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Orchids

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Charles Darwin, in his letter to Joseph Hooker, wrote, “*I never was more interested in any subject in my life, than in this of Orchids*”. The Orchidaceae comprise over 850 genera and 25,000 species representing about 10% of the world’s flowering plants and the largest family in species number. The ease of hybridisation means more than 100,000 hybrids have been created, more than any other floricultural crop.

Orchids have a number of distinguishing characteristics, but no single character defines the family (Figure 1); (a) stamens are on the abaxial side of the flower, (b) stamens and pistil are at least partly fused, (c) large numbers of small seeds per ovary, (d) labellum or lip (a modified petal) occurs opposite the fertile stamen(s), (e) flowers are often resupinate, and (f) pollen is usually held in masses (pollinia). However, it is the fusion of the stamens and pistil to form the column or gynostemium that above all other characters defines the orchid family (except for some members of the Hypoxidaceae and Styliaceae). The family is divided into five subfamilies with the Apostasioideae, being basal. This is followed by Vanilloideae, Cyripedioideae, then the two most species rich subfamilies, the Orchidoideae and Epidendroideae.

The relationship of the Orchidaceae to other monocotyledons is poorly resolved with orchids being either sister to all other Asparagales or sister to the first branching clade of the Asparagales. Equally confused is the geographical origin of the family. Members of the basal subfamily, Apostasioideae, are found in south east Asia, however, one of the closest relatives to the Orchidaceae, Hypoxidaceae, has a Gondwanaland distribution. To date the only unequivocal orchid fossil found is the recently described orchid pollinia on

the back of a bee trapped in amber (Figure 2). This has been used to date the most recent common ancestor of extant orchids to the Late Cretaceous (76-84 myo) coinciding with bee evolution.

Orchids are a cosmopolitan family, growing in all terrestrial ecosystems with the exception of the poles and extremely dry deserts, but reach their zenith in the tropics. Approximately 73% of orchid species are epiphytic or lithophytic, using other plants or similar structures such as fence posts; however, support-host specificity is rare and in no instance are orchids parasites on their supporting species.

Threats to orchids

Orchids are the epitome of plant evolution but sadly they are among the most threatened of all flowering plants where overzealous collection and habitat loss has taken many species towards extinction in the wild.

Orchids represent the container commodity of highest value in commercial horticultural production and are therefore prone to illegal poaching of plants from the wild. For example *Paphiopedilum vietnamense* was first described in 1999 as new to science, by 2003 it was extinct in the wild through poaching. However, orchids are also collected for ethnobotanical uses, for example the pseudobulbs of *Dendrobium* species are used in the Chinese medicinal plant trade, while tuberous terrestrial orchids are collected in east sub-Saharan Africa for the production of a cake called chikanda. Each cake requires 100 tubers and it has been estimated that 2.2-4.0 million tubers are traded illegally between

Tanzania and Zambia. Similarly in Turkey, tubers of terrestrial orchids are used to make an extract known as salep that is used in ice cream manufacturing.

As a result of their complex ecological interactions with pollinators, mycorrhizal fungi and other plants and animals, orchids are often the first biological indicators of ecosystem decay and collapse. Many decades may be needed to return a level of ecological stability conducive to orchid persistence due to the reliance by orchids on insect pollinators and mycorrhiza.

Ecophysiology

Few plants can match the diversity of ecophysiological adaptations encompassed by orchids. Most tree and rock dwelling species possess special water absorptive roots that act like a sponge, absorbing nutrients in the first raid of nutrient rich water flowing down the tree trunk or rock surface. So effective are these special water absorptive roots at sustaining the orchid plant that entire genera of tree-dwelling orchids are leafless, using instead chlorophyll in the upper parts of the slightly flattened roots to support photosynthesis.

Nutrients and water are usually stored by orchids for long periods in expanded petioles, stems or leaves that are often sufficiently fleshy to enable the orchid plant to survive many months without rainfall. Many tree and rock-dwelling orchid species, including the bizarre cucumber orchid (*Dockrillia cucumerina*) from eastern Australia which survives the rigours of living in exposed, hot and often dry environments by using crassulacean

acid metabolism (CAM). CAM metabolism is more commonly found in succulents from desert regions and the development of CAM in orchids has enabled many orchids to conquer epiphytic growth where few other plants can survive (Figure 3).

