K.W. Dixon, S.P. Kell, R.L. Barrett and P.J. Cribb (eds) 2003. *Orchid Conservation*. pp. 69–89.

Chapter 5

DNA DATA AND ORCHIDACEAE SYSTEMATICS: A NEW PHYLOGENETIC CLASSIFICATION

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Orchidaceae are rapidly becoming one of the best-studied families of the angiosperms in terms of infra-familial phylogenetic relationships. These studies demonstrate that several previous concepts about phylogenetic patterns were incorrect, which make all previous classifications in need of review. Therefore, in this paper we describe the emerging patterns and propose a new phylogenetic classification of Orchidaceae that accords with these newly discovered relationships. We recognise five subfamilies: Apostasioideae, Vanilloideae, Cypripedioideae, Orchidoideae and Epidendroideae, the last containing the bulk of the taxa in the family. Apostasioideae are sister to all the rest, followed successively by Vanilloideae, Cypripedioideae and the remainder of the monandrous orchids, Orchidoideae and Epidendroideae. Although only an interim classification, it should help to focus other areas of orchid research and stimulate the creation of new hypotheses that will direct orchid researchers to new questions.

1. Introduction

For many years, orchid classification has been based almost exclusively on features of their gymnostemium or column (Brown, 1810; Lindley, 1840; Pfitzer, 1887; Schlechter, 1926; Swartz, 1800). In the two most recent of these systems, an evolutionary progression was hypothesised from two or three anthers in the apostasioid orchids (*Apostasia* and *Neuwiedia*) through two in the cypripedioids (*Cypripedium, Mexipedium, Paphiopedilum, Phragmipedium*, and *Selenipedium*) to

one in the monandrous orchids (Epidendroideae, Orchidoideae and Spiranthoideae *sensu* Dressler, 1993). Within the monandrous orchids, which contain the great majority of orchid taxa, classification has depended largely on whether pollen in the anther was loose or formed into packets of various sorts, including hard pollinia. In the apostasioids, pollen is powdery as it is in most groups of Asparagales (*sensu* Angiosperm Phylogeny Group (APG), 1998), but in all other orchids, pollen is at least sticky and self-adherent so that it travels in packets, which is probably related to the large number of ovules in the ovaries of most orchids. In the most highly evolved groups of epidendroid orchids (roughly 80% of the species in the family; Dressler, 1993), pollen is firmly bound into hard pollinia deposited as complete units in the stigmatic cavity, but in the other monandrous orchids, there is every possible intermediate stage between free monads and hard pollinia. Most systems have also emphasised the other structures that comprise pollinaria, such as stipes, caudicles, and viscidia, but only a few older classifications (e.g. Pfitzer, 1887) have incorporated any number of vegetative characters.

Because orchid classification has largely been based on the relative degree of organisation of the pollinia, the distinction between Neottioideae and Epidendroideae has been highly problematic, such that the more primitive group, Neottioideae, has been variously narrowly and broadly defined. In Dressler's two schemes (1981; 1993), the neottioid orchids were narrowly treated. In addition to circumscription of the neottioids, the other major group of orchids that has been problematic is the vanilloids. Their columns are much like those of the epidendroids, but vegetatively they are highly divergent from all other orchids (Cameron and Dickison, 1998; Stern and Judd, 2000).

More recently, orchid systematists have begun the process of incorporating other categories of morphological information into their classifications (Dressler and Dodson, 1960; Garay, 1960; 1972; Vermeulen, 1966; Rasmussen, 1985; Burns-Balogh and Funk, 1986; Brieger, Butzin and Senghas, 1995; Szlachetko, 1995), but this process has only infrequently been couched in terms of explicitly phylogenetic studies (Freudenstein and Rasmussen, 1999). Burns-Balogh and Funk (1986) presented their arguments in cladogram format, but no formal analysis was conducted. Dressler (1981; 1993) also conveyed his ideas about relationships in the form of cladograms with characters mapped onto them, but their structure was purely intuitive. The results of the morphological analyses of Freudenstein and Rasmussen (1999) indicated that the high degree of hierarchical structure in all previous classifications of Orchidaceae was not warranted; this assertion was grounded on the fact that their cladistic analyses of morphological data showed little resolution at lower taxonomic levels. They did, in contrast, provide support for some of the various subfamilial groupings recognised in most previous systems of classification, such as Apostasioideae, Cypripedioideae, Orchidoideae and Epidendroideae.

