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## FROM LINNAEUS TO *GENERA ORCHIDACEARUM*: THE EVOLUTION OF ORCHID CLASSIFICATION

Alec Pridgeon

Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, UK

### ABSTRACT

Although Linnaeus may have been published binomials in orchids, systematics of Orchidaceae began in earnest with the classification of Swartz in 1800. Lindley built on Swartz's classification and thousands of specimens for his *Genera and Species of Orchidaceous Plants* (1830-40), but like his predecessors he relied heavily on the structure and position of the anther. Pfitzer (1887) took the bold step of overlaying another level of characters, vegetative characters, onto the conventional column features and attempted to polarize them, primitive and advanced, across the family and was probably influenced by Darwin's works. Schlechter borrowed from both Bentham and Pfitzer to create a classification that Dressler and Dodson (1960) later supplemented and brought into conformity with the *International Code of Botanical Nomenclature* but with only two subfamilies -- Cyripedioideae (including *Apostasia* and *Neuwiedia*) and Orchidoideae. Garay (1972) proposed a system of five subfamilies, the number still used today, although one of them was Neottioideae instead of Vanilloideae.

In 1974 Dressler revised the classification of Dressler and Dodson, adding Garay's subfamily Apostasioideae. By 1981, the number of Dressler's subfamilies had risen to six with the addition of Spiranthoideae, Epidendroideae, and Vandoideae. What set this classification apart from the previous ones was its incorporation of new characters such as subsidiary cell development. Nevertheless, it still stressed the flower, the column in particular. In 1993 he added even more characters after publication of new data on seeds, stigmata, and endothelial thickenings. Problems remained, exemplified by two subtribes and two other genera labeled "misfits and leftovers."

Molecular studies in orchids came to the fore in 1993 when Chase *et al.* published a cladogram based on *rbcL* sequence data for 33 taxa spread across the family in the *Proceedings of the 14th World Orchid Conference*. It provided the first truly phylogenetic evidence that *Vanilla* and *Pogonia* did not belong to Epidendroideae, most Spiranthoideae were part of Orchidoideae, and Neottieae part of Epidendroideae. Like Pfitzer and Dressler before them, they stressed the importance of analyzing vegetative features and taking into account data from many sources toward producing a natural classification. Cameron *et al.* (1999) dramatically expanded the sampling of taxa in another *rbcL* study that offered support for a subfamily Vanilloideae. At the same time, however, it revealed no support



for Spiranthoideae, Neottioideae or Vandoideae nor for relationships among the five subfamilies along the spine of the tree. Freudenstein and Chase (2001) investigated mitochondrial DNA in Orchidaceae and showed that the mitochondrial genome shows the same historical pattern as the plastid genome in Orchidaceae. Chase *et al.* (2003) based their phylogenetic classification on published evidence from morphology and all these genes or gene regions, including a three-gene dataset for the family from Cameron (2001). We now have a robust, natural classification of the orchids being published as *Genera Orchidacearum* that can serve as a framework for answering all sorts of questions about orchid phylogeny, circumscription of taxa at every rank, biogeography, and character trends.

## BEGINNINGS

If you were a European living in the 18th century and were sent specimens of orchids, what would you name them? Even more important, how would you name them? Would you use one word, two words or many words as the medieval botanists, the herbalists, did? How would you determine how closely related they were -- and how could you be more or less sure you were right about their relationships? If you wanted to classify them, which features or characters would you use? And why those particular features? How many are necessary? On what basis do you assign importance to them?

What tools would you use to examine all these new species in the search for characters? DNA nucleotides would not be discovered and named until the end of the 19th century. The scanning electron microscope would not be invented until the 1930s. With only primitive microscopes and certainly without the benefit of DNA sequence analysis, you would be forced to rely on gross morphology, the form of the plant, and to some extent, on microscopic features. The first orchid classifications were comparatively simple, because so few were known. But as more and more orchids were discovered and shipped to Europe from all over the world, problems and contradictions began to arise.

Before Carl von Linné (Linnaeus), species naming practices varied. Many biologists gave the species they described long, unwieldy Latin names. The need for a workable naming system was made even greater by the huge number of plants and animals that were being brought back to Europe from Asia, Africa, and the Americas. After experimenting with various alternatives, Linnaeus (**Fig. 1**) simplified nomenclature immensely by designating one Latin name to indicate the genus, and one as a “shorthand” name for the species. The two names make up the binomial (“two names”) species name. This binomial system rapidly became the standard system for naming species. Although Linnaeus was not the first to use binomials, he was the first to use them consistently.

Linnaeus’s plant taxonomy was based solely on the number and arrangement of the reproductive organs; in ranking, a plant’s class was determined by its stamens (male organs) and its order by its pistils (female organs). This resulted in many groupings that seemed unnatural. Plants without obvious sex organs were classified in Class Cryptogamia, which lumped together the algae, lichens, fungi, liverworts and mosses, and ferns. Linnaeus freely admitted that this produced an artificial classification, not a natural one, which would take into account all the similarities and differences between

