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PREFACE

Orchid biology: from Linnaeus via Darwin to the 21st century

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Orchidaceae are the largest family of flowering plants, with at least 24 000 species, and perhaps better than any other family of flowering plants, orchids represent the extreme specializations that are possible. As a result, they have long fascinated luminaries of the botanical world including Linnaeus and Darwin, but the size of the family has historically been an impediment to their study. Specifically, the lack of detailed information about relationships within the family made it difficult to formulate explicit evolutionary hypotheses for such a large group, but the advent of molecular systematics has revolutionized our understanding of the orchids. Their complex life histories make orchids particularly vulnerable to environmental change, and as result many are now threatened with extinction. In this Special Issue we present a series of 20 papers on orchid biology ranging from phylogenetics, floral evolutionary development, taxonomy, mycorrhizal associations, pollination biology, population genetics and conservation.

Key words: Conservation, Darwin, evo-devo, Linnaeus, mycorrhizas, orchids, Orchidaceae, phylogenetics, pollination.

Orchidaceae are the largest family of flowering plants, with an estimated 800 genera and at least 24 000 species (World Checklist of the Monocotyledons, 2006). Distributed throughout all continents except Antarctica and particularly numerous and diverse as epiphytes in the wet tropics, they have long fascinated biologists by their remarkable range of life history strategies, floral and vegetative morphology and pollination syndromes. For many years there was a great deal of controversy over their phylogenetic relationships and higher-level classification. This uncertainty about relationships was highly inhibitory to development of research projects in other areas of orchid biology because it was difficult to frame evolutionary hypotheses when researchers were not certain of which taxa were relevant to include. Comparative studies were thus rendered highly speculative, and to many researchers this was unappealing, leading them to study other groups of flowering plants. Many other potential students were also frustrated by the immense size of the family, which made it difficult to carry out comprehensive projects. There were some areas of research that provided some data on orchids (e.g. micropropagation, pollination ecology), but in general from the last half of the 19th through most of the 20th century, orchids were understudied relative to the other large families (Asteraceae, Fabaceae, Poaceae, Rubiaceae) and became a backwater for modern approaches to the study of their evolutionary biology.

This all began to change as molecular systematists began to focus their attention on Orchidaceae from the early 1990s onward (starting with Chase *et al.*, 1994). There are now numerous studies that have provided an increasingly detailed phylogenetic framework for the orchids and made development of well-focused comparative studies in other areas of research feasible (a number of such studies are included in this volume). Cameron (2009) examines the utility of markers from different genomes in addressing phylogenetic questions and finds that nuclear ribosomal genes provide a source of reliable phylogenetic data on the genera of subfamily Vanilloideae (Fig. 1). Chase *et al.* (2009) focus on a problematic group of Brazilian members of subtribe Oncidiinae (Cymbidieae; Epidendroideae) and find that recircumscription of *Gomesa* (Fig. 2) provides a reasonable solution to the problems posed by a set of species previously assigned to *Oncidium* (and which are not related to the group of species centred on the type species of *Oncidium*). They also describe a new genus for another problematic South American species. Salazar *et al.* (2009) and van den Berg *et al.* (2009) focus on problems of circumscription in the largely terrestrial, mostly neotropical tribe Cranichideae (Fig. 3; Orchidoideae) and the horticulturally important, epiphytic subtribe Laeliinae (Epidendreae; Epidendroideae), respectively. Bateman *et al.* (2009) focus on phylogenetic relationships in subtribe Orchidinae, in particular *Galearis* and *Platanthera*, and show that some of the problematic species are best treated in these genera. An outgrowth of the application of molecular data to addressing orchid systematic topics has been the landmark *Genera Orchidacearum* series (Pridgeon *et al.*, 1999, 2001, 2003, 2005, 2009), which has also promoted the study of all aspects of orchid biology by providing a phylogenetic framework and summaries of previous research as a basis to enable yet further study. The series also clearly outlines where there are gaps in what is known, stimulating further studies focused on filling these lacunae. Two remaining volumes of *Genera Orchidacearum* are in production (volume five is in press and will appear in 2009; volume 6 is in preparation and expected in 2011), and production of an electronic version is anticipated. Even with the wealth of phylogenetic information available, there are still aspects of the taxonomy of certain groups of orchids that are being hotly debated. Hopper (2009) documents, *inter alia*, the controversy surrounding the competing generic limits proposed for the