Molecular data have come to play an increasingly important role in angiosperm classification (Chase *et al*., 1993; 2000a; b; APG, 1998; Soltis, Soltis and Chase, 1999; Chase, Fay and Savolainen, 2000; Savolainen *et al*., 2000; Soltis *et al*., 2000), and although the main focus has been at the supra-familial level, increasingly efforts are being focused on familial classification (Sheahan and Chase, 1996; 2000; Chase *et al*., 2000c; Richardson, Fay and Chase, 2000). Within Orchidaceae, numerous DNA phylogenetic studies have now been published, ranging from the whole family (Neyland and Urbatsch, 1993; Chase *et al*., 1994; Cameron *et al*., 1999; Molvray, Kores and Chase, 2000; Freudenstein, Senyo and Chase, 2000a; b), subfamilies (Cox *et al*., 1997; Kores *et al*., 1997), tribes (Cameron and Chase, 1999; Douzery *et al*., 1999; Kores *et al*., 2000; Whitten, Williams and Chase, 2000; Goldman *et al*., 2001), subtribes (Chase and Palmer, 1989; 1992; 1997; Chase and Hills, 1992; Yukawa, Cameron and Chase, 1996; Pridgeon *et al*., 1997;

Generic delimitation in several subtribes has also been studied. Whitten *et al*. (2000) demonstrated that generic limits in Stanhopeinae accord nearly perfectly with DNA results, as was also true in the earlier work on Catasetinae (Chase and Hills, 1992; Pridgeon and Chase, 1998), so DNA results do not contradict previous generic schemes based on (intuitively interpreted) morphological information in all cases. Oncidiinae (Williams *et al*., 2001) are a good example in which many genera have long been thought unsatisfactorily circumscribed (Garay and Stacy, 1976; Chase, 1986; 1987), so the gross polyphyly of the two largest genera, *Odontoglossum* and *Oncidium*, came as a surprise to no one. Our list of Oncidiinae genera in the Appendix reflects some of the recent nomenclatural changes, but many more are planned to bring generic delimitation into the line with a strict concept of monophyly. Likewise, many changes are in store for Eulophiinae (Cribb, Pridgeon, Norup and Chase, in prep), Maxillariinae (Whitten, Atwood *et al*., in prep.), and Zygopetalinae (Whitten, Dressler, Williams *et al*., in prep.).

3. Conclusions

All of these changes in taxonomy will be reflected in *Genera Orchidacearum* (Pridgeon *et al*., 1999; 2001; 2003). We expect the classification as outlined here to be ephemeral (hopefully for not longer than the next five years), but it should serve a useful interim purpose of giving other researchers a better place to start than Dressler (1993), which in spite of its admirable qualities is out of date. Nevertheless, we still recommend that orchid researchers continue to consult his treatment; it contains a wealth of information and ideas, many of which are still relevant.

Orchids should be one of the premier groups of flowering plants for evolutionary studies, and the massive amounts of DNA data now accumulating are revolutionising our ideas about these wonderful plants. Darwin's next book after *On the Origin of Species* was focused on orchids, and the reasons for this are clear: orchids should be studied more because they epitomise evolution in its most dynamic aspect, the rapid production of an incredibly diverse array of species. The challenge is to understand how this has come about, and so intensive study of this largest angiosperm family is highly appropriate. We hope that this new classification of the family facilitates research on Orchidaceae in the same manner as have Dressler's previous classifications (1981; 1993) and that it stimulates an understanding of the urgent need to conserve these evolutionary marvels.

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