Mycorrhiza

Orchids are unique among all other plants in their modes of nutrition involving direct and often obligate relationships with organisms as diverse as bacteria and fungi.

Bacterial associations have been shown to involve a complex array of soil borne bacteria that live endophytically in the cells of roots and underground stems of terrestrial orchids with the bacteria providing plant growth regulation compounds that improve seed germination and seedling growth. It is the orchid's relationship with fungi through mycorrhizal interactions that have made these plants masters of nutritional deception (Figure 4). Like no other plant group, orchids use a wide and varied assortment of endophytic fungi from morels (Ascomycetes) to mushrooms (Basidiomycetes) and even species of truffles.

The nutritional dependency of the orchid varies with orchid species and situation.

Whereas epiphytic taxa may be found associating with fungi in the seed germination phase, adult epiphytes may be independent of mycorrhiza for nutrition instead relying on uptake of nutrients directly from rainfall and bark/rock runoff. This explains why epiphytic orchids are more amendable to horticulture than many terrestrial species.

Terrestrial orchids reflect a continuum in mycorrhizal dependency with herbaceous terrestrial taxa (those with underground organs and seasonal growth usually by the emergence of a leaf or flowers) exhibiting a high level of mycorrhizal dependency. Fringed orchids (*Plantanthera*) from the US, bee orchids (*Ophrys*) from Europe and spider orchids (*Caladenia*) are examples of common terrestrial taxa where mycorrhiza are critical for growth and development.

The orchid-fungus association can involve a multitude of fungal partners with direct molecular analysis of underground roots of some northern hemisphere orchids showing up to a dozen or more fungi are present. The relationship between orchid and fungus is best described as mutualistic with the plant providing sugars, B vitamins and a 'safe haven' to the fungus, while the fungus passes to the orchid, water, mineral salts and up to 85% of the plant's carbon requirements. It is also thought that the presence of mycorrhiza imparts a level of protection or 'plant immunisation' for protection against soil pathogens.

Wild germination of orchid seed occurs once the correct fungus enters the seed with the tiny seedling, capable of precisely balancing the amount of nutrient received with the pathogenicity of the associated fungus. A simple shift in soil nutrients such as through the addition of sugars will often tip the orchid-fungus association and result in rapid parasitism and death of the orchid seedling by the fungus.

Some orchids have taken their fungal relationship to a remarkable level with more orchids than any other plant group evolving species that lack any ability to photosynthesise. These mycoheterotrophic orchids have evolved independently more than 20 times often resulting in the orchid plant developing a total and absolute reliance on their fungus partner for sustenance. A number of genera of mycoheterotrophic orchids specifically associate with fungi that also live on the root system of nearby shrubs and trees with radioactive tracing studies showing a direct transfer of non-orchid carbon to the orchid via a 'fungal bridge'.

A pinnacle of mycoheterotrophy is the astonishing story of the world's only fully underground orchid, Australia's *Rhizanthella gardneri* (Figure 5). The large purple and white, waxy flowers were originally discovered in 1929 during land clearing operations in the biodiversity hotspot of south west Australia. At the time the discovery was hailed as the botanical find of the century as here was an orchid that spent its entire existence underground! However it would take another 60 years for scientists to show that the orchid employed a complex yet highly effective three-way relationship, orchid-fungus-shrub root to siphon carbon and nutrients from the shrub to orchid plant.

Seed science

Orchid seed are the smallest by size (0.05-6mm) and weight (0.31-24µg) of all seed-bearing plants. Further, a single fruit capsule can produce up to 4 million seeds.

Containing a rudimentary embryo often encased in a thin almost lose seed coat, the small size and ability of orchid seed to float on the slightest updraft are thought to have been a

key mechanism enabling orchids to become widespread and supreme epiphytic colonisers. Darwin calculated within three generations “*a single plant would nearly ... clothe with one uniform green carpet the entire surface of the land throughout the globe.*” (Darwin, 1862, 344-345). Unlike most other flowering plants, the pollen of orchids, on average, travels a shorter distance than the seed. However, it should be noted that most orchid seeds fall close to the mother plant with only a tiny fraction of the seed germinating and eventually becoming an adult plant.