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FIG. 1. *Eriaxis rigida* (Vanilloideae) is endemic to the Pacific island of New Caledonia, where it grows on ultramafic maquis. Its closest relative, *Clematepistephium smilacifolium*, in contrast, is a climbing vine found in the New Caledonian rainforests (photograph: K. M. Cameron).

FIG. 2. *Gomesa echinata* (previously known as *Baptistonia echinata*; Oncidiinae, Cymbidieae, Epidendroideae) from Brazil (photograph: M. W. Chase).

largely Australian genus *Caladenia* (Fig. 4). Even with a well-resolved phylogenetic tree, debates can still occur, and these need to be resolved as quickly as possible. Most users of taxonomy prefer stability and the simplicity of broader generic limits. In addition to taxonomy, phylogenetic analyses can provide a framework by which the evolution of other kinds of characters can be given an evolutionary perspective. For example, Neubig *et al.* (2009; Fig. 5) and Leitch *et al.* (2009) examine leaf and fruit morphology and genome size, respectively, against the background of phylogenetic relationships.

FIG. 3. *Stenorrhynchos speciosum* (Cranichideae, Orchidoideae) from Costa Rica (photograph: M. W. Chase).

FIG. 4. *Caladenia longicauda* (Caladeniinae, Diurideae, Orchidoideae) from Western Australia (photograph: R. J. Smith).

FIG. 5. *Dichaea morrisii* (Zygopetalinae, Cymbidieae, Epidendroideae) is a frequently encountered species found throughout tropical America. It has muricate ovaries, a homoplasious feature in *Dichaea* (photograph: K. M. Neubig).

With the scientific tools now available for genomics, population genetics, evolutionary development (evo-devo) and fragrance analysis and the ability to frame questions in a phylogenetic context, the true complexity of orchids is being shown to be even greater than previously thought. In this Special Issue, we present papers that describe current ideas about many aspects of orchids and their biology, including evo-devo of flowers, pollination syndromes, mycorrhizal associations, conservation, phylogenetics, taxonomy, genome evolution and invasive species, with examples drawn from four of the five subfamilies (Chase *et al.*, 2003) now generally recognized. Only the small (approx. 15 species in two genera) and relatively poorly understood Apostasioideae are not represented by new research in this volume, and they are clearly a group on which a focused further research effort is required.

Despite the historical high level of interest in the family, the extraordinary diversity has only been fully realised during the last 150 years (Rasmussen, 1999). Linnaeus included only 62 species of orchids in his *Species Plantarum* (1753), albeit including species from as far afield as Asia, the Caribbean and northern South America. Jarvis and Cribb (2009) provide a list of currently accepted names for the orchids included in *Species Plantarum*, because Linnaeus' generic concept was much different than that now followed. One of Linnaeus' more notable generic misplacements was to use the name *Cactus parasiticus* for *Dendrophylax funalis* (Fig. 6), a leafless orchid from the West Indies, (Jarvis, 2007; Jarvis and Cribb, 2009).

Pollination biology has had a long and successful history in orchids. In fact, even Linnaeus made his contribution to this area of research. In his *Öland and Gotland Journey* (see Edmondson, 2007), he observed about *Ophrys insectifera* that 'Its flowers bear such a resemblance to flies, that an uneducated person who sees them might well believe that two or three flies were sitting on a stalk. Nature has made a better imitation than any art could ever perform' (Fig. 7). Of course, this observation did not lead to the conclusion that sexual deceit is operating in *Ophrys*, but it is a clear indication that something unusual was taking place in orchids. Given Linnaeus' religious convictions, it was unlikely that he would ever have viewed orchid pollination syndromes as more than 'just so' stories. Devey *et al.* (2009) present a genetic diversity study of one group of *Ophrys* species, the *O. fuciflora* complex, showing that clear geographical patterns

