

New evidence on the origin of carnivorous plants

 Thomas J. Givnish¹

Department of Botany, University of Wisconsin-Madison, Madison, WI 53706

Carnivorous plants have fascinated scientists and the general public since the pioneering studies of Charles Darwin (1). No doubt part of their wide appeal is that carnivorous plants have turned the evolutionary tables on animals, consuming them as prey, with the green predators often equipped with remarkable lures, traps, stomachs, and—in a few cases—extraordinary speed of movement. To be considered carnivorous, a plant must be able to absorb nutrients from dead bodies adjacent to its surfaces, obtain some advantage in growth or reproduction, and have unequivocal adaptations for active prey attraction, capture, and digestion (2, 3). Some carnivorous species [e.g., *Pinguicula* (butterworts), *Philcoxia*] lack obvious attractants; some rely on passive pitfalls [e.g., *Cephalotus* (Australian pitcher plant), *Sarracenia* (American pitcher plants)] rather than active traps based on sticky tentacles [e.g., *Byblis*, *Drosera* (sundews)] or snap traps [e.g., *Dionaea* (Venus fly-trap), *Utricularia* (bladderworts)]; and some lack digestive enzymes and instead depend on commensal microbes or insect larvae to break down prey (e.g., *Brocchinia*, *Darlingtonia*, some species of *Sarracenia*). Based on these criteria, today we recognize at least 583 species of

carnivorous plants in 20 genera, 12 families, and 5 orders of flowering plants (Table 1). Based on DNA sequence phylogenies, these species represent at least nine independent origins of the carnivorous habit per se, and at least six independent origins of pitfall traps, five of sticky traps, two of snap traps, and one of lobster-pot traps. To the extent to which molecular phylogenies have been calibrated against the ages of fossils of other plants, these origins of carnivory appear to have occurred between roughly 8 and 72 million years ago (Mya). In PNAS, Sadowski et al. (4) contribute to our understanding of the origins of plant carnivory by describing the first fossilized trap of a carnivorous plant, a fragment of a tentacled leaf preserved in Baltic amber from 35 to 47 Mya, and allied to modern-day *Roridula* of monogeneric Roridulaceae (Ericales) from South Africa.

As with most carnivorous plants, the two living species of *Roridula* today grow on open, extremely infertile, moist sites. The occurrence of carnivorous plants on nutrient-poor substrates has been understood since Darwin showed that such plants augment their supply of mineral nutrients through prey capture. The restriction of carnivorous

plants to open, infertile, moist sites, however, remained unexplained until modern cost-benefit models showed that carnivores are likely to obtain an advantage in growth relative to noncarnivores only on such sites, where nutrients and nutrients alone limit plant growth, and where carnivory can accelerate photosynthesis and the conversion of photosynthate to new leaf tissue while decreasing allocation to root tissue (2, 3, 5, 6). Wet soils and fire can favor carnivorous plants, by making N more limiting for growth while making light and water less limiting (3). The wet, sandy, fireswept sites in fynbos occupied by *Roridula* (6) should thus favor carnivory, and indeed *Roridula* often grows in association with large numbers of carnivorous sundews.

Roridula, however, is in other respects highly unusual as a carnivorous plant. Although its glistening, glandular tentacles do trap large numbers of insects, the secretions are resinous rather than aqueous, and so cannot support the activities of digestive enzymes. It does not secrete proteolytic enzymes; several authors thus argued that *Roridula* could not be carnivorous because it could not digest prey or absorb the minerals released (7, 8). The resinous nature of *Roridula* secretions may be an adaptation to the summer drought in the Mediterranean climate it now occupies, in that they do not lose volume or stickiness during long periods of drought; the secretions also do not dissolve during winter rains (9). It turns out that certain hemipterans (*Pameridea*) are capable of negotiating the glandular leaves of *Roridula* without becoming entangled; they eat the prey immobilized by the plant, and then N from their excretions is absorbed by *Roridula* (Fig. 1). This process substantially augments the N supply to the plants, with the plants obtaining 70% or more of their nitrogen supply in this fashion (7, 10). The mutualism appears stabilized by nonlinear interactions: excess densities of *Pameridea* turn counterproductive as the bugs switch to sap-sucking in the absence of prey, leading to negative impacts on *Roridula* and, ultimately, on the bugs themselves (11).

