

## EARLY CACTUS EVOLUTION

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Cactus fossils do not exist (Becker 1960). The little physical evidence cacti have left us include a few seeds and spines sequestered in ancient packrat middens, and pollen released over the last 30,000 years (Van Devender 1988, 1990). Yet we want to know how cacti evolved and what their ancestors looked like.

At least since Darwin, biologists have been able to infer (and test!) ideas about the evolution of organisms. The key to unlocking the evolutionary puzzle lies in understanding basic evolutionary mechanisms, such as selection, inbreeding, and genetic drift, and from there using evidence from living taxa to test hypotheses about their ancestors. Such hypothesis testing is only as good as our evolutionary theories (which are under constant refinement) and the availability of empirical data (which continues to accumulate).

Phylogenetic reconstruction is one such example of evolutionary hypothesis formation. The phylogenetic trees that adorn pages of journals, including this one, are simply hypotheses about the evolutionary history (pedigree) of a group. Since they do not require fossils, phylogenies have emerged as one of the *only* useful tools for unraveling evolutionary histories of cacti, which can be constructed using morphological and/or molecular characters. Theory enters in various ways. For example, most phylogenies are trees, and not nets, because we assume that there is no horizontal gene transfer between distantly related individuals. With additional empirical data, either from extant specimens or fossils, we can test whether one phylogeny is better than another.

In the absence of fossils, phylogenies are essential for making evolutionary inferences. Ancestral (basal) taxa should reflect early evolution. Or at least basal taxa should reflect early evolution because they are believed to undergone fewer evolutionary changes, possibly at a slower rate, than derived taxa.

Good phylogenies matter. If *Ceraria* and *Portulacaria* are most closely related to traditional Didiereaceae than to Portulacaceae, as appears to be the case (Nyffeler and others pp 26–36), we may make erroneous inferences about the evolution of succulence in cacti and related families. This philosophical approach is not without problems, because it is often difficult to discern which characters are basal and which are derived, much as it is difficult to distinguish homology from analogy in evolution (that is, whether a pair of traits are identical by descent or only superficially similar via convergent evolution). For example, *Blossfeldia liliputana* is now often considered to be sister to the Cactoideae (Nyffeler 2002), sometimes in its own subtribe, Blossfeldieae (Crozier 2004; Butterworth 2006), yet it has a litany of highly derived characters (Barthlott and Porembski 1996).

The following five papers cover a lot of ground, from cacti to didierias to portulacas, from morphological to molecular data, from the mid-19<sup>th</sup> century to the present, and with experts from Europe and the Americas. There exist several major cactus architectures: (1) non-succulents (*Pereskia*), (2) leafless stem succulents (for instance, *Rhipsalis*), (3) leaf succulents (marginally *Maihuenia*, *Perskiopsis*, *Quiabentia*, and *Austrocylindropuntia*), (4) caudiciform and pachycaul succulents (*Melocactus*, *Pachycereus*), and (5) geophytes (for instance *Pterocactus*, *Ariocarpus*). As Nyffeler and others convincingly assert, “cacti [are] just another weird Portulacineae,” the relatively small suborder composed of the families Basellaceae, Cactaceae, Didiereaceae, and Portulacaceae—an idea seconded by others in this volume (including Griffith, pp 37–45). But what does this mean for our understanding of the early evolution of cacti? Is succulence a form of canalization, where a group is lacking developmental and phenotypic plasticity, as appears to be the case throughout the suborder Portulacineae? If so, by implication, *Blossfeldia liliputana* is either highly derived or an evolutionary dead-end, the latter scenario being most consistent with recent data. Griffith takes a different view, believing that reversions to non-succulence are relatively common. Epiphytic cacti may provide multiple examples of such reversions, albeit they have not lost all succulence. Atavisms (throwbacks to earlier evolutionary conditions) are widely recognized in plants and animals. Atavisms should be relatively common in groups with substantial gene duplication, in particular polyploidy. Gene duplications result in shutting down of regulatory genes (for instance, epigenetic si-

lencing, non-functionalization, and sub-functionalization; Adams and others 2003; Gorelick 2004; Lynch and Force 2000), which could cause reversions to non-succulence. There seems to be a general consensus, based on both morphological and genetic data, that the most basal extant cacti are in the genus *Pereskia*. However, apparent paraphyly of *Pereskia*, with *Maihuenia*, Opuntioideae, and Cactoideae embedded within it, continues to confound.

