

Supertrees versus Godzilla

Dinosaurs have a widespread, almost universal appeal. Yet, in spite of the attention that they attract, no comprehensive phylogeny for the group exists. Much of this can be traced to the fragmentary nature of fossil material, leading to a high proportion of missing information and difficulties in drawing homologies, especially between specialized structures. 'Jurassic Park' notwithstanding, DNA information for dinosaurs is unknown and likely to remain so. As a result of these difficulties, estimates of dinosaur phylogeny tend to be as fragmentary (both in size and taxonomic coverage) as the data on which they are based. Moreover, many of these estimates are based on subjective, nonrigorous interpretations of the data. It comes as little surprise perhaps that these latter estimates often conflict with one another.

How then to derive a comprehensive estimate of dinosaur phylogeny? To accomplish this, Pisani *et al.* have taken a different approach in a new paper [1]. Dinosaur phylogenies based on a rigorous

methodology (e.g. cladistic analysis) do exist, but tend to be small and restricted in scope. However, because some species are found in more than one tree (i.e. the trees 'overlap'), the trees can be combined as a phylogenetic supertree. This was the method used by Pisani *et al.*, who combined 126 cladograms to produce a supertree of 277 dinosaur genera. The supertree is not complete – very poorly described genera (*nomina dubia*) were necessarily omitted – but it is by far the most inclusive phylogeny ever presented for dinosaurs. As such, it resolves many controversies in dinosaur systematics, both for taxa that are more (e.g. Sauropodomorpha or Iguanodontidae) and less familiar (e.g. Melanorosauridae or Therizinosauroidea). Three major polytomies (one within Sauropoda and two within Theropoda) highlight relationships that continue to be contested or poorly investigated.

Like any phylogeny, Pisani *et al.*'s supertree is not the final word in dinosaur systematics. New fossil discoveries and further primary

cladistic analyses mean that the dinosaur supertree will always be incomplete and in need of revision. In time, a species-level supertree should also be feasible. However, the current dinosaur supertree is still a remarkable step forward in our understanding of the global systematic relationships of this group. Many large-scale questions about dinosaur biology can now finally be asked in a phylogenetic framework. The supertree also produced a somewhat unexpected, but reassuring result. Its well-resolved nature points to a higher level of agreement concerning dinosaur systematics than might have been suspected previously. Thus, in the battle to produce a comprehensive phylogeny of dinosaurs, Round 1, it appears, belongs to the supertrees.

1 Pisani, D. *et al.* (2002) A genus-level supertree of the Dinosauria. *Proc. R. Soc. Lond. Ser. B*
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Optimal foraging and phenotypic plasticity in plants

Do plants forage? The resources that plants consume come from various sources: water and nutrients from the soil, nitrogen and phosphorous from microbial symbionts, light from the solar radiation and, in the case of carnivorous plants, nutrients from animal prey. And, in the heterogeneous world in which plants live, phenotypic plasticity comes in handy: stems elongate in response to shade from neighbors and defenses are induced following herbivory. Recently, biologists have developed conceptual models and experiments that show the use, by plants, of phenotypic plasticity, and yes, even optimal foraging, in terms of ramet-level specialization, for maximal resource acquisition. In a new paper, Ellison and Gotelli [1] show a similar pattern for a carnivorous plant, extending our knowledge of phenotypic plasticity in plant-resource acquisition.

The northern pitcher plant *Sarracenia purpurea* inhabits open areas in bogs and fens; such nutrient-poor sites are thought to favor carnivory in plants. The high carbon:nitrogen (C:N) ratio of such sites is purported to allow for the investment of excess C in prey-capturing (i.e. N-capturing)

organs. Over three years of field experiments, Ellison and Gotelli show that additions of N to natural plant populations in New England led to a reduction in prey-capturing pitchers (modified leaves) and an increase in phyllodia, or leaves that are specialized for C capture. Indeed, at increasing N levels, not only did the capacity for carnivory decrease, but the maximum photosynthesis rates also increased linearly. Results were consistent when nutrients were added to individual plants, whole plots, and when the authors surveyed the natural correlation between nitrate levels and indices of pitcher size across 26 bogs. The concordance of manipulative experiments with the observed geographical pattern is a satisfying indication that the environment is a key player in the distribution of phenotypic variation in resource acquisition.

These results are similar to recent demonstrations of resource quality affecting the relative consumption of different trophic levels in omnivorous animals. But, other than the fantastic natural history, what is the real advance here? First, the strong influence of the biotic and abiotic environment on apparently adaptive

phenotypes, even in organisms that appear to live in homogeneous environments, reinforces the view of economy in nature and the importance of phenotypic plasticity. Second, the results are consistent with Givnish *et al.*'s C–N-based hypothesis for the origin of botanical carnivory. Carnivorous plants are not only found primarily in sunny, moist and nutrient-poor sites, but carnivory is also reduced when these conditions are ameliorated. This phenotypic reallocation can occur within a single growing season, consistent with thinking of the plants as foragers. Finally, from the perspective of global change, Ellison and Gotelli propose that the pitcher:phyllode ratio could be a useful indicator of local rates of N deposition. This study therefore represents an important contribution linking theory, description and experiment, and potential application.

1 Ellison, A.M. and Gotelli, N.J. (2002) Nitrogen availability alters the expression of carnivory in the northern pitcher plant, *Sarracenia purpurea*. *Proc. Natl. Acad. Sci. U. S. A.* 99, 4409–4412

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