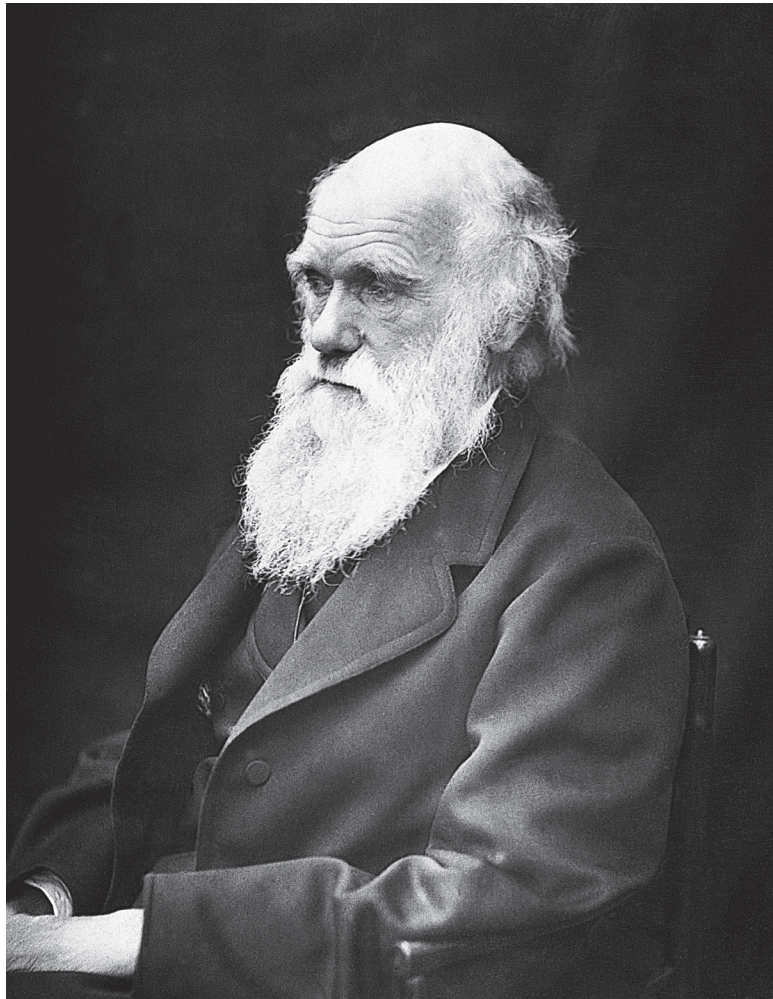


**Figure 1.** Carl von Linné (Linnaeus, 1707-1778), painted about 1775 by Alexander Roslin. Reproduced here by permission of the Linnean Society of London.

organisms. Like many naturalists of the time, Linnaeus attached great significance to plant sexual reproduction, which had only recently been rediscovered.

The sexual basis of Linnaeus's plant classification was controversial in its day; although easy to learn and use, it clearly did not give good results in many cases. Some critics also attacked it for its sexually explicit nature: one opponent, Prussian botanist Johann Siegesbeck (1737), called the sexual system "loathsome harlotry." What has survived of the Linnean system is its method of hierarchical classification and custom of binomial nomenclature.

Although Linnaeus may have been published binomials in orchids, 69 species in 7 genera in the first edition (1753) and 85 in the second edition (1762-63) of *Species Plantarum*, systematics of Orchidaceae began in earnest with the classification by Olof Swartz (1805), who provided a key to his 25 genera, observed that some orchids have one anther and others two, and divided the monandrous



**Figure 2.** Charles Robert Darwin (1809-1882). Photograph taken by his son Leonard about 1874 and published in Shropshire Archaeological Society's Transactions (1884).

orchids into three groups on the basis of the position of the anther. Louis Claude Richard (1817) stressed the structure of pollinia and the column in characterizing orchids; he also introduced many terms associated with the column that we still use today – rostellum, viscidium, and gynostemium. John Lindley (1830-40) built on Swartz's classification and thousands of specimens for his *Genera and Species of Orchidaceous Plants*, including 394 genera and an estimated 3000 species in 7 tribes. But at the tribal level, he, too, relied heavily on the structure and position of the anther. George Bentham (1881) recast Lindley's classification by adding the rank of subtribe but still focused on column features. Heinrich Gustav Reichenbach (1854-90) criticized Bentham and Pfitzer for deviating too much from details of the column in their systems.

## THE FIRST REVOLUTION

Charles Darwin's (**Fig. 2**) *On The Origin of Species* (**Fig. 3**) was published on 24 November 1859, 502 pages long. The first printing of 1250 copies sold out that same day (Desmond and Moore, 1991). Evolution -- descent with modification -- was not a new idea by any means. The idea has existed since ancient times, notably among Greek philosophers such as Epicurus and Anaximander. However, scientific theories of evolution were not established until the 18th and 19th centuries, by scientists such as Jean-Baptiste Lamarck and his Darwin's grandfather, Erasmus Darwin. Lamarck's theory of heritability of acquired characteristics was the idea that an organism can acquire characteristics during its lifetime and pass them on to its offspring. One example he gave was that giraffes stretching their necks to reach leaves high in *Acacia* trees strengthen and gradually lengthen their necks. These giraffes have offspring with slightly longer necks. The theory was later discredited.

