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Molecular Phylogenetic and Evolutionary Studies of Parasitic Plants

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The parasitic nutritional mode is a frequently evolved adaptation in animals (Price, 1980), as well as in flowering plants (Kuijt, 1969). Heterotrophic angiosperms can be classified as either *mycotrophs* or as *haustorial parasites*. The former derive nutrients via a symbiotic relationship with mycorrhizal fungi. Haustorial parasites, in contrast, directly penetrate host tissues via a modified root called a haustorium and thereby obtain water and nutrients. Although such categories are often a matter of semantics, we use the term *parasite* in a strict sense to refer to haustorial parasites. Angiosperm parasites are restricted to the dicot subclasses Magnoliidae, Rosidae, and Asteridae; have evolved approximately 11 times; and represent approximately 22 families, 265 genera, and 4,000 species, that is, about 1% of all angiosperms (Fig. 8.1). Owing to their unique adaptations, parasitic plants have long been the focus of anatomical, morphological, biochemical, systematic, and ecological research (Kuijt, 1969; Press and Graves, 1995). For the vast majority of parasitic plants, negative effects upon the host are difficult to detect, yet others (e.g., *Striga, Orobanche*) are serious weeds of economically important crops (Kuijt, 1969; Musselman, 1980; Eplee, 1981; Stewart and Press, 1990; Press and Graves, 1995).

The degree of nutritional dependence on the host varies among haustorial parasites. Hemiparasites are photosynthetic during at least one phase of their life cycle and derive mainly water and dissolved minerals from their hosts. Obligate hemiparasites require a host plant to complete their life cycles whereas facultative hemiparasites do not. Hemiparasites can be found in Laurales (*Cassytha*), Polygalales (*Krameria*), and all families of Santalales. In Solanales (*Cuscuta*) and Scrophulariales, some species are chlorophyllous hemiparasites whereas other species are achlorophyllous holoparasites. Holoparasites represent the most extreme manifestation of the parasitic mode because they lack

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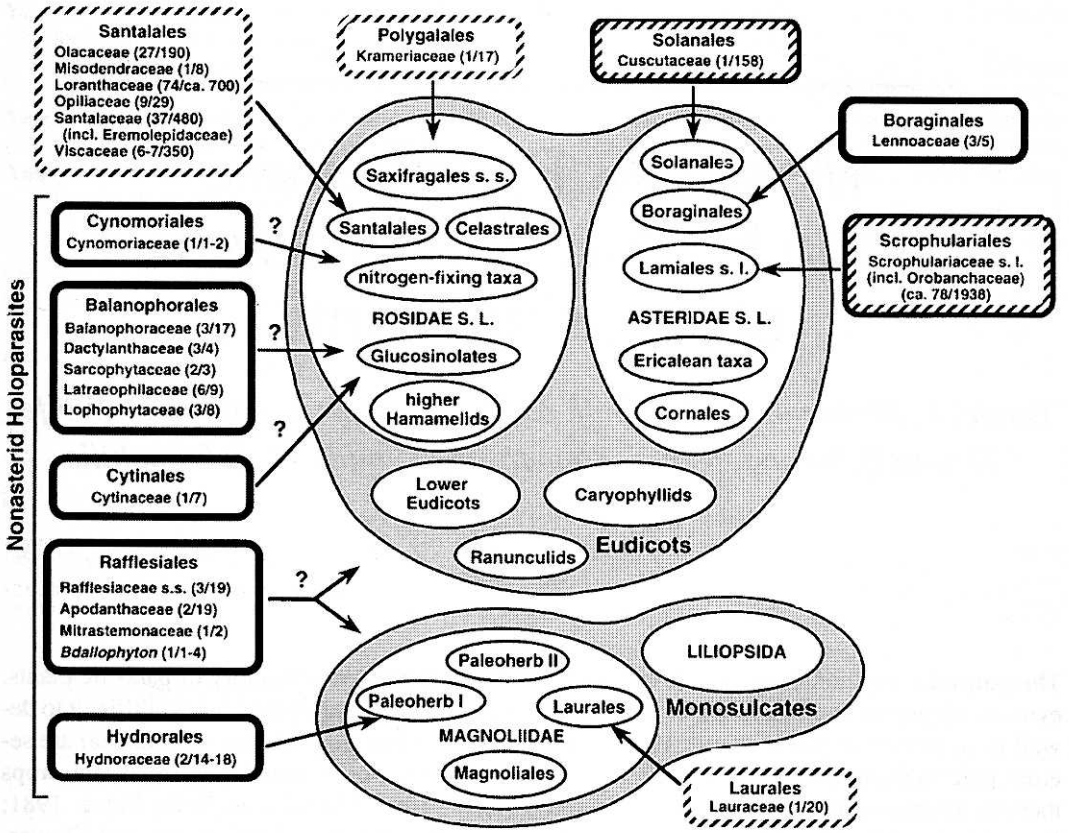

Figure 8.1. The distribution of haustorial parasitism among angiosperms. This generalized diagram incorporates information from global molecular phylogenetic studies using *rbcL* (Chase, Soltis, Olmstead et al. 1993) and nuclear 18S rDNA (Soltis, Soltis, Nickrent et al., 1997). No attempt was made to show all taxa, only to indicate groups that were supported by both studies. Hemiparasitic angiosperms are enclosed within dashed borders and holoparasites by black borders. Both trophic modes occur in Scrophulariaceae s. l. and *Cuscuta*. Arrows that touch a group indicate that strong evidence exists for the placement of that parasitic taxon within the group. Uncertain affinities are indicated by arrows with question marks. The familial classification of the nonasterid holoparasites is modified from Tahktajan (1987); however the placement of these orders is not concordant with his superordinal classification. The number of genera and species is indicated in parentheses following each family name. For Scrophulariaceae s. l., only the parasitic members are tabulated.

photosynthesis and must rely upon the host for both water and inorganic and organic nutrients. Six groups (orders or families—Fig. 8.1) are represented entirely by holoparasites: Balanophorales, Cynomoriaceae, Cytinaceae, Hydnoraceae, Lennoaceae, and Rafflesiales.

The relationships shown in Figure 8.1 are based upon those of Takhtajan (1987) as well as results of recent molecular analyses. For this paper, Santalales are considered, in a strict sense, to include Olacaceae, Misodendraceae, Loranthaceae, Opiliaceae, Santalaceae, and Viscaceae. This composition differs from that of Cronquist (1988) by excluding Balanophoraceae, Medusandraceae, and Dipentodontaceae. Morphological, cytological, and molecular evidence all point toward the separation of Cynomoriaceae from Balanophoraceae and of Cytinaceae from Rafflesiaceae (Takhtajan, 1987; Nickrent and Duff, 1996; Pazy et al., 1996). Traditional classifications have often allied these holoparasites with Santalales; however, considerable variation can be seen in alternate classifications and such an affinity is not apparent from molecular investigations (see below). Given this, the term *nonasterid holoparasites* will be used to distin-