

Parasitic plants

Although not generally recognized, parasitic organisms make up a large percentage of the Earth's total biodiversity. The word "parasite" generally conjures up images of organisms such as microbes and worms, but this life-form has evolved repeatedly in many groups, including flowering plants (angiosperms). A parasitic angiosperm is one that attaches to a host root or stem via a modified root called the haustorium, thereby deriving some or all of its water and nutrients. Some parasitic plants are green and photosynthetic, but they still obtain water and solutes from their host. These are called hemiparasites (somewhat of a misnomer in that they are fully parasitic). Other parasitic plants have lost their ability to conduct photosynthesis and are thus fully heterotrophic (that is, obtaining nourishment from exogenous organic matter). These are called holoparasites, and they obtain carbohydrates from host phloem as well as water from the host xylem. Here a plant is considered parasitic only if it forms a direct haustorial connection to a host plant. This excludes plants such as Indian pipe (*Monotropa*) that attach to mycorrhizal fungi and are technically known as mycoheterotrophs.

Because of their curious nature, the natural history of parasitic plants has been studied for centuries. Work from the mid-1800s onward focused

mainly on the morphological and anatomical features of these plants, with particular attention to adaptations associated with their parasitic habit. Since then, data from physiology, biochemistry, genetics, ecology, pathology, and phylogeny have resulted in a virtual explosion of information about these plants. It should be pointed out, however, that the vast majority of parasitic plants do not harm economically valuable crops. Indeed, of the 268 genera and 4558 species of parasitic plants (see **table**), only about 25 genera can be considered crop pests.

Recently, great advancements have been made in the area of the evolutionary biology of parasitic plants. Current information on parasitic angiosperms can be organized according to two interrelated disciplines: molecular evolution and molecular phylogeny. Parasitic plants have provided excellent models to study genetic changes at the molecular level because they represent natural genetic mutants that differ from typical land plants in fundamental ways. Indeed, the holoparasites stretch the definition of plant itself, having lost one of the key traits associated with this lineage: photosynthesis. Accompanying these changes at the molecular level are changes in morphological features as well. Reduction and complete loss of typical plant organs has compromised previous efforts to classify several parasitic plant families. More recently, molecular data have helped rectify this situation, but these studies have also produced some real surprises.

Molecular phylogenetics. Phylogenetics is primarily concerned with the branching events that took place during the evolutionary history of a group of organisms. With regard to parasitic plants, a basic question is: "How many times did parasitism evolve among angiosperms?" Previous morphology-based classifications provided many hypotheses, but different researchers often had conflicting ideas about the relationships of these plants, particularly the holoparasites. Thus, until recently, no definitive answer to this question could be given because well-supported phylogenetic trees were not available for all groups. As shown in the table, all parasitic angiosperms can now be placed in the global angiosperm phylogeny. For the most part, these placements are robust, being supported by analyses using genes from the nucleus, plastid, and mitochondrion. These results indicate that parasitism arose independently in 12 lineages (clades) of flowering plants.

Rafflesiaceae are a notable family for which evidence about their evolutionary relationships has been elusive. This family is considered here in the strict sense, that is, including only the large-flowered genera *Rafflesia*, *Rhizanthus*, and *Sapria*. *Rafflesia* is commonly known as the "Queen of the Parasites" because some members have the largest flowers among all angiosperms [exceeding 1 m (3.3 ft) in diameter] (see **illustration**). The placement of these amazing parasites in the global angiosperm phylogeny has been extremely difficult because of morphological reductions in vegetative parts—there are no stems, leaves, or roots, only an endophyte—the vegetative portion of the parasite that lives