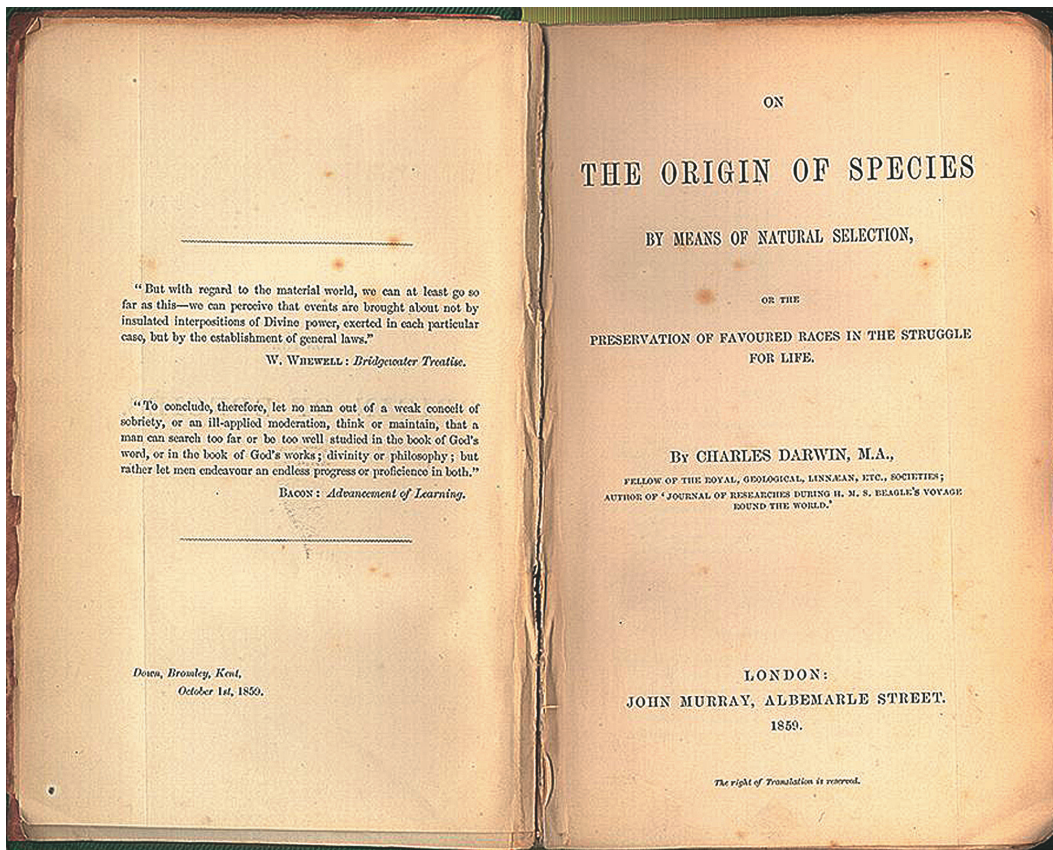
There are five overriding ideas in the *Origin*:

- 1) Variation exists in natural populations.
- 2) Many more offspring are born each season than can possibly survive to maturity.
- 3) As a result, there is a struggle for existence.
- 4) Characteristics beneficial in the struggle for existence will tend to become more common in the population, changing the characteristics of a species.
- 5) Over time, and given a steady input of new variation into a population, these processes lead to the emergence of new species.

The second and third of these ideas were heavily influenced by Thomas R. Malthus' famous "An Essay on the Principle of Population," which went through six editions between 1798 and 1826. The fourth of these points is a summation of natural selection, and the fifth addresses the process of speciation.

Darwin's dilemma in the *Origin*, his Achilles heel, had to do with the first of these -- how to explain the source of variation on which natural selection worked. In the absence of any better theory, he was compelled to adopt the then-popular concept of blending heredity. That is, any differences in traits of parents are blended in their offspring. These differences, or "fortuitous novelties" as he called them, derive from changes in the environment, drifting dangerously toward Lamarckian inheritance. He argued in the *Origin* that sexual reproduction would actually reduce variation, not promote it.

Pfitzer (1887) took the bold step of overlaying another level of characters -- vegetative characters such as veneration, number of pseudobulb internodes, and growth habit -- on the conventional column features and attempted to polarize them, primitive and advanced, across the family and was probably influenced by Darwin's works. Schlechter (1926) borrowed from both Bentham and Pfitzer to create a classification that Dressler and Dodson (1960) later supplemented and tweaked a bit to



**Figure 3.** Dedication and title pages of the first edition of *On the Origin of Species*. Note that Darwin dedicated his masterpiece to 1) William Whewell (1794-1866), who wrote extensively on numerous subjects from geology and astronomy to the history of science and moral philosophy, and 2) Sir Francis Bacon (1561-1626), English statesman and advocate of modern science.

bring it into conformity with the *International Code of Botanical Nomenclature* but with only two subfamilies -- Cyripedioideae (including *Apostasia* and *Neuwiedia*) and Orchidoideae.

To this mix Garay (1972) added yet more types of characters such as those related to floral vascularization, embryology, and seeds and proposed a system of 5 subfamilies, still used today, although one of them was Neottioideae instead of Vanilloideae. All of these gentlemen knew that their system would not be the last word as there were still too many unanswered questions. Garay's methodology, to uncover primitive features in living species, differed by 180 degrees from phylogenetics.

In 1974, Robert L. Dressler revised the classification of Dressler and Dodson (1960), adding Garay's subfamily Apostasioideae. By 1981, the number of his subfamilies had risen to six with the addition of Spiranthoideae, Epidendroideae, and Vandoideae. What set this classification apart from

the previous ones was its incorporation of new characters such as subsidiary cell development. Nevertheless, it still stressed the flower, the column in particular.