There are continuing disputes not just about whether succulence is ancestral or derived in cacti and related plants, but also concerning a suite of related characters, including leaf venation and wood anatomy (see Butterworth and Edwards, pp 46–53, and Griffith, pp 37–45). Succulent tissues can have very different wood architectures compared with non-succulent sister taxa (Mauseth and Stone-Palmquist 2001). Debates on cactus wood go back at least to Bailey's (1960–1968) classic studies, which were published in a 17-part series titled "Comparative anatomy of the leaf-bearing Cactaceae," and continued in more recent studies by Gibson (1973, 1976, 1977), Carlquist (1999), and Mauseth (Mauseth and Plemons-Rodriguez 1998). But no single character—neither wood, leaves, succulence, nuclear, or chloroplast DNA, photosynthetic mode, nor position of ovary—will provide sufficient insight into early cactus evolution. We will need a preponderance of evidence. We therefore include here a detailed, thorough systematic treatment of the three best-studied putatively-basal cactus genera: *Pereskia*, *Maihuenia*, and *Blossfeldia*. Leuenberger (pp 54–93) does not explicitly weigh-in on the questions of early cactus evolution, but instead compiles a wealth of objective information that others can use to test their hypotheses.

The questions asked here about early cactus evolution are not new (Metzing and Kiesling, pp 6–23). Systematics began with people being typological, believing that classification reflected platonic ideals. After Charles Darwin, especially with the modern synthesis, systematics instead examined adaptive traits, which were ostensibly molded by selection. Only in the last half century, with the advent of molecular techniques, has systematics instead sought out neutral traits, because they would be most informative insofar as convergent evolution would not muddle classification. The problem with morphological characters (and, to a lesser extent, molecular characters) is that it is not obvious whether a trait is adaptive or not, nor whether two traits are homologous. Extraction and separation of plant and animal proteins (allozymes) showed that there is lot more (selectively neutral?) variation in the biological world than anyone had previously suspected (Hubby and Lewontin 1966; Lewontin and Hubby 1966). DNA sequencing opened new avenues toward understanding evolution (Kreitman 1983), where most mutations are believed to be deleterious (the view from 1900–1965) or neutral (the view since the late 1960s), that is, not adaptive. Molecular information is thus independent of and often complementary to morphological data. Too bad we cannot yet map genotype to phenotype, but meanwhile we should never forget the importance of morphologically-based hypotheses and their underlying data, just as humans did not abandon stone once the stone-age ended (Gorelick 2002)—advice that the authors in this volume have nicely heeded.

Naively, one would yearn for a police-sketch of the first cactus. Was it tall and thin or short and fat? Was it spiny? Did it breathe during the day or night? What colors were its parts? A more sophisticated approach would be to ask what the *lineage* from which cacti evolved looks like. There will of course be lots of variation in the answers to these questions, because cacti (as well as all other plants in the order Caryophyllales) evolved from a large number of ancestors. Reticulation, the mixing of genes of two or more disparately related individuals, abounds in plants, which means that depiction of evolutionary histories as trees is quantitatively wrong. Nonetheless, we should be able to paint some sort of impressionistic portrait of early cacti and their suborder Portulacineae.

While there has never been a consensus—see the fluidity of ideas in Metzing and Kiesling or the ever-changing molecular phylogenies coming out of Rob Wallace's lab—it may be safe to say that the cacti, in particular, and the Portulacineae, in general, are taxa that have somehow managed to maintain the ability to evolve both succulent and non-succulent forms. Over the past 150 years, a large majority of scientists have believed that the ancestors of today's living cacti and their living basal ancestors were tall, thin, non-succulent plants. And while this view has not changed too drastically with the advent of DNA data, molecular work has generated a few more adherents to the idea that cacti evolved from short, fat, succulent ancestors (Lütolf 1969 as cited in Hershkovitz and Zimmer 1997; Griffith 2004).

Evolutionary biology is not, however, a beauty contest. At the end of the day, the minority might be correct. Read the following five papers on early cactus evolution and decide for yourself, bearing in mind that these papers represent only a stage set for further work. For better or worse, consensus on the nature of the earliest cacti, and whether their various morphological, anatomical, and molecular characters are truly ancestral, is still far off. Evolution has never been unidirectional or simple—in large part due to complex dynamics (of genes with each other and with the environment) and randomness (mutation and drift)—especially for cacti!

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