NEWS AND COMMENTARY

Parallel evolution

Hearing echoes

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For animals, belonging to two most distinct lines of descent, may have become adapted to similar conditions, and thus have assumed a close external resemblance; but such resemblances will not reveal—will rather tend to conceal their blood-relationship.

Darwin, On the Origin of Species, 1st ed., p. 427

How repeatable is evolution? Not so long ago, the answer to this question would have told us as much about the scientist as it does about evolution: surveying the broad brush of biodiversity, the naturalist sees parallelism everywhere. In the sky, there are flying birds, gliding mammals and even true flying mammals. In the sea, there are fishes, seals, whales and dolphins. Not so, says the molecular taxonomist: everywhere in the genome, the tick-tock of the molecular clock tells us that species are splitting away from each other. The convergence that the naturalists see everywhere, according to the molecular taxonomist, is nothing more than an evolutionary echo. Adaptations may be shaped by the hand of selection for sure. But mutations are, as we all know, random.

A readjustment may well be in order, thanks to recent studies by Li *et al.* (2010) and Davies *et al.* (2012) in this current issue. In contrast to traditional views that convergent evolution reflects only functional but not mechanistic convergence in achieving analogous adaptations, molecular evolutionary biologists use the term ‘parallel evolution’ to convey the mechanistic parallelism between independent cases. This molecular parallelism can be both deep and far-reaching: the same recurring mutations—the equivalent of hitting evolutionary jackpots (twice)—appear in different echolocating bats from distinct origins. Wait! Make that different echolocating

bats and whales from distinct origins. What’s more, this phenomenon does not occur just once, but was found in as many as four (perhaps more?) genes implicated in hair-cell formation, the same cells that are missing among whom hearing is high-frequency-challenged (Li *et al.*, 2010; Liu *et al.*, 2011; Davies *et al.*, 2012).

How would these evolutionary echoes be represented by molecular trees, the favourite tool of the molecular taxonomist? Because the guiding principle behind all trees is Ockham’s razor, which strives to use the fewest possible steps to describe as much of the data as possible, the otherwise reliable tool commits an oversimplification (Figure 1). In the topsy-turvy world of parallel molecular evolution, forcing the lowest number of mutations at genes controlling high-frequency-hearing places all the distantly-related echolocating bats together, leaving the non-echolocating old world fruit bats dangling out there on their own branches. At the gene *Prestin*, where this phenomenon of extreme parallel evolution was originally reported, even echolocating whales join the gaggle before the fruit bats get a look in (Figure 1, middle panel). The two additional genes, described by Davies *et al.* (2012), recapitulate the results at *Prestin*: the pattern is more widespread (two additional genes and more species) but less sharp (fewer recurring mutations, less discrepancy between the gene and the species tree, Figure 1, right panel).

Davies *et al.* (2012) raise an interesting question: how often do we hear evolutionary echoes like this? Indeed, the picture may be emerging that convergent phenotypes may often correspond to parallel mechanisms down to the finest molecular level, as unlikely as that proposition may appear at first glance. Surely, the chances of evolution ending up favouring the same mutation(s) will be vanishingly small if thousands of viable alternatives exist. But when potentially advantageous

mutations are limited (comparatively few hearing genes?), selection may be stuck with choosing among the few strong alternatives. Under such conditions, theoretician Allen Orr argues that having organisms independently hitting upon the same evolutionary solution may not only be plausible but also be surprisingly probable: $P=2/(n+1)$, n being potentially advantageous mutations (Orr, 2005).

Painstaking experimental evolution work in viruses, bacteria and yeast provides some of the strongest empirical support for rampant molecular parallelism (see review by Elena and Lenski, 2003). Natural examples, like those detected by Davies *et al.* (2012), have also started to accumulate, showing that parallelism is not just a laboratory curiosity. Parallel mutations in multiple species at the same genes conferring insecticide resistance are not only common but have also arisen rapidly (French-Constant *et al.*, 2004). Melanic or light-coloured mutants are common enough that parallel mutations in melanocortin receptor (*MclR*) were found in blond beach mice and woolly mammoth (Römler *et al.*, 2006)! As evolutionary genetics increasingly attains molecular resolution, striking examples keep popping up everywhere. The ion channel Nav1.4a/b that produces electric discharges in electric fish suggests, like echolocation, that parallel evolution can be found in the most sophisticated evolutionary innovations (Zakon *et al.*, 2008). It does not have to be restricted to the coding region either. In pelvic-reduced sticklebacks, similar mutations that delete the same distant *cis*-acting enhancer have occurred at least nine different times, showing remarkable precision and repeatability (Chan *et al.*, 2010). If we include cases where pre-assembled adaptive mutations can be passed around as favoured—but rare—alleles (that is, parallel selection favouring the same standing variants rather

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Figure 1 Tangled branches. Parallel mutations at the hearing genes *Prestin* (Li *et al.*, 2010), *Tmc1* and *Pjvk* (Davies *et al.*, 2012) cause the trees, built from its coding sequences (middle and right panel), to mistake long-diverged echolocating species as close relatives (left panel).

than parallel mutations in independent lineages), parallel evolution can be positively prevalent, as evidenced by the many loci controlling parallel marine–freshwater adaptations in sticklebacks (Jones *et al.*, in press).

Indeed, such evolutionary echoes keep emerging from all corners: those naturalists who see parallel adaptation everywhere, armed with fresh molecular evidence, may now feel vindicated. Are we hearing the rumbles of an evolutionary revolution in the making then? Not so fast: it is important to take it all in context. After all, molecular taxonomists, despite often having to contend with the vagaries of conflicting gene trees from different genes, still find that much of the genome reliably reveals the history of descent connecting species. It may be only fair to point out that spectacular parallelisms in nature have a much easier time getting noticed and published. Rather than asking how common is parallel evolution, perhaps it would be better to celebrate the astounding adaptive feat of these organisms, and ask oneself, in the face of evolution's repeat

performances and endless resourcefulness, shouldn't we have seen/heard it coming?

CONFLICT OF INTEREST

The author declares no conflict of interest.

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