## THE SECOND REVOLUTION

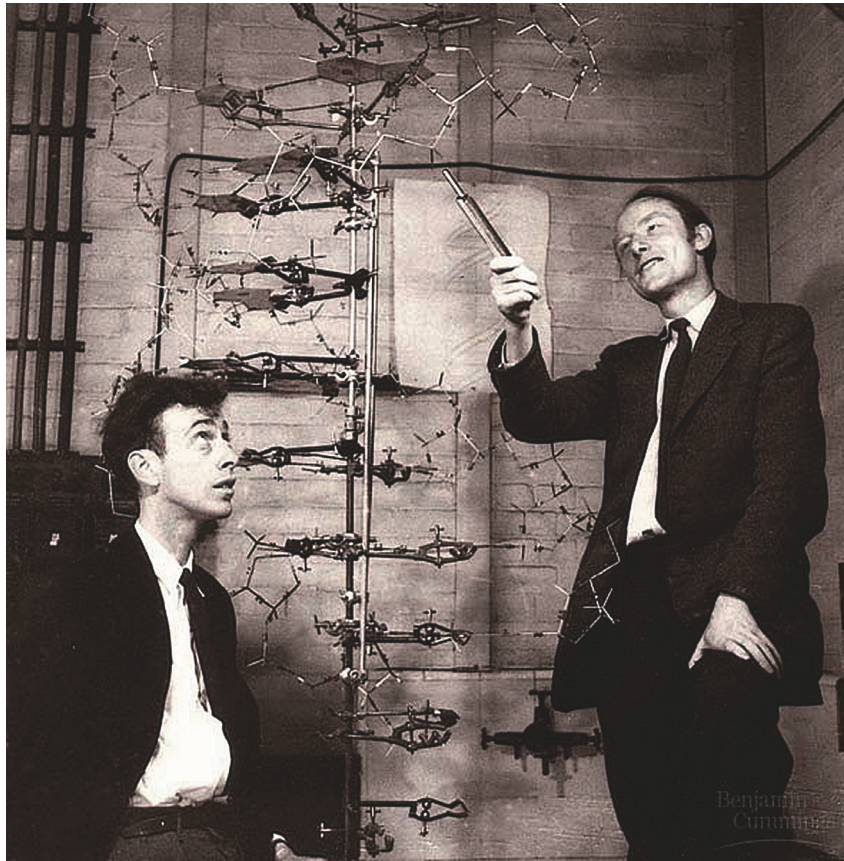
To set the stage for what would occur in the next few decades, a two-page paper by the American James Watson and British Francis Crick (**Fig. 4**) appeared in the journal *Nature* in 1953 (Watson and Crick, 1953a; **Fig. 5**), by coincidence exactly two centuries after publication of *Species Plantarum*. It ushered in an age that has not only changed the way we think about systematic and evolutionary relationships but even enabled us to change our own constitution and clone organisms, which has its own set of ethical, legal, and religious implications. That short paper, barely over a page long, described the double helix structure of DNA and ended with the famous words, “It has not escaped our notice that the specific pairing we have postulated immediately suggests a possible copying mechanism for the genetic material.” In a follow-up paper (Watson and Crick, 1953b), they speculated on how base-pairing allows DNA replication.

It was Watson who fit the final piece into place. He was in the lab, pondering his cardboard replicas of the four bases that, we now know, constitute DNA’s alphabet: adenine, thymine, guanine and cytosine, or A, T, G and C (Watson, 2003). He realized that an adenine-thymine (purine-pyrimidine) pair held together by two hydrogen bonds was identical in shape to a guanine-cytosine (purine-pyrimidine) pair. These pairs of bases could thus serve as the rungs on the twisting ladder of DNA.

We now know that there is not one but three different genomes in a plant cell. Nuclear DNA, usually biparentally inherited, is often the most variable compared to the other genomes. Most phylogenetic work has used ribosomal DNA, which has major roles in protein synthesis, including binding certain proteins into ribosomes. Although some regions of ribosomal DNA, particularly the coding genes, are highly conserved (e.g. 18S rDNA), other regions are more rapidly evolving and systemat-ically useful at the species level and among closely related genera (ITS rDNA).

Two other cell organelles also possess DNA. One of these is the mitochondrion, which provides energy for cellular functions in plants and animals. Mitochondrial DNA studies have been used more extensively in evolutionary studies of animals than in plants, primarily because plant mitochondrial DNA is often too conservative in plants to be useful. The other cell organelle with DNA is limited to plants, the plastid. The entire plastid genome, with about 120 genes, has been mapped now for several species such as *Nicotiana* (tobacco) and *Oryza* (rice). Like mitochondrial DNA, it is inherited from only one parent (usually maternal). Different plastid genes evolve at different rates, and so biologists have been able to use specific genes to show relationships at different levels of classification. The most commonly used gene, *rbcL*, codes for the large subunit of the enzyme ribulose 1,5-bisphosphate carboxylase/oxygenase, or “RUBISCO.” This enzyme is probably the most abundant protein on the planet because it is involved with the fixation of carbon dioxide from the atmosphere in all green plants including algae. For systematic purposes it has been used to show evolutionary relationships at





**Figure 4.** James D. Watson (1928- ) and Francis H. C. Crick (1916-2004), with a model of the double helix of DNA. Photographer unknown, dated 1953.

the genus level and above in plants. Plastid gene regions variable enough to be useful among closely related genera and species are, for example, *matK* and *trnL*.

At about the same time that Watson, Crick, and their colleagues were puzzling over the structure of DNA, the phylogenetic method called cladistics was being formulated by a German entomologist named Willi Hennig (1950, 1966). It attempts to reconstruct the evolutionary history or phylogeny of a group of organisms on the basis of shared derived characters called synapomorphies. Evolutionary relationships are then represented in a branching diagram called a cladogram. The guiding principle of cladistics is that shared derived characters define monophyletic groups called clades that include all the descendants of a common ancestor and that ancestor. A shared character is one that two lineages have in common, and a derived character is one that evolved in the lineage leading up to a clade and that sets members of that clade apart from other individuals. For example, amphibians, turtles, lizards, snakes, crocodiles, birds, and mammals all have (or historically had) four limbs. If you look at a modern snake you might not see obvious limbs, but fossils show that ancient snakes did have limbs, and some modern snakes such as ball pythons retain rudimentary limbs. ‘Presence of four limbs’



(Reprinted from *Nature*, Vol. 171, p. 737, April 25, 1953)

## MOLECULAR STRUCTURE OF NUCLEIC ACIDS

### A Structure for Deoxyribose Nucleic Acid

**W**E wish to suggest a structure for the salt of deoxyribose nucleic acid (D.N.A.). This structure has novel features which are of considerable biological interest.

A structure for nucleic acid has already been proposed by Pauling and Corey<sup>1</sup>. They kindly made their manuscript available to us in advance of publication. Their model consists of three intertwined chains, with the phosphates near the fibre axis, and the bases on the outside. In our opinion, this structure is unsatisfactory for two reasons: (1) We believe that the material which gives the X-ray diagrams is the salt, not the free acid. Without the acidic hydrogen atoms it is not clear what forces would hold the structure together, especially as the negatively charged phosphates near the axis will repel each other. (2) Some of the van der Waals distances appear to be too small.

