

Orchid Research Newsletter No. 66

When the Molecular Systematics Laboratory at the Royal Botanic Gardens, Kew, first opened under the leadership of Mark Chase and Mike Bennett as Keeper of the Jodrell, the main target marker was *rbcL* for family-wide systematic studies of Orchidaceae and other families. Internal transcribed spacers of nuclear ribosomal DNA were used for studies below the family level. Those of us unfortunate to have lived through those days of manual sequencing in the early 1990s know how laborious it was to label nucleotides with radioactive phosphorus 32 or sulfur 35 with all the safety measures that that entailed, pour polyacrylamide gels between two glass plates without even the smallest air bubble, expose the sequencing gel to x-ray film, and then manually call the bases one by one off the autoradiogram, hoping to get 100 bases of the more than 1300 base pairs in the *rbcL* sequence and then enter them into the computer database. In many cases, the results were ambiguous, which entailed judgment calls. And this did not even include data analysis with software much, much slower than today. All this work produced only a trickle of data and a lack of strong support for many branches leading to the major clades.

Manna from heaven came in the form of automated sequencing later that decade. Automated sequencers used the Sanger method, which relied on the introduction of dideoxynucleotides into the growing DNA strand by DNA polymerase, creating fragments separated by size on the gel by electrophoresis. Nucleotides were labeled by fluorescent dyes rather than sulfur 35, and read by a laser. Electropherograms still needed interpretation and some manual base calling in positions with ambiguity, especially toward the ends of the reads where the signal trailed off. But then overlapping sequences using other primers improved reliability. Read lengths of 800 bases were now possible, but the amount of DNA could fit on a single run was still limited. This was the technology most widely used, both here at RBG Kew and around the world.

Orchid sequence data began to flow more freely and quickly across the entire family in the laboratories at RBG Kew and elsewhere. More and more genes and gene regions (primarily plastid markers) were being sequenced. But we still had to amplify the DNA by the polymerase chain reaction in a thermal cycler, check it on agarose gels, and clean the products before sequencing. From DNA extraction to getting a sequence could take as long as a week or even two depending on how booked up the sequencer was. But by 2005 we and our colleagues around the world had a robust, natural classification of the orchids that could serve as a framework for answering all sorts of questions about orchid phylogeny, circumscription of taxa at every rank, biogeography, and character trends.

At the Wellcome Trust Sanger Centre near Cambridge it took 10 years for researchers to sequence only one third of the human genome using capillary electrophoresis and the dideoxynucleotide-chain termination method developed by Frederick Sanger for long, continuous reads. The sequencing instruments made by Applied Biosystems back then could produce a million DNA bases/machine/day there, which at the time seemed phenomenal.

What a difference only a few years makes in an ongoing technological revolution. Next-generation sequencing (NGS) has turned the sequencing world topsy-turvy. With NGS, genomic DNA is extracted, fragmented into smaller segments, and sequenced in a massively parallel fashion using machines developed mostly in the last five years by the Illumina Corporation based in San Diego, California. To give you an idea of the speed, the entire human genome can now be completely sequenced in 27 HOURS and analyzed in another day or two. A billion base pairs can be analyzed by one machine in one day.

Applying NGS to orchids, a paper by Cai *et al.* (2014) with multiple authors appeared last November in *Nature Genetics*. They reported the first whole-genome sequence of an orchid species, not for some twig epiphyte with only a few chromosomes and a short generation time such as *Erycina pusilla*, but for *Phalaenopsis equestris* (pictured here) with a diploid chromosome number of 38, crassulacean acid metabolism, and a relatively long generation time. However, its genome size is small compared to other species in the genus as well as other genera. The authors found 29,431 protein-coding genes in 3,694 gene families. Over 60% is repetitive DNA, twice what it is in rice but about the same as sorghum. Interspersed repeats and transposable elements (“jumping genes”) make up 59% of the genome.



Phalaenopsis equestris var. *rosea*
(Photo: Alec Pridgeon)

They then used the Ramirez *et al.* (2007) study of the orchid fossil *Meliorchis caribea* to determine that 71% of the long terminal repeats (a type of retroposon) arose during an insertion between 11.7 and 43 million years ago. In quantifying gene expression levels, they discovered that 2,283, 1,499, 947, and 1,288 genes were preferentially expressed in flower, leaf, stem, and root, respectively. Most of the type II MADS-box genes had been duplicated, especially in the B-class AP3, C/D class and E-class clades, which are associated with the labellum and gynostemium in orchids. Five MADS-box genes were exclusively expressed in the flower and probably have a role in floral morphogenesis.

The importance of this paper cannot be overemphasized because not only is it the first published whole genome of an orchid species but also a CAM plant, which has a carbon fixation pathway in photosynthesis that confers drought tolerance. It also shows the extent of small-scale duplications as well as a whole-genome duplication event in orchid evolution. According to our colleague in China, Luo Yi-bo, his team led by Liu Zhong-jian in Shenzhen has nearly finished sequencing the whole genome for ten other orchid species. We extend our hearty congratulations to them for this outstanding achievement. As you might expect, the pace will accelerate now that the first few are completed. We will easily have whole-genome sequences for a wide spectrum of orchids in the next year or two.