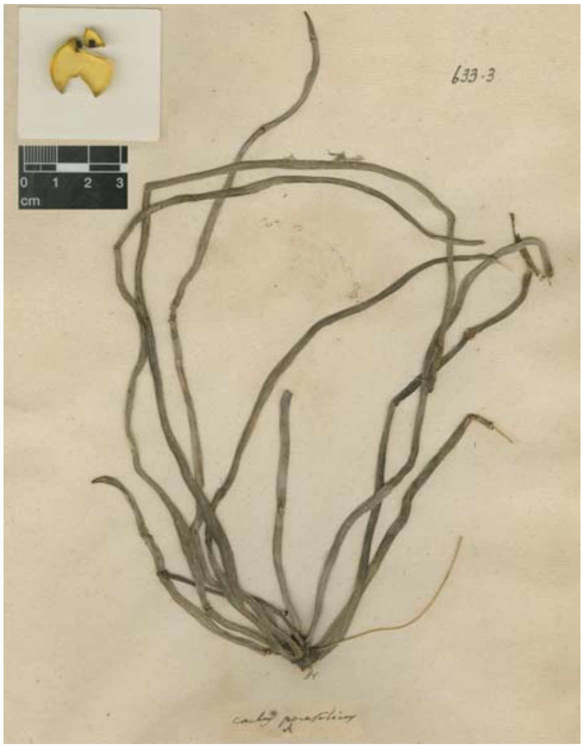

FIG. 6. The specimen of *Dendrophylax funalis* (Angraecinae, Vandeae, Epidendroideae) from the Linnean Herbarium. Linnaeus mistakenly called this *Cactus parasiticus*, causing taxonomic problems in Cactaceae (image reproduced with kind permission of the Linnean Society of London).

FIG. 7. *Ophrys insectifera* (Orchidinae, Orchidoideae) on Gotland. 'Its flowers bear such a resemblance to flies, that an uneducated person who sees them might well believe that two or three flies were sitting on a stalk' (Linnaeus; see Edmondson, 2007; Photograph: K. W. Dixon).

underlay patterns of floral variation in this genus. Cortis *et al.* (2009) also examine the nature of species boundaries in sympatric *Ophrys* species on the Mediterranean island of Sardinia, demonstrating that although the two species hybridize in sympatry as a consequence of pollinator overlap and weak mechanical isolation, post-zygotic barriers reduce hybrid frequency and fitness and prevent extensive gene introgression, despite the fact that in *Ophrys* it is pre-mating barriers that are often considered predominant.

Other population studies in this volume focus on genetic variation differences between populations on the edges of the range of a species versus its centre (Duffy *et al.*, 2009), plastid microsatellite marker variation in *Cypripedium calceolus*, a species of special conservation in England (Fay *et al.*, 2009), and the difficulties of understanding patterns of morphological and ecological variation in *Dactylorhiza incarnata s.l.* on the Baltic island of Gotland (Sweden) when genetic variation is extremely limited (Hedrén and Nordström, 2009; Fig. 8).

Although many researchers focus on rare and endangered orchids and the whole family is listed in Appendix II of the CITES regulations (implying that all species are of some conservation concern), some orchid species are in fact invasive, and there is some concern that they could displace native species from some sites. *Disa bracteata*, a South African species is now widespread in Australia and occurs in large numbers at many sites (Swarts and Dixon, 2009). Likewise, *Oeceoclades maculata*, a tropical African species, is now widespread in the American tropics, and Cohen and Ackerman (2009) examine its distribution relative to native species that appear to have similar habitat preferences in order to determine if *O. maculata* poses a threat to these species.

FIG. 8. *Dactylorhiza incarnata* var. *ochroleuca* (Orchidinae, Orchideae) on Gotland (photograph: M. Hedrén).