Another three-chain structure has also been suggested by Fraser (in the press). In his model the phosphates are on the outside and the bases on the inside, linked together by hydrogen bonds. This structure as described is rather ill-defined, and for this reason we shall not comment on it.

We wish to put forward a radically different structure for the salt of deoxyribose nucleic acid. This structure has two helical chains each coiled round the same axis (see diagram). We have made the usual chemical assumptions, namely, that each chain consists of phosphate di-ester groups joining  $\beta$ -D-deoxyribofuranose residues with 3',5' linkages. The two chains (but not their bases) are related by a dyad perpendicular to the fibre axis. Both chains follow right-handed helices, but owing to the dyad the sequences of the atoms in the two chains run in opposite directions. Each chain loosely resembles Furberg's<sup>2</sup> model No. 1; that is, the bases are on the inside of the helix and the phosphates on the outside. The configuration of the sugar and the atoms near it is close to Furberg's 'standard configuration', the sugar being roughly perpendicular to the attached base. There is a residue on each chain every 3.4 Å. in the z-direction. We have assumed an angle of 36° between adjacent residues in the same

Figure 5. First page of Watson and Crick (1953a) paper describing DNA structure.

is a shared derived character inherited from a common ancestor that helps to distinguish this particular clade of vertebrates.

In 1993 Dressler added even more characters to his classification after publication of new data on seeds, stigmata, and endothelial thickenings. His reasoning was cladistic in nature but without formal cladistic analysis. Problems remained, exemplified by two subtribes and two other genera labeled “misfits and leftovers.” As a result, no one was entirely satisfied with the 1993 version, including Dressler.

## MODERN ORCHID SYSTEMATICS

Only a year later, Chase *et al.* (1994) published a cladogram based on *rbcL* sequence data for 33 taxa spread across the family in the *Proceedings of the 14th World Orchid Conference*. It provided the first truly phylogenetic evidence that *Vanilla* and *Pogonia* did not belong to Epidendroideae, Spiranthoideae (excluding *Tropidia*, *Diceratosteles*, and others) were part of Orchidoideae, and Neottioideae part of Epidendroideae. Like Pfitzer and Dressler before them, they stressed the importance of analyzing vegetative features and taking into account data from many sources toward producing a natural classification.

Freudenstein and Rasmussen (1999) scored 71 characters using Dressler’s 1993 classification and excluded 10 other characters for a variety of reasons. Their results showed substantial structure but high levels of homoplasy in the nonvandoid epidendroids. The independence of vegetative characters from floral elements as evidence was clearly shown by the position of *Tropidia* in Epidendroideae instead of its traditional placement in Spiranthoideae.

With the advent of automated DNA sequencing and improved reagents, Cameron *et al.* (1999) dramatically expanded the number of taxa sampled to 171 in another *rbcL* study that showed the same relationship of *Tropidia* to Epidendroideae and offered support for a subfamily Vanilloideae. At the same time it revealed no support for Spiranthoideae, Neottioideae or Vandoideae nor for relationships among the five subfamilies along the spine of the tree. Most subtribes were monophyletic, but not so the tribes. More gene regions were required to help solve these problems.

Freudenstein and Chase (2001) investigated mitochondrial DNA in Orchidaceae, sequencing an intron in the gene for NADH dehydrogenase, which has a high proportion of length mutations, that is, insertions and deletions (indels). Inclusion of indels in an analysis of base substitutions yielded significantly more resolved trees than use of substitutions alone. In this study, the overall signal mirrored that of Cameron *et al.* (1999), which means that the mitochondrial genome shows the same historical pattern as the plastid genome.

Chase *et al.* (2003) based their phylogenetic classification on published evidence from morphology and all these genes or gene regions, including a three-gene dataset for the family from Camer-

on (2001). Finally, Freudenstein *et al.* (2004) expanded the combined *rbcL/matK* dataset to encompass 173 taxa, resolving some relationships that were only weakly supported in the Cameron *et al.* (1999) analyses and strengthening others from those earlier studies. In the short span of a decade, molecular systematists from around the world did something that Garay thought impossible, focused as he was on the search for primitive characters. Phylogenetic analyses search for shared derived characters rather than differences. We now have a robust, natural classification of the orchids that can serve as a framework for answering all sorts of questions about orchid phylogeny, circumscription of taxa at every rank, biogeography, and character trends.

*Genera Orchidacearum* (Pridgeon *et al.*, 1999, 2001, 2003, 2005) is the first real attempt to monograph the world's 800 or so orchid genera using phylogenetics, and especially molecular phylogenetics, written by 82 different collaborators from around the world to date. It represents a synthesis of our knowledge of the nomenclature, distribution, anatomy, palynology, cytogenetics, phytochemistry, phylogenetics, ecology, pollination, uses, and cultivation for each genus. For virtually every genus there is a diagnostic line drawing, usually one or more color illustrations, and a distribution map.

The system followed in *Genera Orchidacearum* comprises five major lineages based mostly on the classification of Chase *et al.* (2003): 1) At the base are the two genera of Apostasioideae from tropical Asia and northern Australia. *Apostasia* and *Neuwiedia* are terrestrial, have 2 or 3 anthers, and the lip is similar to the petals. Pollen grains are shed separately as monads and are powdery; 2) Vanilloideae are distributed worldwide. They are vines or herbs with tunicate or crustose or winged seeds, different from the dust seeds of more advanced subfamilies. Pollen from the single anther is usually shed as monads. Many species of *Vanilla* are economically important; 3) The five genera of Cypripedioideae, the slipper orchids, are widespread from the temperate zones to the tropics. They are terrestrials, epiphytes or lithophytes with usually showy flowers having a pouched or saccate lip and two anthers. Pollen is powdery or sticky; 4) Orchidoideae include over 3500 species. They are usually terrestrials with tubers or fleshy rhizomes, spirally arranged leaves, and 2 or 4 pollinia attached by stalks called caudicles to viscidia; 5) Epidendroideae is by far the largest subfamily with about 18,000 species in 650 genera. Most occur in the tropics but they extend from the Arctic Circle to Argentina, Tasmania, and New Zealand. Most have fleshy stems or pseudobulbs, fleshy leaves, and pollen shed as pollinia, but naturally there are many exceptions to these. All have one anther.

