are attracted and feed on exudates from the highly modified pitchers that feed these mammals or roost within the pitchers (Chapters 5, 13, 26). Other species are partly detritivorous (Chapter 17).

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## 1.3 Other plants that share some carnivorous characteristics

The ability to trap passively small insects, digest them, and absorb at least some nutrients from their carcasses has been observed in many other plant species. Spomer (1999) detected surface proteinase activity in 15 species of North American plants (including the common potato, *Solanum tuberosum*) with glandular leaves, stems, or flowers; he called these plants protocarnivorous, but we think this term should be avoided because it implies that plants with surface proteinases are ancestral to carnivorous plants or that evolution of plants is progressing toward carnivory. Two of the 19 species he studied, *Geranium viscosissimum* and *Potentilla arguta*, also absorbed carbon from  $^{14}\text{C}$ -labeled algal protein into their leaves, a phenomenon that has been observed infrequently in carnivorous plants (Chapter 16). Similarly, some *Stylidium* species entrap insects in their inflorescences and have some protease activity associated with their sticky glands (Darnowski et al. 2006).

Although thousands of vascular plants have sticky, glandular organs that can ensnare insects, and most plants can absorb nutrients through their stems and leaves, most of these plants grow in relatively fertile soils, whereas carnivorous plants normally grow only in nutrient-poor soils or dystrophic, barren waters (Chapters 2, 17–19). Sticky glandular organs with proteinase activity apparently have evolved as a defense against small arthropod herbivores or microbial pathogens (Chapter 16) but the episodic capture of very small prey appears to contribute little to the mineral nutrient budget in plants such as *Geranium viscosissimum*, *Potentilla arguta*, or *Stylidium* spp. In contrast, prey capture and digestion account for most nutrients obtained by carnivorous ones (Płachno et al. 2009a; Chapter 17–19).

## 1.4 The benefits and costs of carnivory

The quantity (biomass) of captured prey per plant and the efficiency of prey use are the principal factors determining the ecological benefits and evolutionary fitness of carnivory under natural conditions (e.g., Givnish et al. 1984, Adamec 1997a, 2011c, Farnsworth and Ellison 2008; Chapters 2, 17, 18). There are, however, substantial structural, physiological, and ecological costs to attracting, capturing, and digesting prey (e.g., Givnish et al. 1984, Ellison and Gotelli 2002; Chapter 18). For carnivory to evolve, the marginal benefits of either direct or indirect carnivory (§1.2) must exceed their marginal costs (Givnish et al. 1984; Chapter 18). These benefits most often outweigh the costs in nutrient-poor, well lit, and wet environments (Givnish et al. 1984, Benzing 1987, 2000; Chapters 2, 18).

Even after the plants have digested and mineralized nutrients from their prey, the dismembered carcasses still may contain relatively high amounts of mineral nutrients, especially nitrogen in chitin (Adamec 2002; Chapter 17). After traps senesce and decay, the carcasses and dead traps that contact wet topsoil decompose in proximity to the plant's (usually weakly developed) roots. Because of this additional decomposition, spent prey carcasses can be said to fertilize the soil close to the roots, which can thus take up additional, prey-derived nutrients.

## 1.5 The future: learning from carnivorous plants

In *Insectivorous Plants*, Darwin wrote that “as it cannot be doubted that this process [carnivory] would be of high service to plants growing in very poor soil, it would tend to be perfected through natural selection” (Darwin 1875: 362–363). Many noncarnivorous plants also grow in nutrient-poor soils, and an obvious question is, if carnivory is so useful in such environments, why aren't all plants that grow in them carnivorous?

In the last century and a half, as researchers have defined and delimited plant carnivory, they have also sought to understand its evolution and explain its rarity. The results have shed new light on the evolution and workings of physical and chemical defenses across the plant kingdom (Chapter 16), identified key genetic changes responsible for the shift from defensive chemistry to offensive carnivory (Fukushima et al. 2017), and highlighted the myriad ways that plants can extract scarce nutrients from nutrient-poor substrates (Benzing 1987, Givnish 1989; Chapter 18). Carnivorous plants illustrate general principles of coevolution and convergent evolution; in turn, a better understanding of both processes in carnivorous plants has led to the concept of evolutionarily convergent interactions that are revealing new symbiotic relationships among animals, plants, fungi, and microbes (Bittleston et al. 2016b). As more and more genomes of carnivorous plants are sequenced and annotated (Chapter 11), the data are being combined with detailed natural history observations and experimental results to test and develop new theories about plant form, function, ecology, and evolution. It is reasonable to suggest Darwin's “most wonderful plants in the world” increasingly will become model biological systems for field research (Chapters 24, 25) and

classroom study (Ellison 2014) in the same way that *Escherichia coli*, *Arabidopsis thaliana*, and *Drosophila melanogaster* have been used in the laboratory.

This vision will be realized only if viable populations of carnivorous plants persist in the field. The widespread fascination with carnivorous plants, their rarity, and their occurrence in unique, often patchy habitats makes them very vulnerable to over-collection and poaching, land-use changes, and ongoing climatic change. While scientists, land-use managers, and conservation professionals are working to preserve populations of threatened and endangered carnivorous plant species and their habitats (Chapter 27), researchers are using their unique distributional characteristics to test assumptions and reveal shortcomings in existing models used to forecast how species respond to climatic change (Chapter 28). The refined models, based on ideas gleaned from studying carnivorous plants, will benefit all species, rare or common, carnivorous or not.

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