Pollination

Most orchids are pollinated via an insect vector, with birds being a rare exception. Pollinators visit orchid flowers for potential rewards, these may include oils, floral fragrances, pollen, even sheltering site, however floral nectar is the most common reward. In return, the orchids benefit from the movement of pollinia between flowers; the efficiency of this strategy varies since orchids are often pollinator-limited. However, there is a trend towards a reduction in the number of pollinator species per orchid species resulting in increased specialization. This relationship between the orchid and its pollinator/s is often one-sided, with the orchid relying far more on its pollinator than the pollinator on the orchid. Probably the most famous is the interaction between Darwin’s long-spurred comet orchid from Madagascar (*Angraecum sesquipedale*) and the equally long-tongued hawkmoth, which he postulated pollinated the orchid but had not seen. This interaction has been described as a classic ‘arms-race’ between the orchid’s spur and the hawkmoth’s tongue, resulting a gradual ‘proliferation’ in length of the two organs. That

is not to say the hawkmoth is exclusively dependent on the orchid, rather it may only have adapted to access another nectar resource.

Approximately one-third of orchids have evolved mechanisms of deceit, where the pollinator receives no reward. Mechanisms of deceit include food (either through Batesian mimicry or without a model), sexual (pseudocopulation), brood site and territorial antagonism. The presence of a reward has been shown, on average, to result in a two-fold increase in fruit set, in both temperate and tropical orchids. Further, temperate orchids produce twice as many fruits per flowering event as their tropical counterparts. It has been suggested that this is related to aspects of population structure and pollinator community. However, one factor that has not been considered is the preponderance of Orchidoid orchids in the temperate regions with their sectile pollinia. Via an insect pollinator, pollen can be deposited on several flowers, compared to Epidendroid orchids, common in tropical regions but rare in temperate zones, with consolidated pollinia, which go for an 'all or nothing' strategy.

In the absence of an effective pollinator some orchids utilise autopollination (10-15%) and very rarely apomixis. Unlike many other flowering plants, orchids place the pollinia on the pollinators in specific microsites to reduce cross pollination between species rather than using chemical inhibition. As a result most orchids are self compatible, with self-incompatibility (i.e. Dendrobiinae – c. 72%, Laeliinae, Oncidiinae – c. 73% and possibly Vandaeae – c. 30% spp) and 'quasi-dioecy' (i.e. *Catasetum*, *Cycnoches* and *Mormodes*) being rare. Once a flower is pollinated, it can take several to many months for the fruit to

develop. While an orchid may be pollinator-limited within a season, the resource requirement to maintain fruits can lead to resource-limitation over the orchid's lifetime.

Sexual deceit mechanisms in orchids rely on the production of a chemical copy by the orchid of the pheromone produced by the female insect. Visual cues to add further enticement to the potential male pollinator include modifications to the labellum to resemble insect forms – from the bumblebee mimic in European *Ophrys* replete with 'legs' and bristles to the hammer orchids (*Drakaea*) of Western Australia, home to more species of sexually deceptive orchids than any other region, where the labellum is the only significant floral structure remaining and mimics the dull-coloured flightless female of thynnine wasp species (Figure 6). A pinnacle of sexual deception is found in the demure Australian flying duck orchids (*Paracaleana* and *Caleana*) that use a triple-whammy pollination system involving a chemical cue and insectiform labellum combined with a touch-sensitive hinge on the labellum that catapults and momentarily holds the male insect against the pollination structures.

It is suggested that deception leads to an increase in fitness of the plant through reallocation of resources of what would have been expended on the production of a reward. Also, due to the lack of reward to maintain pollinator interest, fewer flowers are visited within an individual inflorescence resulting in great levels of outcrossing.

However, why orchids should have such high levels of deception has given rise to numerous hypotheses. Firstly, why bother constantly luring back pollinators when a single visit will efficiently transfer pollinaria? Secondly, as orchids more often form

small populations, this limits the ability of the pollinator to learn that they have been duped. Finally, the presence of a reward maintains pollinator interest on a single inflorescence leading to an increased risk of geitonogamous self-pollination, particularly when the pollen is packaged as pollinia. Deception would therefore reduce geitonogamy through increase out-crossing.