Two of the benchmark studies in molecular systematics of Orchidoideae were those Pridgeon *et al.* (1997) and Bateman *et al.* (2003). Initially using ITS sequences alone, it was clear that *Orchis* as traditionally understood was polyphyletic and spread among three clades, two with a diploid chromosome number of 40 or 42 and one with 32 or 36. *Orchis morio* and its relatives fell into the same clade as the previously monospecific *Anacamptis*. Another clade of *Orchis* including *Orchis ustulata* with  $2n = 40$  or 42 was sister to the formerly monospecific *Neotinea*. The type clade with *Orchis militaris*, also with  $2n = 40$  or 42, included *Aceras anthropophorum* as basally divergent.

Primarily because DNA sequencing has uncovered genetic relationships obscured by morphological homoplasy, long-standing questions about relationships of many genera have now been resolved. For example, Bentham and Hooker (1883) placed *Meiracyllium* in Pleurothallidinae. Schlechter (1926) put it close to *Sophranitis* in Laeliinae, and Dressler (1981, 1993) put it in its own subtribe of Epidendreae because its rostellum and pollinia had little in common those of Laeliinae. Dressler and Dodson (1960) and Garay (1974) suggested a link with *Arpophyllum*. Van den Berg *et al.* (2005) reported that ITS and plastid DNA sequences placed *Meiracyllium* firmly in Laeliinae, but its sister relationships are still unclear.

Relationships of *Arpophyllum* have also been historically problematic. Various workers used floral features to include it in Laeliinae, Pleurothallidinae, Ponerinae, Sobraliinae, and even close to *Dendrobium*. This could have gone on interminably with one opinion marching after another until van den Berg *et al.* (2005) clearly showed with 100% bootstrap support that it is sister to Laeliinae. Soto Arenas and Salazar Chávez (2004) speculated that the morphological traits of *Arpophyllum* are plesiomorphic among epidendroids and that its distribution indicates that it is a relict of the boreo-tropical orchid flora of North America.

*Dilomilis* and *Neocognauxia* had been included in Laeliinae by Dressler, but combined DNA sequence analyses showed a strongly supported sister relationship to Pleurothallidinae. These two genera and a third one segregated from *Dilomilis*, *Tomzanonia*, lack the articulation between the ovary and pedicel that characterizes Pleurothallidinae, but they were included in that subtribe in volume 4 of *Genera Orchidacearum* on the basis of evidence from multiple DNA regions, number of pollinia (8, like *Octomeria*), the ancestral reed-stem condition in other clades of Epidendroideae, seed morphology, and the expanded leaf sheaths of *Fronitaria*, which are interpreted as a reversal to the reed-stem condition. As in so many other groups, DNA sequences have helped us to circumscribe more natural and phylogenetically informative groups.

*Claderia* contains only two species, one widespread in southern Thailand, the Malay Peninsula, Singapore, Sumatra, Borneo, and Sulawesi, the other in New Guinea. Plants have an unusual habit, starting life as a leaf-litter terrestrial. The elongate, creeping rhizome climbs an adjacent tree trunk, and the lower part of the plant may eventually rot to leave the plant as a scandent epiphyte. The systematic position of the genus has always been debated. Mansfeld (1937) placed *Claderia* in the monogeneric Claderiinae but never formally established the subtribe. Dressler (1981) noted that *Claderia* fits Cymbidieae in its floral features and placed it in alliance 1 (with *Bromheadia*) of the five alliances of Cyrtopodiinae on account of their possession of “slender reed-like stems.” Dressler (1993) noted Mansfeld’s attribution of the genus but confessed that he was unsure where it belonged in Epidendroideae and included it among his “misfits and leftovers.” Szlachetko (1995) validated Claderiinae and considered it a subtribe of Polystachyae, along with Polystachyinae, Collabiinae, and Bromheadiinae. Recent inclusion of the rDNA ITS sequence of *C. viridiflora* in a Eulophiinae-Cymbidiinae data set (Pridgeon, unpublished) yielded strong support (87%) for placement of *Claderia* in Cymbidieae, where it is sister to *Dipodium* in the strict consensus tree (but with less than 50% bootstrap support).

Having a reliable phylogeny for Orchidaceae has facilitated elucidation of character-state trends in several areas:

*Cytogenetics.* In tribe Orchideae there are four basic chromosome numbers,  $x = 16, 18, 20,$  and 21, yielding diploid complements ranging between 32 and 42, rarely 44 and 46. Habenariinae are generally 40 or 42 as are *Orchis s.s.*, *Dactylorhiza*, *Gymnadenia*, etc. More derived taxa such as *Ophrys*, *Serapias*, *Anacamptis s.l.* have 36, rarely 32. But accompanying general reduction in chromosome number there are specializations in the karyotype such as increasing asymmetry. According to Chase and Palmer (1997), there is also evidence for aneuploid reduction series in Oncidiinae, from  $n = 28$  and 30 as the ancestral condition and  $n = 5-24$  in the derived groups.