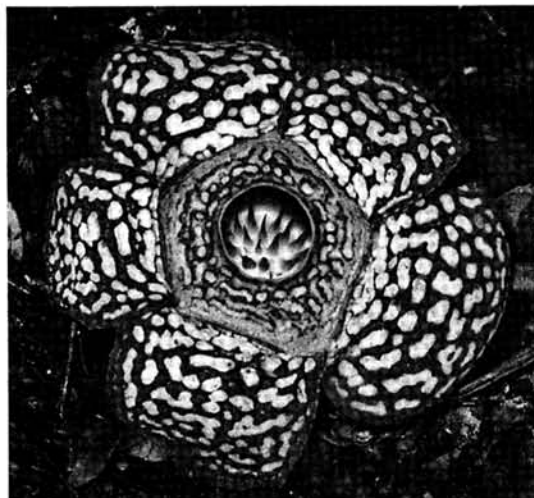
Parasitic plants				
Clade	Example genera	No. genera/species	Family	Order
1	<i>Cassytha</i>	1/16	Lauraceae	Laurales
2	<i>Hydnora, Prosopanche</i>	2/15	Hydnoraceae	Piperales
3	<i>Olax, Ximeria</i>	14/104*	"Olacaceae"	Santalales
3	<i>Misodendrum</i>	1/10	Misodendraceae	Santalales
3	<i>Arjona, Quinchamalium, Schoepfia</i>	3/50	Schoepfiaceae	Santalales
3	<i>Amyema, Nuytsia, Tristerix</i>	73/906	Loranthaceae	Santalales
3	<i>Agonandra, Opilia</i>	11/34	Opiliaceae	Santalales
3	<i>Comandra, Santalum</i>	37/531	"Santalaceae"	Santalales
3	<i>Arceuthobium, Phoradendron, Viscum</i>	7/546	Viscaceae	Santalales
3	<i>Balanophora, Helosis, Thonningia</i>	17/43	Balanophoraceae	Santalales
4	<i>Cynomorium</i>	1/2	Cynomoriaceae	Saxifragales
5	<i>Krameria</i>	1/18	Krameriaceae	Zygophyllales
6	<i>Rafflesia, Rhizanthus, Sapria</i>	3/30	Rafflesiaceae	Malpighiales
7	<i>Bdallophyton, Cyrtinus</i>	2/7	Cyrtinaceae	Malvales
8	<i>Apodanthes, Berlinianche, Pilostyles</i>	3/23	Apodanthaceae	Cucurbitales
9	<i>Mitrastemon</i>	1/2	Mitrastemonaceae	Ericales
10	<i>Lennoa, Pholisma</i>	2/5	Boraginaceae	Euasterid
11	<i>Cuscuta</i>	1/170	Convolvulaceae	Solanales
12	<i>Orobanche, Pedicularis, Striga</i>	88/2046	Orobanchaceae	Lamiales
	Total parasitic plants	268/4558*		

*Not counting 13/64 autotrophic (nonparasitic) "Olacaceae."

inside the host vine *Tetrastigma* (Vitaceae). Molecular phylogenetic methods have placed Rafflesiaceae in Malpighiales and recently more specifically near the spurge family Euphorbiaceae. This result is surprising because spurges typically have small flowers, thus indicating that the stem lineage leading to *Rafflesia* underwent a massive increase in flower size (ca. 79-fold).

With 163 genera and over 2200 species, the sandalwood order (Santalales) is one of the largest clades of parasitic plants. One of the most important innovations to evolve in Santalales is stem parasitism, which includes mistletoes.

The order Lamiales is a clade containing the family Orobanchaceae. Among flowering plants, parasites in the genera *Orobanche* (broomrape) and *Striga* (witchweed) inflict the most damage upon crops and are thus the subject of intensive efforts to reduce their impact on world agriculture.



Rafflesia pricei. Mature open flower, about 30 cm (12 in.) in diameter, from Tambunan, Sabah, Malaysia (Borneo). (Photograph by D. L. Nickrent)

Molecular evolution. Molecular evolution is concerned with the rates and patterns of change in macromolecules (DNA, RNA, and protein) and mechanisms underlying those changes. This is an active field intimately associated with molecular phylogeny. This is especially true with model-based phylogeny inference methods for which mathematical algorithms aim to accurately model molecular processes such as base substitutions. As mentioned above, parasitic plants represent natural genetic mutants that provide a window into understanding how evolutionary processes work at the molecular level. The use of parasitic plants as genetic models will be demonstrated by discussing three areas: evolutionary rate increases, plastid genome evolution, and horizontal gene transfer.

One of the earliest concepts developed when molecular data were applied to evolutionary questions concerns the molecular clock, that is, the number of DNA base substitutions (for example, changing an adenine to a guanine) accumulated per unit time (that is, the rate). Initially thought to be constant across different organismal lineages, later work showed that this strict molecular clock could not be applied to all organisms and all genes. Studies of some animals and plants suggested that differences in accumulated substitutions could be best explained by the generation time: Slowly reproducing organisms had fewer substitutions than rapidly reproducing ones. When DNA sequences of ribosomal genes of holoparasitic angiosperms such as *Balanophora* and *Rafflesia* were obtained, it was found that they exhibited substitution rates as high as 3.5 times that seen in nonparasitic, autotrophic plants. Because these parasites did not have rapid generation times and because some rapid generation plants such as *Arabidopsis* did not show the same rate increases, factors other than generation time were discussed.

