Evolution by leaps and bounds

One of the most perplexing features of evolutionary biology to those encountering it for the first time is the apparently tedious, stepwise process of darwinism. How could the diversity of life be produced by the steady accumulation of tiny heritable differences? The most obvious answer is that given time enough, all things are possible, even by tiny steps. But perhaps evolution can take shortcuts, leaps instead of steps. Two discussion papers in *Evolution and Development* review potential mechanisms for taking evolutionary leaps – macromutation and modularity[1,2].

R.A. Fisher's microscope analogy has provided a persistent image of change by tiny modifications: as you get closer to the correct focus, a small change will have a fair chance of being beneficial, but a large change will almost certainly make the focus worse. Similarly, as a trait approaches some adaptive optimum, micromutations of small effect may be selected for, but macromutations of large effect are likely to be deleterious. But how should macromutations be defined? Clarke and Arthur explore the example of chirality. Most snail species are characterized by shells that coil to the right (dextral). But the evolution of left-handed shells (sinistral) has occurred in hundreds of species. In some species, which are polymorphic for both dextral and sinistral shells, shell chirality is determined by a single genetic locus. Reversing shell coiling has a large phenotypic effect, requiring re-organization of many anatomical features, yet it arises from a single developmental change, the orientation of the first cleavage in the egg. So whether change in chirality constitutes a macromutation depends on whether you consider the origin of the trait (single genetic change) or the consequences (broadscale phenotypic change). Clarke and Arthur point out the poverty of a circular definition, where a macromutation is considered one with a small chance of being favoured by selection, or of a definition based on frequency of occurrence. They suggest the type of mutation is more important than the magnitude: mutations that 'stretch' an existing structure are more likely to contribute to evolutionary change than mutations that create a new structure.

In contrast, evolutionary development has explored macromutational origins of major phenotypic features. For example, if *Hox* genes define body plan modules then perhaps structures such as limbs can be acquired or lost in single genetic events. The contribution of developmental modularity to evolution is reviewed in Raff and Raff's report on a symposium on 'Modularity in Development and Evolution'. Although the participants of the symposium could not provide a precise definition of modularity, they agreed that it spanned many levels of organization, from genes to cells to structures to suites of phenotypic traits. Some great leaps in evolution involve acquisition of modules, such as the rapid evolution of antibiotic resistance in bacteria by lateral transfer of genes. Yet if modularity is too broadly defined, it becomes an empty concept, encompassing virtually all evolutionary change (for example the losses, co-option and modification of reptile jaw bones into mammalian jaw and ears). After all, no one, including Darwin, ever said that in the stepwise modification of traits under natural selection, some steps would not be bigger than others.

1 Clarke, B. and Arthur, W. (2000) What constitutes a 'large' mutational change in phenotype? *Evol. Dev.* 2, 238–240
2 Raff, E.C. and Raff, R.A. (2000) Dissociability, modularity, evolvability. *Evol. Dev.* 2, 235–237

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Different tests, different conclusions: evolutionary trees

A phylogeny obtained from molecular sequence data will often conflict to some extent with preconceptions based on taxonomy or other types of characters. In this situation, it is useful to estimate whether we would be able to reject a topology that is consistent with other sources of information, given the data at hand. Previously, many systematists have used the Kishino–Hasegawa test to compare an optimal topology with constrained alternative topologies. The assumptions of the Kishino–Hasegawa test, however, are violated when one of the topologies being tested is known to be optimal *a priori* to the test being performed. Although this problem was first noted in 1996, it is only more recently that alternative parametric and nonparametric tests have been designed to circumvent it.

The recent paper by Goldman *et al.*[1] is a highly accessible review of the problems facing previously implemented maximum likelihood tests of topology, and it provides descriptions of alternative parametric and nonparametric tests. Goldman *et al.* use an intuitive example of two sprinters to explain why the Kishino–Hasegawa is potentially misleading when applied incorrectly. Also of interest to empirical systematists will be the results from analyses of the two data sets: HIV *gag* and *pol* sequences, and mammalian mitochondrial amino acid sequences. Goldman *et al.* clearly illustrate the massive difference in statistical power between the nonparametric and parametric tests. In the case of the HIV sequences, using a test based on parametric bootstrapping, they were able to reject their null hypothesis with an extremely small *P* value. Using the nonparametric Shimodaira–Hasegawa test, however, they were unable to reject the null hypothesis, with a relatively large *P* value. Goldman *et al.* then discuss various explanations for this apparent difference in statistical power. These results will be of great interest to systematists because the two basic statistical approaches can imply radically different biological conclusions.

This paper is likely to have a large impact on the way systematists test their hypotheses, and will prompt the reassessment of many studies where overconfidence might have been given to the results of a test because of inappropriate statistical assumptions. Goldman *et al.* end by emphasizing that researchers must think very hard about the precise hypotheses that are being tested, because the nature of these hypotheses can have a large impact on the type of test that is required and, therefore, the ultimate biological conclusions. As pointed out by the authors, further research is now needed into the statistical and biological assumptions of maximum likelihood tests of topology.

1 Goldman, N. *et al.* (2000) Likelihood-based tests of topologies in phylogenetics. *Syst. Biol.* 49, 652–670

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