While the study of orchid mycorrhizal diversity has lagged behind orchid pollination biology, it is postulated that increased mycorrhizal specialisation by orchids is driving deceptive pollination syndromes. The evolution of dioecy on islands due to the need to increase genetic diversity after a founder event is well known. It is therefore possible that colonisation of new 'mycorrhizal islands' is driving the requirement for outcrossing, leading to the promotion of deceit pollination.

Final remarks

Pollinator-limitation and resource constraints results in only a small proportion of an orchid population giving rise to the subsequent generation. This proportion is further limited, as most orchid populations, particularly in the tropics, are small, due to the fluid nature of the niches they occupy and the availability of mycorrhiza 'islands'. This low reproductive success results in a small effective population size (N_e), followed by genetic drift as the potential initial cause of evolution. Subsequent diversification and speciation occurs through Darwinian adaptation to better fit the new generation to the local pollinator population.

While much still remains to be learnt within orchid biology, there is now a mass of literature on the pollination biology and phylogenetic relationship. However, much of this has been the description of patterns, what is now need are studies into the processes that drive diversification in this most remarkable of flowering plant families.

Further Reading

- Arditti, J., and Ghami, A. K. A. (2000). Numerical and physical properties of orchid seeds and their biological implications. Tansley Review No. 110. *New Phytol.* 145, 367-421.
- Cozzolino, S., and Widmer, A. (2005). Orchids diversity: an evolutionary consequence of deception? *Trends Ecol. Evol.* 20, 487-494.
- Darwin, C. (1862) *The Various Contrivances by which Orchids are Fertilised by Insects*, (London: John Murray).
- Dixon, K. W., Kell, S. P., Barrett, R. L., and Cribb, P. J. (2003). *Orchid Conservation*, (Kota Kinabalu, Sabah: Natural History Publications).
- Dressler, R. L. (1990). *The Orchids: natural history and classification*, (Cambridge: Harvard University Press).
- Jersáková, J., Johnson, S. D., and Kindlmann, P. (2006). Mechanisms and evolution of deceptive pollination in orchids. *Biol. Rev. Camb. Philos. Soc.* 81, 219-235.
- Pridgeon, A. M., Cribb, P. J., Chase, M. W., and Rasmussen, F. N. (2001-6). *Genera Orchidacearum*, vols. 1-4. (Cambridge: Cambridge University Press).

Tremblay, R., Ackerman, J. D., Zimmerman, J. K., and Calvo. R. N. (2005). Variation in sexual reproduction in orchids and its evolutionary consequences: a spasmodic journey to diversification. *Biol. J. Linn. Soc.* 84, 1-54.

<http://apps.kew.org/wcsp/home.do> (World Checklist of Monocotyledons)

Figure captions

Figure 1. *Sophranitis jongheana*, a typical orchid flower with three sepals, two lateral petals, the third petal is highly modify to for the labellum or lip, clasping the column (gynostemium) which is formed through the fusion of the stamens and pistil. Photograph courtesy of P. Cribb.

Figure 2. The first definitive fossil record of an orchid, *Meliorchis caribea* pollinarium on the back of a bee (*Proplebeia dominicana*), preserved in amber. Photograph courtesy of S. Ramirez.

Figure 3. An estimated 73% of orchid species grow as epiphytes or lithophytes, in this case *Sophranitis coccinea* from Brazil. Photograph courtesy of P. Cribb.

Figure 4. Scanning electron microscope image of orchid mycorrhiza in the underground stem of an Australian spider orchid (*Caladenia*). Photograph courtesy of Tien Huynh.

Figure 5. The remarkable underground orchid from south west Australia (*Rhizanthella gardneri*).

Figure 6. One-third of orchids do not produce a reward for pollinators, while food deception is the most common form, it is sexual deceit that is most intriguing. This mechanism can be extremely elaborate, here the hammer orchid (*Drakaea*) mimics the flightless female of thynnine wasps. The male wasp is enticed by a single chemical compound the orchid produces which mirrors the female's own pheromone, as well as the insectiform labellum. As the male tries to fly off with what he thinks is a female the hinge labellum catapults the male wasp against the column.