Parasitic plants have also been important in the study of plastid genome evolution. Plastids are derived from cyanobacteria that became incorporated into eukaryotic cells hundreds of millions of years ago. This endosymbiotic event was followed by the massive loss of genes from their genome (plastome), most of which now reside in the host cell nucleus. Today, most land plant plastids are streamlined organelles with ~100 genes for which order is highly conserved. The primary function of the plastid is photosynthesis and, as expected, some of the genes needed for this process are coded by the plastome (for example, photosystem I and II genes, *rbcl*, etc.). However, several thousand genes are needed for the processes that take place in the plastid; thus, the majority of genes are coded by the nucleus and the products (proteins) are imported into the plastid. What then happens to the plastid and plastome of a holoparasitic angiosperm that does not photosynthesize? Answers to this question began emerging following study of beechdrops (*Epifagus*, Orobanchaceae), a root holoparasite of beech trees (*Fagus*) in North America. The complete plastome sequence of *Epifagus* showed that it is about half the size of a typical angiosperm plastome, the difference mainly attributable to the loss of all photosynthetic and respiratory genes. More recently, the complete plastome sequences of additional parasitic plants (*Cuscuta* and *Pholisma*) have been completed and they too have lost these genes.

The loss of genes in parasitic plant plastomes may be viewed as a continuation of a process that began soon after the initial endosymbiotic event. How far then can this process proceed? In other words, can the plastome be lost entirely? All plastids examined to date contain a plastome, albeit some are small. Whereas the plastome of *Epifagus* is 70 kilobases (kb) long, its relative *Conopholis* has been reduced to 40 kb. Although a complete plastome sequence is not available, Southern blot data suggest a plastome as small as 20 kb in *Cytinus* (Cytinaceae). A number of hypotheses have been advanced as to why nonphotosynthetic plastids retain plastomes [for example, the plastome has a gene (or genes) essential for survival, but which cannot be transferred to the nucleus], but overall none of them provide explanations that are satisfactory for all organisms. To date, only one lineage of holoparasite has eluded polymerase chain reaction (PCR) amplification of any plastome genes, namely Rafflesiaceae, again highlighting that one explanation may not serve all examples. Given the high substitution rates in holoparasites such as *Rafflesia*, molecular methods such as PCR and Southern blotting are compromised because the target genes may be too divergent to accept primers and probes designed from more "typical" plants. Ultimately, complete genome sequencing will provide the answer to the fate of the plastome in *Rafflesia*.

Parasitic plants have played a key role in uncovering another biological phenomenon that has only recently received wide attention: horizontal (or lateral) gene transfer (HGT) [where genetic material

(DNA) is exchanged among organisms that are distantly related]. The most prevalent form of genetic inheritance is vertical transmission, that is, a parental generation providing genes to the next (filial) generation, and so on. Indeed, this form of inheritance provides the cornerstone for Darwinian evolution. However, HGT between unrelated species can occur in bacteria and fungi, although its frequency, mechanism, and significance in eukaryotes are not understood. It should be pointed out that HGT here does not refer to transmission of mobile genetic elements, but to larger segments of DNA (for example, whole genes) from the mitochondrion and nucleus. Widespread transfer of mitochondrial genes in flowering plants and a gymnosperm has been demonstrated, and this same phenomenon was documented for a parasitic plant. Ironically, the transfers are not unidirectional (host to parasite), but movement of parasite genes into hosts has been documented as well. These involved the discovery of the mitochondrial gene *atp1* from *Cuscuta* in *Plantago* and mitochondrial *nad1* and *matR* genes from Santalales in the fern *Botrychium*. The mechanism of HGT is still a matter of speculation; however, the role played by parasitic plants in providing interspecific conduits is being investigated.

For background information see AGRICULTURAL SCIENCE (PLANT); CELL PLASTIDS; PARASITOLOGY; PLANT CELL; PLANT GROWTH; PLANT KINGDOM; PLANT PATHOLOGY; PLANT PHYLOGENY; RAFFLESIALES in the McGraw-Hill Encyclopedia of Science & Technology.

Daniel L. Nickrent

Bibliography. C. C. Davis et al., Floral gigantism in Rafflesiaceae, *Science*, 315:1812, 2007; J. Kuijt, *The Biology of Parasitic Flowering Plants*, University of California Press, Berkeley, 1969; D. L. Nickrent et al., Phylogenetic inference in Rafflesiales: The influence of rate heterogeneity and horizontal gene transfer, *BMC Evol. Biol.*, 4:40, 2004; D. L. Nickrent, J. P. Der, and F. E. Anderson, Discovery of the photosynthetic relatives of the "Maltese mushroom" *Cynomorium*, *BMC Evol. Biol.*, 5:38, 2005; D. L. Nickrent et al., Molecular phylogenetic and evolutionary studies of parasitic plants, pp. 211-241, in D. Soltis, P. Soltis, and J. Doyle (eds.), *Molecular Systematics of Plants II: DNA Sequencing*, Kluwer Academic, Boston, 1998; M. C. Press and J. D. Graves (eds.), *Parasitic Plants*, Chapman and Hall, London, 1995.