In contrast to Linnaeus, Darwin remains one of the major figures in orchid pollination biology. In fact, Darwin found the subject of orchid pollination so interesting that he wrote a whole book on the subject (Darwin, 1862), with the specific goal of demonstrating that outcrossing is so important to the process of evolution by natural selection that angiosperms and in particular orchids have gone to great lengths to produce extremely complicated floral morphologies that make it unlikely that their pollinators will be able to make geitonogamous (self) pollinations. In many orchids, genetic incompatibility reinforces floral morphology to ensure that only outcrossing can occur; such a case is documented by Cheng *et al.* (2009). If special creation is responsible for life on Earth, then why are the higher levels of variability present in outcrossed progeny so important that such extreme morphologies and genetic incompatibility exist to make self-pollination less likely or even impossible? These bizarre pollinator relationships would be unnecessary if evolution was not responsible for all of biological diversity. Self-pollination is sufficient to produce the offspring needed fo the next generation, thus eliminating the need for outcrossing and pollinators altogether. Peter and Johnson (2009) demonstrate that although geitonogamy occurs in their study species, outcrossing is the predominant pattern, demonstrating again that floral morphology is highly influential in facilitating outcrossing, even though bee behaviour favours geitonogamy.

The most visibly obvious manifestation of the diversity of orchids is their floral complexity: orchids uniquely fuse their gynoecia and androecia, and one of the three petals is modified into a landing platform or attracting structure, the lip or labellum. It has long been assumed that in orchids the basic controls on floral morphology that operate in other monocots must have been modified. Mondragón-Palomino and Theißen (2009) examine the developmental and evolutionary aspects of their ‘orchid code’, in which they hypothesize that orchid floral morphology is controlled by four *DEF*-like MADS-box genes interacting with other floral homeotic genes. In this paper, they demonstrate that all frequently occurring orchid terata (including peloric forms) can be explained by loss or gain of function in various floral organs of one of the genes involved.

The complex life histories of many orchids, including interactions with mycorrhizal fungi and specialized pollinators, make them particular vulnerable to climate change and human activity, and Swarts and Dixon (2009) provide a schematic representation of the spectrum of orchids ranging from generalists such as the often weedy *Microtis media* capable of forming associations with a range of mycorrhizal fungi and not being dependant on a pollinator, through to extreme specialists, such as the underground orchid *Rhizanthella gardneri*, which is dependant on a specialist pollinator, a specialist seed-dispersal agent and, finally, a specialist fungus that is in turn dependant on a specific associated shrub. An understanding of the complexities of these interactions is essential in the development of viable integrated conservation activities. In the face of climate change and increased threats due to anthropogenic disturbance, such conservation activities will become ever more important.

FIG. 9. *Hippotion celerio* visiting flowers of *Mystacidium capense* (Angraecinae, Vandeae, Epidendroideae) in South Africa (photograph: S. D. Johnson).

Roy *et al.* (2009) have studied mycorrhizal associations in another specialist, the ghost orchid *Epipogium aphyllum*, demonstrating that most of the plants formed symbioses with *Inocybe* spp, the first time that mycoheterotrophic orchids have been shown to form associations with members of this genus. The fungus in turn formed ectomycorrhizal associations with surrounding trees, indicating that these are probably the ultimate carbon source for the orchids. Certainly our knowledge of the requirements for germination and seedling growth has moved on since Darwin wrote to Hooker in 1863 'I have not a fact to go on, but have a notion (no, I have firm conviction!) that they [orchids] are parasites in early youth on cryptogams!' (Darwin, 1863).

The diversity of orchid research activity demonstrated in this volume is testament to their appropriateness for evolutionary study. Perhaps better than any other family of flowering plants, orchids represent the extreme specializations that are possible, and it is often through the study of extremes that general principles are more clearly determined. We hope that this volume will entice students into the study of orchids and bring even more evidence to bear on how this huge diversity evolved. Darwin was right to have focused his book subsequent to *The Origin of Species* on orchids: their diversity and great beauty could only be the product of a phenomenon that is driven by high levels of variability and complexity, which create a feedback loop that generates ever greater levels of specialization, much as selection on nectar-spur length produces species of comet orchids (*Angraecum* spp.) and their allies (Fig. 9) with ever longer spurs and hawkmoths with ever longer tongues (Micheneau *et al.*, 2009).

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