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Questioning the Tree of Life

The Tree of Life (ToL) is conceived as a unique representation of the evolutionary relationships between species, depicting the true evolutionary relationships amongst organismal lineages as a single ever-bifurcating pattern. It takes the form of nested hierarchies that are presumed to be the consequences of descent with modification and speciation. All life-forms, past and present, are assumed to have a single place in this one true tree, and all future organisms are also anticipated to find their place as the tree continues to grow. Over the last several years, the increased availability of molecular data from many organisms, especially genomic sequences of microbes, has thrown these traditional assumptions into disarray. Major challenges arise from increasing awareness of processes such as lateral gene transfer (LGT), and endosymbiosis, in which one organism becomes part of another. Organisms that acquire genetic resources horizontally as well as vertically violate standard representations of species lineages. A fundamental problem in constructing the ToL lies in establishing the evolutionary relationships between the three domains or superkingdoms (Bacteria, Archaea and Eukarya) and the role horizontal transfer events had in making these groups distinguishable. Such events are not solely a problem for the placement of microbes in the ToL. The blurring of species boundaries by hybridization is well known in plants, fungi and, increasingly, in animals. Genetic flux across all domains of life (such as that facilitated by the cross-taxa dispersal of viruses), plus other activities that produce conflicting phylogenetic signals, demand more complex ways of representing evolutionary processes than can be captured by a single tree of bifurcating branches.

My lecture will examine assumptions about the tree of life, the ways in which those assumptions are being challenged, and the implications of these challenges for broader aspects of biology and philosophy of biology. I will focus on how some molecular phylogeny is re-evaluating the tree's epistemological status and downgrading it from a biological fact to a hypothesis that remains unconfirmed in relation to most life and evolutionary history. Problems in selective attempts to use only data that support tree-like patterns — always an overwhelming minority of the total data available for prokaryotes — make it necessary to consider non-tree-like representations of evolutionary history, such as webs or networks. However, it is also important to reflect on arguments in phylogeny that are more sanguine about the reconstruction of a universal tree and the strategies they propose for doing so.

READING MATERIAL for the Tree of Life lecture (suggestions only)
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'ONE-SHOT' INTRODUCTION:

Doolittle, W.F. 2000. Uprooting the tree of life. *Scientific American*, 282: 90-95.

CLASSICS AND CONTEXT:

Doolittle, W.F. 1999. Phylogenetic classification and the universal tree. *Science* 284: 2124-2128.

Gogarten, J.P., Doolittle, W.F., & Lawrence, J.G. 2002. Prokaryotic evolution in the light of gene transfer. *Molecular Biology and Evolution*, 19: 2226-2238.

Pennisi, E. 2003. Modernizing the tree of life. *Science*, 300: 1692-1697.

Stanier, RY., and van Niel, C.B. 1941. The main outlines of bacterial classification. *Journal of Bacteriology*, 42: 437-466.

Woese, C.R. 1987. Bacterial evolution. *Microbiological Reviews*, 51: 221-271.

Zuckerkandl, E., and Pauling, L. 1965. Molecules as documents of evolutionary history. *Journal of Theoretical Biology*, 8: 357-366.

ADVANCED, SPECIALIZED READING

Beiko, R.G., Harlow, T.J., & Ragan, M.A. 2005. Highways of gene sharing in prokaryotes. *Proceedings of the National Academy of Sciences USA*, 102: 14332–14337.

Dagan, T., & Martin, W. 2006. The tree of one percent. *Genome Biology*, 7: 118.

Doolittle, W.F., & Bapteste, E. 2007. Pattern pluralism and the Tree of Life hypothesis. *Proceedings of the National Academy of Sciences USA*, 104: 2043-2049.

Hacking, I. 2007. Root and branch. *The Nation*, October 8th. www.thenation.com/doc/20071008/hacking

Keeling, P.J., and Palmer, J.D. 2008. Horizontal gene transfer in eukaryotic evolution. *Nature Reviews Genetics*, 9: 605-618.

Kurland, C.G., Canback, B., and Berg, O.G. 2003. Horizontal gene transfer: A critical view. *Proceedings of the National Academy of Sciences USA*, 100: 9658-9662.

Mallet, J. 2005. Hybridization as an invasion of the genome. *Trends in Ecology and Evolution*, 20: 229-237.

McBreen, K., & Lockhart, P.J. 2006. Reconstructing reticulate evolutionary histories of plants. *Trends in Plant Science*, 11: 398-404.

O'Malley, M.A., & Boucher, Y. 2005. Paradigm change in evolutionary microbiology. *Studies in History and Philosophy of Biological and Biomedical Sciences*, 36: 183-208.

Puigbò, P., Wolf, Y.I., and Koonin, E.V. 2009. Search for a 'Tree of Life' in the thicket of the phylogenetic forest. *Journal of Biology*, 8: 59 doi: 10.1186/jbiol159

Sober, E., & Steel, M. 2002. Testing the hypothesis of common ancestry. *Journal of Theoretical Biology*, 218: 395-408.

ADDITIONAL ONLINE RESOURCES:

Tree of Life Web Project. 2007. Explore the tree of life. www.tolweb.org/tree

Questioning the Tree of Life Network.
http://centres.exeter.ac.uk/egenis/research/QuestioningtheTreeofLife.htm

Special issue of *Biology and Philosophy* on the Tree of Life (Online First, print publication imminent; 15 papers by biologists, philosophers and historians):
http://www.springerlink.com/content/102856/?Content+Status=Accepted

Cracraft, J., Donoghue, M., Dragoo, J., et al. 2002. *Assembling the tree of life: harnessing life's history to benefit science and society*. National Science Foundation/ American Museum of Natural History. http://atol.sdsc.edu/pdf_docs/atol.pdf

Special issue of *Philosophical Transactions of the Royal Society London, B*, on The Network of Life (11 papers on whether networks are better than trees for representing evolution):
http://rstb.royalsocietypublishing.org/content/364/1527.toc