

Prokaryote phylogenies, lateral transfer, and
ontic-epistemic confusion¹

Leigh Van Valen
Department of Ecology and Evolution
University of Chicago
1101 E. 57 St.
Chicago, Ill. 60637

As is now recognized, lateral transfer of genes is quite common among prokaryotes. As a result, actual as well as inferred phylogenies of different genes from the same species can differ widely. Such discrepancies contribute importantly to divergent phylogenies inferred for prokaryotes, although some classes of genes appear to be less successful invaders than others and are therefore more reliable indicators of phyletic relationship.

Two related proposals have taken the prevalence of lateral transfer as the basis for radical reconceptualization. Ford Doolittle (1999; Gogarten et al., 2002) and others hypothesize that, especially in earlier prokaryote evolution, there were no actual phyletic lineages at all. Instead, there was a somewhat subdivided universal population, with a continuity of gene flow throughout. As an extension of an earlier viewpoint of his, Woese (2000, 2002) envisions a similar but less organized stage before the origin of cells like those we know, with the earliest divergence of extant organisms marking the end of such "communal" evolution in "common ancestral chaos."

As a side comment, there is no justification for positioning the end of the hypothesized chaos so late. How many branchings occurred earlier but left no extant survivors is of course unknown, and setting this value at 0 is merely an extreme possibility. An evolutionary interval of transition from a pre-cell grade to a fully cellular grade, from which the initiator of the clade of extant organisms later emerged, would be the parsimonious inference.

In an evolutionary interval of universal partial panmixia, as with less extreme scenarios of lateral transfer, general adaptations would spread widely because for them there is the equivalent of only a single evolving population. (Special adaptations could be prevented from spreading by sufficiently strong adverse selection outside their proper adaptive zones.) To the extent that lateral transfer is restricted, this scenario grades into the parsimonious one of the preceding paragraph.

So. Does appreciable discordance among inferred, and even real, phylogenies of different genes actually give evidence against the occurrence of multiple evolving lineages? If one looks a bit more closely, the apparent evidence evaporates.

Consider an actual evolving lineage, such as that of *Escherichia coli* today. Genes wink in and wink out, the old and the new being retained against entropy to the extent that they

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are advantageous enough in common enough circumstances. Newly acquired segments of DNA, like new mutations, are almost always eliminated. Occasionally, though, a newly inserted gene or other invading element will survive even though it had not been previously selected to do so in this lineage.

Now generalize over a large set of such successful insertions. Each one occurred in a specific lineage, but the lineage itself maintained its identity during the process. The only situation where specific lineage continuity would be in question is with the merger of two previously distinct lineages, as with the origin of the eukaryotic cell, and even in such cases each earlier lineage would continue as the resulting one.

The perspective just outlined doesn't eliminate the possibility that there was once (or more than once) a universal semi-panmixia, of course. What it does claim to do is eliminate the phylogenetic evidence for such a phenomenon.

The above argument exemplifies a genuinely fundamental distinction which is surprisingly often overlooked, and not just in the evolutionary half of biology. Philosophers call it the ontic-epistemic distinction. Roughly, ontic refers to the world itself, and epistemic refers to our ways of inferring what the world is like — reality and evidence, so to speak.

In the present case there is evidence for a phylogenetic pattern involving horizontal transfer on a large scale. Such transfer can happen, however, without a universal semi-panmixia, and in fact that appears to be the situation today. We may or may not be able to infer accurately the actual lineages of prokaryotes during, say, the Phanerozoic, but they were there.

Ontic-epistemic confusion is also prevalent at the level of concepts. Criteria for recognizing examples of homology, species, life, and so on are sometimes used to define the concepts themselves. In some cases definitional criteria are also directly useful in inference, but the appropriate direction is from the concept to the evidence, not the other way around.

Similarly, in ecology it's common to dismiss the possibility of there being more niches in situations where there are more species, simply because niches are most easily recognized by their having occupants.

References

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