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WHY IS ORCHIDACEAE SO LARGE, ITS SEEDS SO SMALL, AND ITS SEEDLINGS MYCOTROPHIC?

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The biology of the orchids is sometimes summarized as five facts: (1) Orchidaceae is probably the largest of all angiosperm families; (2) its seeds are among the smallest of any taxon; (3) the resulting seedlings are mycotrophic; (4) many of its species are rare or widely dispersed; and (5) they often rely on very specialized pollination relationships for sexual propagation. Is there any adaptive or evolutionary significance in this association of conspicuous family characteristics? Pollinator behavior has certainly played a major role in orchid speciation and currently facilitates the diffuse distribution of many populations, but what about the tiny seeds and unusual mode of seedling nutrition?

Individual seeds of flowering plants range in mass from a high of several kilograms for *Lodoicea* (Arecaceae) to 0.01-0.1 mg for many orchids. Among closely related individuals of just about any group of spermatophytes, however, seed weight is remarkably constant. At least three distinct requirements oblige close adherence to some optimal profile: (1) the heterotrophic demand of a seedling before it achieves autotrophy; (2) the requirement for dispersal to propitious sites; and (3) the need for sufficient fecundity to maintain a parent population. Seed characteristics that vary among taxa represent adaptive tradeoffs designed to facilitate survival under combinations of constraints in native habitats.

A discussion of the patchy and infertile nature of the epiphytic biotope has been presented previously, as was the rationale for the high fecundity and vagility required of plants living in the crowns of trees (Benzing, 1978; Benzing & Davidson, 1979; Benzing & Renfrow, 1980). These studies further revealed that, for the extreme epiphyte, small seeds are particularly adaptive as a means of increasing mineral economy and countering high rates of juvenile mortality. Numerous terrestrial orchids also inhabit such stressed environments as infertile acid bogs and porous soils, and many of these sites are patchy and/or disturbed as well, suggesting that the family has probably been facing many of the same physical constraints for some time. I propose that the seeds of orchids have become unusually small in response to strong *r*-selecting forces imposed by unpredictably disturbed, patchy and stressed habitats. The miniaturization required to achieve a "dust" type seed -- the basis of the impressive fecundity mounted by these organisms -- seems to have been made possible by major shifts in juvenile nutrition that, in effect, obviated the need for maternally supplied food at germination and for varying periods of time afterward.

Mycorrhizal fungi initiate the orchid life cycle by invading the quiescent seed. Whether this relationship is universal in the family and persists in epiphytes is not really known, but most orchid biologists believe symbiotic germination to be routine. This conviction supports my contention quite well, since it explains how young orchid seedlings survive in the field with so little food of parental origin. The fungal associate, through its practice of secreting various hydrolytic exoenzymes, is capable of reducing insoluble organic substances to consumable byproducts (Smith, 1966, 1967, 1973). Some of these find their way to the orchid embryo and so relieve it of reliance on endogenous sources of nutrients. In some cases, dependence on the

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fungus continues, and the orchid matures as a mycorrhizal saprophyte or, more likely, an epiparasite on the root systems of nearby vascular autotrophs. Regardless of the nutritional competence of offspring as adults, a maternal parent, freed from the usual task of provisioning its young with substantial nutrient stores, is amenable to selective forces that encourage the production of unusually large numbers of small seeds. An appropriate pollen delivery system -- in this case, usually involving a pollinium -- is, of course, necessary to ensure that numerous ovules are fertilized following each successful pollination.

The occurrence of a broad constellation of primitive floral and vegetative characters (e.g., mesomorphic shoot, C_3 metabolism), small seeds and at least crude pollinia in terrestrial Cypripedioideae and Spiranthoideae suggests that the requisite adaptations for high fecundity emerged before Orchidaceae invaded the forest canopy and assumed much of its present diversity and size. A small seed may have indirectly enhanced this diversification process by making possible the adoption of specialized animal-mediated breeding systems characterized by high pollinator fidelity. These relationships, while very effectively contrived to promote outcrossing among conspecifics and isolation of closely related populations, are often inefficient, yielding few fruits. Were these occasional capsules to release more conventional numbers of larger propagules than they typically ripen, fecundity would likely be too low to sustain widely dispersed taxa of the type so common in many orchid genera. Had this constraint been in force throughout its history, Orchidaceae would have been much less effectively equipped to invade such habitats as the forest canopy where patchiness and disturbance foster patterns of localized colonization and extinction that favor rapid evolution and speciation, and ultimately large numbers of species and great diversity.

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