The next decade will bring even more staggering changes in methodology. What if we did not even have to amplify the DNA to sequence it? What if we did not have to add fluorescent labels to the nucleotides? What if we needed only a single strand of DNA

and then relied on other methods for detecting the nucleotides? First of all, we could save thousands of dollars in hardware, software, and reagents and bring the cost for a complete genome (human or otherwise) to below \$1000. The answer lies in nanotechnologies, the manipulation of matter at the scale of a nanometre (one-billionth of a metre).

Oxford Nanopore Technologies, Ltd. and also Pacific Biosciences of California, Inc. have produced commercial devices that read DNA bases directly by passing a single strand of DNA through a nanopore only about 2 nm in diameter. Nanopores can be biological and formed by a pore-forming protein in a membrane like a lipid bilayer, solid-state and comprising synthetic materials such as silicon nitride or graphene, or a hybrid of these constructed of a pore-forming protein set in synthetic polymer. As electric current flows through the pore, different DNA bases disrupt the current in different ways, letting the machine electronically read out the sequence. Because of the hairpin structure of DNA, both strands – sense and antisense – can be sequenced one after the other. Oxford Nanopore reported reading a stretch of DNA roughly 48,000 bases long. There are nanopore research groups and companies all over the world, mostly in the Europe and the United States but also as far-flung as Israel and New Zealand.

Oxford Nanopore's new product line will begin shipping later this year and is called a MinION, regrettably often confused with the cartoon characters Minions. It is a miniaturized portable device, roughly the size of two decks of cards, that can plug directly into a computer's USB port and is capable of sequencing small volumes of DNA as well as micro RNAs and proteins. Happily, it works on both PCs and Macs! A larger desktop machine can handle larger volumes; clusters of these machines will be used for sequencing whole genomes. Although the company has not yet announced pricing for the desktop machine, the portable version could cost less than £600. Just between us, it has been undergoing early beta testing in the UK, and there are still bugs in the system. One of them is that the error rate is still up to 15%, even with the dual read via the hairpin, mostly having to do with the base-calling software. The quality of the pores is also variable. However, these problems will surely be solved in the foreseeable future; compare the original iPhone with the iPhone 6 to see just how fast technology is corrected and expanded.

The result of all this new technology is a flood of data giving us a structural knowledge of genomes. But the task before future generations is building a functional knowledge of genomes, that is, how genes are expressed and regulated, which ones are silencers, which ones are promoters, and which ones are enhancers. Interpreting the data is without doubt the major bottleneck now and in the decades ahead.

Alec Pridgeon

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Upcoming Conferences

We welcome any news about future orchid conferences for promotion here. Please send details to Alec Pridgeon (a.pridgeon@kew.org) as far in advance of the event as possible, remembering that the *Orchid Research Newsletter* is published only in January and July of each year.

The Fifth Scientific Conference on Andean Orchids will be held 19-21 November 2015, on the beautiful and safe campus of the Pontificia Javeriana University (PUJ). Over the course of the Conference, one day of talks will each be devoted to systematics, ecology, and conservation science. Poster sessions in all three areas of investigation will supplement the lecture series. Simultaneous translation will be available for all talks. The *Proceedings* of the Conference will be published in an indexed journal dedicated to biodiversity research. Single-day and multiple-day tours will be available with expert guides, providing an excellent opportunity to see and photograph a diversity of spectacular orchids *in situ*. The webpage for the conference is www.andeanorchidconference.org, which is still under development, so please check back often.

The 12th Asia Pacific Orchid Conference will be held in Bangkok, Thailand, 19-17 March 2016. For up-to-date news, consult the website address (www.apoc12.com).

The 22nd World Orchid Conference will take place 5-13 November 2017 in Guayaquil, Ecuador, at the spacious Guayaquil Convention Center. There will be two concurrent sessions with simultaneous translation for each of the four days of lectures beginning Wednesday, 8 November 2017. Proposed abstracts for those wishing to speak at the Conference will begin to be accepted for consideration no earlier than 1 November 2015. Format for the abstracts and the mailing address for their submission will be relayed on the website (www.woc22.com) by 1 September 2015. Poster presentations, especially by students, are encouraged. Students whose posters are accepted may be eligible for scholarships toward their registration fees. Abstracts of all posters accepted will be included in the Conference *Proceedings*. More publicity will follow in subsequent issues of the *Orchid Research Newsletter* and orchid magazines among other publications.

News from Correspondents

Please submit any news about recently completed research, future research plans and needs, change of address, upcoming or recent fieldwork, etc. to Alec Pridgeon (a.pridgeon@kew.org). Graduate students are especially encouraged to share the subjects of their thesis or dissertation with the international community.

Recent Orchid Nomenclature

New orchid names may now be accessed on the IPNI website:

(www.ipni.org/ipni/plantsearch?request_type=search&output_format=query&ret_defaults=on). Click on "Show additional search terms" on the right-hand side of the screen. After the search page appears, type in **Orchidaceae** under family name and (for example) **2010-11-30** under "Record date" and "Added since." This will pull up a list of all names added to the IPNI database since 30 November 2010. Also be sure to check the World Checklist of Selected Plant Families (<http://apps.kew.org/wcsp/>) for accepted names and synonyms as well as for building your own checklists.