Table 1. Currently recognized groups of carnivorous plants

Order	Family or clade	Genus/genera*	No. of taxa
Poales	Bromeliaceae I	<i>Brocchinia</i> ^P	2
	Bromeliaceae II	<i>Catopsis</i> ^P	1
	Eriocaulaceae	<i>Paepalanthus</i> ^P	1
Caryophyllales	DNDD clade		
	Droseraceae	<i>Aldrovanda</i> ^S , <i>Dionaea</i> ^S , <i>Drosera</i> ^T	115
	Nepenthaceae	<i>Nepenthes</i> ^P	90
	Drosophyllaceae	<i>Drosophyllum</i> ^T	1
	Dioncophyllaceae	<i>Triphyphyllum</i> ^T	1
Oxalidales	Cephalotaceae	<i>Cephalotus</i> ^P	1
Ericales	RS-Actinidiaceae clade		
	Sarraceniaceae	<i>Darlingtonia</i> ^P , <i>Heliophora</i> ^P , <i>Sarracenia</i> ^P	32
	Roridulaceae	<i>Roridula</i> ^T	2
Lamiales	Byblidaceae	<i>Byblis</i> ^T	6
	Lentibulariaceae	<i>Genlisea</i> ^L , <i>Pinguicula</i> ^T , <i>Utricularia</i> ^S	330
	Plantaginaceae	<i>Philcoxia</i> ^T	1

Taxa include all members of each genus, except for the monocot genera in order Poales, where the number of carnivorous species within the genus is listed. Independent origins of carnivory per se are indicated by boldface entries in the family/clade column.

*Trap types indicated by superscript: L, lobster-pot trap; P, pitfall; S, snap trap; T, sticky trap.

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¹Email: givnish@wisc.edu.



Fig. 1. Growth form of *Roridula gorgonias* at Fernkloof Nature Reserve near Hermanus, showing glandular tentacles that immobilize insect prey. Close-up of leaves, showing a *Pamerideia* bug (center) that eats immobilized prey and delivers nutrients to the plant via excreta.

Although the *Roridula* system is truly remarkable, similar kinds of complex digestive mutualisms may occur in other carnivorous plants. For example, *Nepenthes bicalcarata* provides domatia for ants, despite ants being the most frequent prey of many *Nepenthes*. Givnish (5) and Hölldobler and Wilson (12) proposed that the resident ants and plants might have a mutualistic relationship of some kind. In fact, the resident ant *Camponotus schmitzi* protects *N. bicalcarata* from weevils that attack their tendrils, and in addition facilitates the plant's uptake of nutrients (13). The ants can swim in the pitcher fluid without adverse effect, retrieve large prey items, and excrete wastes into the pitcher, accelerating nutrient uptake; ant wastes account for 42–76% of total N uptake and ants prolong pitcher lifetimes (13). In other systems, the prey processed by a digestive mutualist may not even be captured by the plant's own traps. *Nepenthes lowii* attracts tree shrews (*Tupaia montana*) to their exceptionally large, broad traps with secreted rewards, and they defecate into the pitcher while marking it as their territory. Their feces account for 57–100% of all leaf N (14). *Nepenthes rafflesiana* var. *elongata*, with smaller but elongate traps, provides a roost for a small bat and obtains nutrients from its feces (15). Whether these systems are best viewed as coprophagy or indirect forms of carnivory involving digestive mutualists that deliver the remains of prey is worth debating. Clearly, however, both plants benefit from animals whose death results in their acquisition of nutrients; we might consider them

“apparent carnivorous plants,” in homage to Holt's concept of apparent competition (16).

The new fossil *Roridula* not only is the first fossil trap leaf uncovered, it is one of the very few undoubted fossils of carnivorous plants of any kind. *Archaeamphora* from Chinese sediments 112 Mya was originally described as Sarraceniaceae, but now there is strong doubt that it was a member of that family or even a carnivorous plant; the unusual leaves may simply not have been traps (17). *Paleoaldrovanda*, putatively a member of Droseraceae based on a “seed,” may actually have

been a fossil insect egg (18). The remaining fossils considered legitimate remains of carnivorous plants include one seed (now destroyed) of *Byblis* (Byblidaceae) from Australia (19), and palynomorphs possibly allied with Nepenthaceae (20). The last two fragments, however, do not demonstrate that the plants to which they belonged were, in fact, carnivorous, which makes the find by Sadowski et al. (4) particularly important. The age of the amber *Roridula*, 35–47 Mya, nicely brackets the divergence between *Roridula* and noncarnivorous Actinidiaceae roughly 39 Mya, as estimated from a calibrated DNA phylogeny (21). This result lends credence to the age estimates based on molecular data, and to the inference from phylogenetic reconstruction that early Roridulaceae were carnivorous. The identity of the fossil *Roridula* appears to be beyond doubt. The former occurrence of *Roridula* around the Baltic—whereas its present-day distribution is restricted to the Cape Floristic Province of southwest South Africa—implies that this group was once far more widespread. The distributions of families in the Clethraceae-Sarraceniaceae-Roridulaceae-Actinidiaceae clade suggest that it originated in southeastern North America or northern South America. In the next few years, further investigations of the Baltic amber might tell us what other plants grew in association with fossil *Roridula*, and thus the nature of the vegetation in which fossil *Roridula* grew. Based on cost-benefit models, the distribution of present-day *Roridula*, and the current distributions of almost all other carnivorous plants, it seems most unlikely that fossil *Roridula* grew below a dense canopy of the conifer forests that produced amber!

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