*Pollen.* In both Laeliinae and Pleurothallidinae the number of pollinia in the basalmost nodes is eight, whereas the derived number is two. Numbers have likely been reduced many times through phylogeny and not necessarily in a linear fashion. Granular pollinia, that is, those having exine on all constituent pollen grains, are generally present in Orchidoideae and basalmost Epidendroideae, whereas solid pollinia, the internal grains of which do not have an exine, generally occur in derived Epidendroideae. Within tribe Epidendreae, ovoid pollinia are found in *Arpophyllum*, flattened pollinia in derived Laeliinae, and clavate pollinia in Pleurothallidinae.

*Vegetative anatomy.* Conical silica bodies occur in most orchids that have vascular bundle sheaths and/or fiber bundles, but spherical types generally occur in more derived clades of Epidendroideae such as Vandaeae, Eriinae, Podochilinae, and Dendrobiinae (Møller and Rasmussen, 1984).

## WHAT LIES AHEAD?

Will this be the last word? Are orchid names going to be fixed after all this DNA work is done? Certainly, binomials will be less prone to change as scientists and hobbyists demand to see evidence for new names before adopting them. This has been the most significant change in the philosophy behind orchid nomenclature in the last decade. The days of authoritarianism, that is, names by fiat, are now anachronistic, if not archaic. But are they never going to change again? Of course not. They should, however, be the most stable they have ever been.

What about hybrids? In today's world, and for the same reasons that binomials are more stable, the names of primary hybrids should be safer from incursions by taxonomists. Note that I qualified that with "in today's world."

The seeds of change in the way we think about plants, and all organisms for that matter, are germinating in research labs around the world, and inevitably a new system of nomenclature, a new paradigm, is going to replace or at least coexist with the present one to accommodate the results of bioengineering. In the next decade or two I suspect we're going to be seeing orchids genetically engineered for color, warmth-tolerance, shape, and ploidy. Genes governing reproductive isolation can



theoretically be knocked out or turned off, so there could be a wider spectrum of hybridizing within the family, even between subfamilies, which means exponentially more nothogenera. Genes from other groups of plants will be inserted into orchid genomes and vice-versa.

The most exciting new research is in evolutionary developmental biology, so-called “evo-devo.” The ABC floral development model proposes that class A genes alone are responsible for the development of sepals but act together with class B genes to effect petal development. Similarly, class C genes alone are responsible for initiating the development of carpels but act together with class B genes to determine the development of stamens. Support for a dual gene interaction with class B genes comes from the nature of class B mutants. A defective B gene leads to the absence of petals and stamens; in their places develop additional sepals and carpels. Similar organ replacement occurs when other classes of genes undergo mutation. Theoretically, then, it is possible to eliminate the sepals or sepals and petals of orchid flowers, leaving only the column (clearly not a desideratum in the horticultural world). Or the column could be eliminated, leaving only the perianth. Considering the actions of these and other genes alone or in combination with those of orchids or other plant families, the number of possibilities is unlimited.

How will we designate these “designer plants” to differentiate them from naturally occurring genomes? Can they in fact still be considered orchids? What will be the minimum number of unaltered genes required for a plant to be considered an orchid? Within this century, we or others are going to be faced with the same issue that Linnaeus and his peers faced: “What, indeed, is an orchid?”

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## Literature cited

- Bateman, R. M., Hollingsworth, P. M., Preston, J., Luo, Y.-b., Pridgeon, A. M., and Chase, M. W. 2003. Molecular phylogenetics and evolution of Orchidinae and selected Habenariinae (Orchidaceae). *Botanical Journal of the Linnean Society* 142: 1-40.
- Bentham, G. 1881. Notes on Orchideae. *Journal of the Linnean Society (Botany)* 18: 281-360.
- Bentham, G. and Hooker, J. D. 1883. *Genera plantarum*, vol. 3. L. Reeve & Co., London.
- Cameron, K. M. 2001. An expanded phylogenetic analysis of Orchidaceae using three plastid genes: *rbcL*, *atpB*, and *psbA*. *American Journal of Botany* 88: Supplement [abstract 2].
- Cameron, K. M., Chase, M. W., Whitten, W. M., Kores, P. J., Jarrell, D. C., Albert, V. A., Yukawawa, T., Hills, H. G., and Goldman, D. H. 1999. A phylogenetic analysis of the Orchidaceae: evidence from *rbcL* nucleotide sequences. *American Journal of Botany* 86: 208-224.

