periment is between normal and rhombohedral pressure-temperature–quenched C_{60} at ambient conditions, 709 $Å^3$ and 603 $Å^3$, respectively. These effects would be partially offset by the reduced (negative) contribution from the entropy term *TS* associated with the onset of orientational order. Calorimetry experiments on RbC_{60} show small reversible heats of transition that are more likely associated with first-order orientational ordering transitions than with bond formation or large volume changes (*7*). A calculation of $(C_{60})_2$ dimers (*11*) shows no carbon distortions and an 8.5 Å center-to-center distance, equal to the undistorted C_{60} skeleton diameter (about 7 Å) plus a C–C single bond length, considerably smaller than the observed values. Also in the RbC_{60} case, polymer formation on cooling from 150°C competes with phase separation into C_{60} and R_3C_{60}; in the potassium analog, slow cooling leads to phase separation, whereas quenching produces a similar metastable orthorhombic structure but with a larger minimum inter-ball distance 9.61 Å (*12*). There is ample motivation to tackle these issues; particularly intriguing is the possibility that the mono-anion polymer is metallic while the mono-anion cubic van der Waals solid is not.

It is also probably true that we have not heard the last from practitioners of the more traditional polymerization reactions. The ever-growing list of mono-functionalized fullerenes will certainly present opportunities for rational polymer synthesis using solution techniques. In the best of all possible worlds we will end up with two families of fullerene polymers: the all-carbon versions described here and those originally envisioned with heteroatom linkages between molecules.

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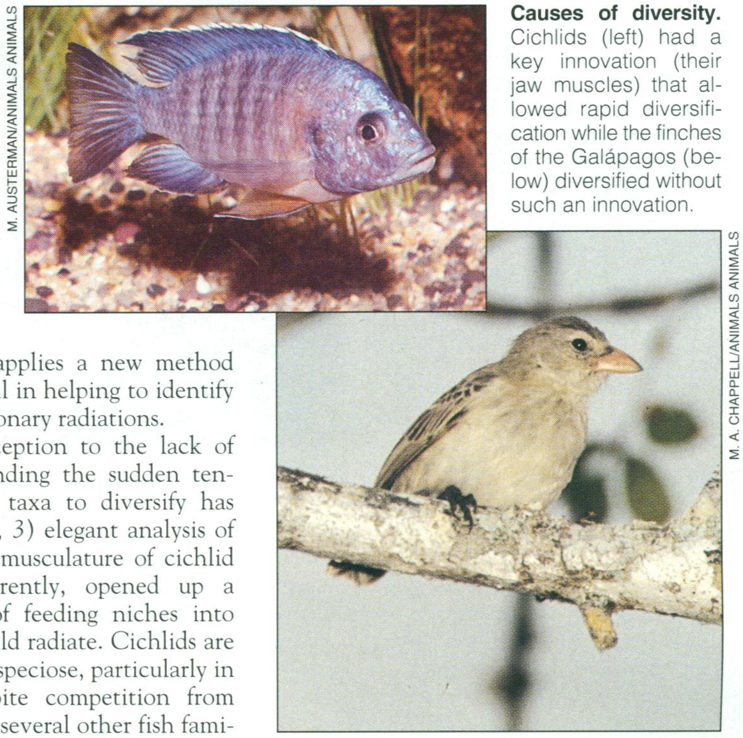
Getting to the Roots of Flowering Plant Diversity

Sean Nee and Paul H. Harvey

The fossil record tells us that speciation and extinction rates have, on occasion, changed dramatically. Much has been written recently about possible causes of mass extinctions, particularly the one at the close of the Cretaceous period, which has been claimed to be associated with the impact of a sizable asteroid and the loss of humankind's beloved dinosaurs. Rather less attention has been paid to the reasons for suddenly increased rates of diversification in particular lineages. A paper by Sanderson and Donoghue in this week's *Science* (*1*) applies a new method that may prove useful in helping to identify the causes of evolutionary radiations.


M. AUSTERMAN/ANIMALS ANIMALS

M. A. CHAPPELL/ANIMALS ANIMALS

Causes of diversity. Cichlids (left) had a key innovation (their jaw muscles) that allowed rapid diversification while the finches of the Galápagos (below) diversified without such an innovation.