Recent Literature

We sincerely thank Paolo Grünanger for supplying new book titles and references from European orchid journals. If you are aware of any recent citations not listed here and henceforth, please send them – in the exact style below – to Alec Pridgeon (a.pridgeon@kew.org) for publication in the following issue (January or July). Write "ORN references" in the subject line of the email. Book citations should include author(s), date of publication, title, publisher, and place of publication (in that order). Journal titles should be spelled out in full.

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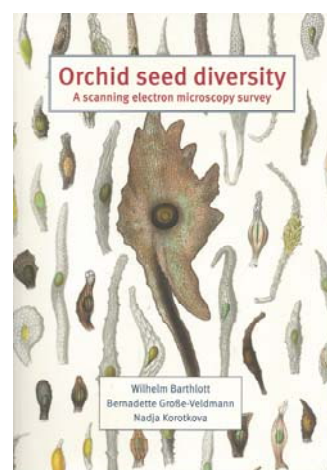
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Book Review

Barthlott, W., Große-Veldmann, B., and Korotkova, N. 2014. Orchid seed diversity: a scanning electron microscopy survey. Softcover, 245 pp. 620 micrographs, 33 figures. Botanic Garden and Botanical Museum Berlin-Dahlem, Berlin. Englera 32. ISBN 978-3-921800-92-8. Price: €25. For information on ordering, visit www.bgbm.org/englera.



Forty years in the making, this SEM survey of orchid seed morphology was begun by Bernhard Ziegler as a dissertation under the guidance of Wilhelm Barthlott. Ziegler (1981) examined the seeds of 310 genera and almost 900 species and assigned combinations of character-states into 20 types named after genera. Barthlott expanded the study here to 350 genera and 1100 species from 1400 collections, took 7000 micrographs for this monograph, and reduced the number of recognized seed types to 17. Nadja Korotkova analyzed the data in a phylogenetic context and compared them to published molecular trees. Bernadette Große-Veldmann continued the character reconstruction as her B.Sc. thesis. By any measure, this volume is a major achievement in orchid morphology.

The survey opens with summaries of current knowledge of orchid phylogeny based on molecular work, morphology of orchid seeds, descriptions of terminology and seed characters (shape, size, colour, number and shape of testa cells, testa cell pattern, anticlinal wall curvature, transverse anticlinal walls, intercellular gaps, surface structure of periclinal walls, cuticular layer, and modifications of testa cell corners). Following are descriptions of the seed types (reduced from 20 to 17 and all referenced to the various micrographs) and then materials and methods including character-coding.

The bulk of the volume is devoted to the illustrated survey arranged by subfamily, tribe, subtribe, and genus. For each genus, the authors provide descriptions using the characters listed above, additional literature references, and illustrations for most. Where no data are available for a recognized genus is made clear as a signal for future research. Regrettably, the authors did not always follow the classification presented in the six volumes of *Genera Orchidacearum* (*GO*) as they claim in the methods section, and so the reader will see several genera listed either in the classification or as unplaced that were synonymized in *GO* many years ago as the result of extensive DNA sequencing, e.g., *Odontoglossum*, *Osmoglossum*, *Palumbina*, *Rodrigueziopsis*, *Eulophidium*, *Cryptophoranthus*, *Physothallis*, *Physosiphon*, *Schomburgkia*, and *Nanodes*. Some of these genera were sunk either in volume 4 (2005) or volume 5 (2009) of *Genera Orchidacearum*, which the authors profess to have followed, so it is difficult to comprehend some of the generic usage here. Other genera such as *Cirrhopetalum*, *Epigeneium*, *Cadetia*, *Doritis*, and *Tainiopsis* were lumped either in volume 6 (2015) or by Chase *et al.* (2015) after this work appeared, so those inclusions might be understandable. For the same reason, the recently reinstated genus *Psychopsiella* (Oncidiinae) and new genera such as *Danxiaorchis* (Calypsoinae) are not listed.

Following the descriptions, illustrated by superb scanning electron micrographs, is the discussion of the systematic and diagnostic value of the characters. The authors conclude that combinations of characters are most useful, and they were adopted by Dressler (1993). Some single characters such as intercellular gaps and undulate anticlinal walls are synapomorphies for some taxa, but most are homoplastic even though consistent within their respective clades at the tribal and subtribal levels. This was also the overall conclusion reached by Molvray and Chase (1999), who also argued that classifying taxa by seed type can be misleading because it is the variable characters, not the types or syndromes, that can and should be used in phylogenetic analyses.

The book closes with 26 pages of phylogenetic trees with character reconstructions for the ones discussed in the book and finally the references. *Orchid Seed Diversity* is a remarkable contribution to orchid morphology that has been eclipsed in this age of molecular systematics. It remains to be seen what selective value these characters have (if any) and under what environmental conditions they evolved.

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