- Chase, M. W., Cameron, K. M., Barrett, R. L., and Freudenstein, J. V. 2003. DNA data and Orchidaceae systematics: a new phylogenetic classification. In *Orchid conservation* (ed. K. W. Dixon, S. P. Kell, R. L. Barrett, and P. J. Cribb), pp. 69-89. Natural History Publications, Kota Kinabalu, Sabah, Malaysia.
- Chase, M. W., Cameron, K. M., Hills, H. G., and Jarrell, D. 1994. DNA sequences and phylogenetics of the Orchidaceae and other lilioid monocots. In *Proceedings of the 14th World Orchid Conference* (ed. A. M. Pridgeon), pp. 61-73. HMSO, Edinburgh.
- Chase, M. W. and Palmer, J. D. 1992. Floral morphology and chromosome number in subtribe Oncidiinae (Orchidaceae): evolutionary insights from a phylogenetic analysis of chloroplast DNA restriction site variation. In *Molecular systematics in plants* (ed. D. E. Soltis, P. S. Soltis, and J. J. Doyle), pp. 324-337. Chapman and Hall, London.
- Darwin, C. 1859. *On the origin of species by means of natural selection, or the preservation of the favoured races in the struggle for life*. Murray, London.
- Desmond, A. and Moore, J. 1991. *Darwin*. Michael Joseph, London.
- Dressler, R. L. 1974. Classification of the orchid family. In *Proceedings of the 7th World Orchid Conference* (ed. M. Ospina), pp. 259-274. Seventh World Orchid Conference, Medellín, Colombia.
- Dressler, R. L. 1981. *The orchids: natural history and classification*. Harvard University Press, Cambridge, Massachusetts.
- Dressler, R. L. 1993. *Phylogeny and classification of the orchid family*. Cambridge University Press, Cambridge, United Kingdom.
- Dressler, R. L. and Dodson, C. H. 1960. Classification and phylogeny in the Orchidaceae. *Annals of the Missouri Botanical Garden* 47: 25-68.
- Freudenstein, J. V. and Chase, M. W. 2001. Analysis of mitochondrial *nad1b-c* intron sequences in Orchidaceae: utility and coding of length-change characters. *Systematic Botany* 26: 643-657.
- Freudenstein, J. V. and Rasmussen, F. N. 1999. What does morphology tell us about orchid relationships? – A cladistic analysis. *American Journal of Botany* 86: 225-248.
- Freudenstein, J. V., van den Berg, C., Goldman, D. H., Kores, Paul J., Molvray, M., and Chase, M. W. 2004. An expanded plastid DNA phylogeny of Orchidaceae and analysis of jackknife branch support strategy. *American Journal of Botany* 91: 149-157.
- Garay, L. A. 1972. On the origin of the Orchidaceae, II. *Journal of the Arnold Arboretum* 53: 202-215.
- Garay, L. A. 1974. Synopsis of the genus *Arpophyllum*. *Orquídea (Mexico City)* 4: 3-19.
- Hennig, W. 1950. *Grundzüge einer Theorie der phylogenetischen Systematik*. Deutsche Zentralverlag, Berlin.
- Hennig, W. 1966. *Phylogenetic systematics*. Transl. by D. D. Davis and R. Zangerl. University of Illinois Press, Urbana, Illinois.
- Lindley, J. 1830-1840. *The genera and species of orchidaceous plants*. J. Ridgway, London.
- Linnaeus, C. 1753. *Species plantarum*. L. Salvius, Stockholm.
- Linnaeus, C. 1762-1763. *Species Plantarum*. 2nd ed. Salvius, Stockholm.
- Mansfeld, R. 1937. Über das System der Orchidaceae-Monandreae. *Notizblatt des Botanische Gartens und Museums zu Berlin-Dahlem* 9: 561-591.
- Møller, J. D. and Rasmussen, H. 1984. Stegmata in Orchidales: character state distribution and polarity. *Botanical Journal of the Linnean Society* 89: 53-76.

- Pfitzer, E. 1887. *Entwurf einer natürlichen Anordnung der Orchideen*. Carl Winter's Universitäts Buchhandlung, Heidelberg.
- Pridgeon, A. M., Bateman, R. M., Cox, A. V., Hapeman, J. R., and Chase, M. W. 1997. Phylogenetics of subtribe Orchidinae (Orchidoideae, Orchidaceae) based on nuclear ITS sequences. 1. Intergeneric relationships and polyphyly of *Orchis sensu lato*. *Lindleyana* 12: 89-109.
- Pridgeon, A. M., Cribb, P. J., Chase, M. W. and Rasmussen, F. N. 1999. *Genera orchidacearum, volume 1. General introduction, Apostasioideae, Cypripedioideae*. Oxford University Press, Oxford, United Kingdom.
- Pridgeon, A. M., Cribb, P. J., Chase, M. W. and Rasmussen, F. N. 2001. *Genera orchidacearum, volume 2. Orchidoideae (part one)*. Oxford University Press, Oxford, United Kingdom.
- Pridgeon, A. M., Cribb, P. J., Chase, M. W. and Rasmussen, F. N. 2003. *Genera orchidacearum, volume 3. Orchidoideae (part two), Vanilloideae*. Oxford University Press, Oxford, United Kingdom.
- Pridgeon, A. M., Cribb, P. J., Chase, M. W. and Rasmussen, F. N. 2005. *Genera orchidacearum, volume 4. Epidendroideae (part one)*. Oxford University Press, Oxford, United Kingdom.
- Reichenbach, H. G. 1854-1900. *Xenia orchidacea*. 3 vols. Brockhaus, Leipzig.
- Richard, L. C. 1817. *De orchideis Europaeis annotationes, praesertim ad genera dilucidanda spectantes*. A. Belin, Paris.
- Schlechter, R. 1926. Das System der Orchidaceen. *Notizblatt des Botanischen Gartens und Museums zu Berlin-Dahlem* 9: 563-591.
- Siegesbeck, J. G. (1737). *Epicrisis in clar. Linnæi nuperrime evulgatum systema plantarum sexuale, et huic superstructam methodum botanicam*.
- Soto Arenas, M. A. and Salazar Chávez, G. A. 2004. Diversidad de orquídeas de Oaxaca. In *Biodiversidad de Oaxaca* (ed. A. García Mendoza and M. de J. Ordoñez), pages 271-295. Instituto de Biología-UNAM/World Wild Life Fund, Mexico City.
- Swartz, O. 1805. Genera et species orchidearum. *Neues Journal für die Botanik* 1: 1-108.
- Szlachetko, D. 1995. Subtribe Claderiinae. *Fragmenta Flora Geobotanica*, Suppl. 3: 80.
- Van den Berg, C., Goldman, D. H., Freudenstein, J. V., Pridgeon, A. M., Cameron, K. M., and Chase, M. W. 2005. An overview of the phylogenetic relationships within Epidendroideae inferred from multiple DNA regions and recircumscriptions of Epidendreae and Arethuseae. *American Journal of Botany* 92: 613-624.
- Watson, J. D. 2003. *DNA: The secret of life*. Alfred A. Knopf, New York.
- Watson, J. D. and Crick, F. H. C. 1953a. A structure for deoxyribose nucleic acid. *Nature* 171: 737-738.
- Watson, J. D. and Crick, F. H. C. 1953b. Genetical implications of the structure of deoxyribonucleic acid. *Nature* 171: 964-967.