One notable exception to the lack of success in understanding the sudden tendency of particular taxa to diversify has been Karl Liem's (*2*, *3*) elegant analysis of changes in the jaw musculature of cichlid fishes which, apparently, opened up a whole new range of feeding niches into which the group could radiate. Cichlids are now extraordinarily speciose, particularly in African lakes, despite competition from species belonging to several other fish families. The change in jaw musculature in cichlids may therefore have been a so-called key innovation. Such key innovations are not prerequisites for adaptive radiations. For example, there was not necessarily anything special about the species of finch that originally invaded the Galápagos Islands and led to the radiation known as Darwin's finches (*4*). Notwithstanding the occasional importance of such vicariance events or changes in the environment that may turn a mundane character into a key innovation, it is natural to seek traits associated with the origin of a radiation. The first step in such an analysis is to pinpoint the origin of the radiation as accurately as possible. One reason is that the number of candidates for the key innovation can be minimized if the number of differences between a radiating taxon and its nonradiating relatives can be reduced. Because closest relatives generally share the greatest number of characters, the comparison should be made between the closest relatives possible. Sanderson and Donoghue provide a powerful and elegant procedure for achieving that end.

The aim is to identify nodes in a phylogenetic tree from which one daughter lineage shows higher rates of branching than the other. The source material, then, is the number of descendent clades arising from each daughter branch of a node. Even if two clades do not differ in features promoting diversification, large inequalities in clade size can arise by chance, prompting one to ask whether observed differences are statistically anomalous with reference to a particular null model. Sanderson and Donoghue are, in essence, asking two questions. First, are the angiosperms significantly more diverse than their sister group the Gnetales? Second, is there a significant difference in diversity between the two most basal angiosperm clades? A positive answer to both questions, which is what they obtain, implies that some angiosperms acquired features or inhabited environments

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that promoted diversification after angiosperm diversification had already begun.

The analysis performed, maximum likelihood estimation of the paramaters of a pure birth process, is sophisticated and is adapted to deal with the uncertainties in relative timings of the first bifurcation in the angiosperm clade. The intricacies of the analysis, and the assumption that plant lineages have never gone extinct, should not raise doubts about the robustness of Sanderson and Donoghue's conclusions because those same conclusions can be drawn from a simpler analysis. Under the null hypothesis that lineages do not differ from each other in any feature affecting diversification, if we have a number of parent lineages at a particular point in the past, and a larger number of progeny lineages in the present day, the distribution of progeny among the parents will follow a distribution well known to ecologists as MacArthur's broken stick distribution. The result makes no assumptions about how the clades have been growing—whether, for example, lineage extinction rates are high or zero. Nor does it matter whether the progeny represent only a phylogenetically random sample of the clade, rather than the entire clade (5).

JANE GRUSHOW/GRANT HEILMAN

RUNK/SCHOENBERGER/GRANT HEILMAN

Flowering plants diversified after their origin. (Top) Bull bay, southern magnolia (*Magnolia grandiflora*). (Bottom) Water lily (*Nymphaea sp.*).

In the special case of two ancestral lineages, which is relevant to making sister group comparisons, all possible divisions of the observed total number of species between the two sister groups are equally likely (6). So, if the larger group has r species and the sister group has $n - r$ in a clade of size n, the probability of an inequality of clade size as large as or larger than that observed is simply $2(n - r)/(n - 1)$. If that statistic is applied to the data in fig. 2 of Sanderson and Donoghue's paper by simply comparing the angiosperm diversity with that of the Gnetales, even discarding the diversity of the putative basal angiosperm clade (such as the Magnoliales in their fig. 2A) to get a conservative test, we find that, indeed, angiosperms are more diverse than Gnetales. Comparing the diversity of the two basal angiosperm sister groups, we find a significant inequality whether we use the Magnoliales, the Nympheales, the Chloranthaceae, or the Ceratophyllaceae for comparison. Hence, there has been an increase in angiosperm diversification rates after the angiosperms had started to diversify.

There is one small but notable difference between the results of the simple analysis performed here and the more sophisticated one reported by Sanderson and Donoghue. The simple analysis finds the Magnoliales to be significantly less diverse than the rest of the angiosperms ($P = 0.024$), whereas their's does not. The source of the discrepancy is not obvious but may derive from the numerical procedures they used.

As molecular phylogenies become more common, we can expect that studies of lineage diversification will exploit the additional information that they contain about the relative timings of nodes (5). Sequence divergence provides information about relative times, and the phrase "molecular clock" no longer contains the assumption that lineages are endowed with synchronized metronomes. Imperfect information is not the same as no information, as those who exploit the fossil record are well aware. Increasingly sophisticated techniques, often based on maximum likelihood methods allied to Sanderson and Donoghue's, are being developed to make the best use of that information (7).

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