Not-so-early bursts and the dynamic nature of morphological diversification

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In *Wonderful Life*, Stephen Jay Gould attempted to explain how the bizarre animal fossils from the 500 million-y-old Burgess Shale fauna teach a valuable lesson about the nature of morphological evolution (1). Finding such a remarkable diversity of body plans so early in the history of metazoan life should not be surprising, he argued, for this is an all-too-common pattern. Rather than gradually accumulating, as earlier iconography tended to illustrate, morphological diversity has often generated rapidly during the early phases of clade history. After an initial and rapid exploration of possibilities, successful forms proliferate while those less fortunate are quickly erased by extinction. Gould's inverted iconography is, in fact, quite consistent with long-standing ideas in paleontology regarding early rapid morphological diversification in higher-level clades (2, 3), and this concept has since become entrenched in modern macroevolutionary biology as the early burst model of adaptive radiation (4). In PNAS, Hopkins and Smith (5) investigate rates of morphological evolution in the post-Paleozoic fossil record of echinoids (sea urchins, sand dollars, and their kin). The authors find that there is no evidence for an early burst of morphological innovation

in echinoids as a whole. Instead, Hopkins and Smith document a third way: echinoid evolution is characterized by slow rates and constraints in stem lineages, but later pulses of evolutionary bursts are associated with shifts in feeding morphology.

Paleontologists have traditionally used measures of raw morphological variation, referred to as disparity, through time to make inferences about underlying rates of evolutionary change. These approaches work because, all else being equal, faster rates of change result in greater disparity, whereas slower rates result in less disparity. By computing disparity in different time intervals and looking at where peak disparity is achieved, it becomes possible to make inferences about how evolutionary rates have changed through time (6). Disparity tends to peak a little over halfway through a clade's lifetime under constant rates of evolution (Fig. 1A), whereas early rapid rates that slow through time result in much earlier peak disparity (Fig. 1B). This latter pattern seems to be very common in the fossil record (7), suggesting that early bursts really are the rule. The problem is that different evolutionary processes can generate similar disparity profiles. For example, we could also obtain an early peak in disparity if rates are constant,

but the range of possible evolutionary outcomes is constrained (Fig. 1C), perhaps by ecological or developmental factors (8). In this scenario, an early peak in disparity reflects saturation of morphospace, rather than early rapid rates of evolution, meaning the distribution of trait values among species will look very different. It's also difficult to predict the shape of a disparity profile when evolutionary dynamics within a particular clade are more heterogeneous.

These limitations can be overcome by directly estimating rates of evolution along the branches of a phylogenetic tree. The last 15 y have seen an explosion of such methods for examining rates on phylogenetic trees, in particular using molecular phylogenies of extant species. At their most complex, these methods allow for the comparison of evolutionary scenarios where rates can vary along individual branches (9, 10), or even for distinct evolutionary regimes to occur in different parts of the tree (11). What we have learned about early bursts from these approaches is rather different from results based on disparity in the fossil record. Although a few clades show evidence for early rapid morphological evolution, the vast majority do not, and even constant-rate models seem preferable (4). Hopkins and Smith (5) take advantage of a well-resolved phylogeny of living and fossil echinoid families, spanning 250 million years, to ask whether analysis of a phylogeny including extinct species could yield support for the early burst model. Most phylogenetic methods for inferring evolutionary rates are only applicable to single, continuously varying traits, such as body size, but Hopkins and Smith (5) wanted to infer evolutionary rates using a matrix of discretely coded characters spanning the entire echinoid body plan. They therefore used a phylogenetic approach that computes rates from the number of inferred character state transitions along branches of a time-calibrated phylogenetic tree (12). Although this approach meant that the authors were not

Fig. 1. Morphological evolution on the same phylogeny under (A) a constant rate of evolution, (B) an early burst of evolution, and (C) a constant rate of evolution in a bounded space. The red dashed lines show the approximate position of peak disparity. (A–C) Lower shows how evolutionary rate varies through time for each of the same processes. Despite earlier peaks in morphological disparity for both early-burst and bounded evolution models, evolutionary rates only vary in the former.

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able to directly compare the fit of alternative modes of evolution, the advantage over disparity-based approaches remains; by directly computing rates rather than extrapolating them from disparity profiles, Hopkins and Smith (5) were able to test whether evolutionary rates were faster early in echinoid history or else showed some alternative pattern. In the process, the authors were able to obtain a far more-nuanced understanding of how morphospace was explored than has previously been possible for fossil clades.

Hopkins and Smith (5) found no evidence for an early burst of morphological evolution in echinoids; in fact the opposite appears to be true, with rates becoming faster from the Jurassic onwards compared with earlier periods in their evolutionary history. Although this finding seems to initially validate the conclusions, based on living groups, that early bursts are uncommon, examination of rates through time within subclades of echinoids reveals two instances of rapidly accelerating and subsequently declining evolutionary rates. These peaks are nested within a clade, called the irregular echinoids, that includes the sand dollars and heart urchins. Furthermore, each of these nested bursts seems to be associated with the evolution of novel feeding strategies: the origin of deposit-feeding irregular echinoids in the Jurassic and of sieve-feeding sand dollars in the Eocene. This pattern is consistent with the idea that ecological opportunity generates bursts of morphological innovation whenever it occurs, regardless of where in clade history that might be (13, 14). Indeed, a few recent studies examining patterns of species diversification using molecular phylogenies of extant species have noted similar nested bursts associated with the evolution of key innovations or novel ecological strategies (15, 16). It's not clear what the specific ecological drivers were for the bursts of ecomorphological innovation found in irregular echinoids. What Hopkins and Smith (5) clearly show though, is that although bursts of morphological or lineage diversification may occur at any time during a clade's history, our ability to detect them is wholly dependent on the scale at which we look.

Application of phylogenetic rate estimates to a phylogeny of fossil species also yields valuable information about why some

lineages fail to diversify morphologically, even when ecological opportunity presents itself. When Hopkins and Smith (5) plotted echinoid morphological variation through time, they found that modern day regular echinoids, the sister lineage to sand dollars and heart urchins, have failed to diversify

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beyond the range of forms found in their ancestors over 200 million y ago. Even at low rates of evolution, regular echinoids should have expanded their range of variation somewhat over this time frame. This finding suggests instead that their evolution was constrained to repeat the same set of outcomes again and again. The constraint may have been ecological; competitive exclusion can limit the width of the adaptive zone a clade occupies and reduce phylogenetic signal in its trait values (17). However, the fact that regular echinoids failed to diversify

in same way as irregulars in the Jurassic and Eocene suggests instead some other limit to their evolvability. The late evolutionary theorist Leigh Van Valen famously remarked that evolution is the control of development by ecology (18). It could be that regular echinoids lacked the developmental machinery to produce morphologically novel forms. Alternatively, something about the regular echinoid body plan may mean that even minor changes in form cause functional inviability, limiting their potential to innovate. Regardless, Hopkins and Smith's (5) results emphasize that by focusing only on ecological opportunity, we may miss the importance of development in generating or limiting diversity over macroevolutionary timescales.

That early bursts of morphological diversification might not always occur early in clade history should probably not surprise us but, as Gould (1) so persuasively argued, iconography can be incredibly compelling. Hopkins and Smith (5) provide a striking demonstration of how significant bursts of morphological evolution can be completely missed when viewed exclusively from the perspective of these models. In doing so, Hopkins and Smith highlight the important role that phylogenetic studies of the fossil record must inevitably play as we strive to gain a new perspective on the tempo and mode of macroevolution.

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