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Review

The not so universal tree of life *or* the place of viruses in the living world

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Darwin provided a great unifying theory for biology; its visual expression is the universal tree of life. The tree concept is challenged by the occurrence of horizontal gene transfer and—as summarized in this review—by the omission of viruses. Microbial ecologists have demonstrated that viruses are the most numerous biological entities on earth, outnumbering cells by a factor of 10. Viral genomics have revealed an unexpected size and distinctness of the viral DNA sequence space. Comparative genomics has shown elements of vertical evolution in some groups of viruses. Furthermore, structural biology has demonstrated links between viruses infecting the three domains of life pointing to a very ancient origin of viruses. However, presently viruses do not find a place on the universal tree of life, which is thus only a tree of cellular life. In view of the polythetic nature of current life definitions, viruses cannot be dismissed as non-living material. On earth we have therefore at least two large DNA sequence spaces, one represented by capsid-encoding viruses and another by ribosome-encoding cells. Despite their probable distinct evolutionary origin, both spheres were and are connected by intensive two-way gene transfers.

Keywords: universal tree; viruses; phages

1. *E PLURIBUS UNUM*: ABOUT UNITY IN BIOLOGY

When reading the books of Aristotle on animals, one gets the impression that the roots of biological research go back to classical Greece. His books offer careful descriptions, sharp reasoning, the beginning of experimentation and entertaining errors. Despite this hopeful start, it took nearly 2000 years before biology became an established branch of science. Today we continue Linné's eighteenth-century efforts to put a systematic grid on the diversity of life, which has been for biologists a source of aesthetic fascination and scientific despair. The closer biologists looked into the biosphere, the more species were discovered. To date, zoologists have described more than a million animal species and botanists a quarter of a million flowering plant species (May 1988; Brusca & Brusca 2003), it is now the turn of microbiologists to add perhaps millions of species to the long list of life. How can biologists cope conceptually and technically with this enormous species number? A deep sigh of relief came for biologists already in 1859 with the publication of Charles Darwin's book 'On the Origin of Species'. Suddenly, biologists had a unifying theory for their branch of science. One could even argue that the holy grail of a great unifying theory was achieved by Darwin and Wallace at a time when Maxwell was unifying physics, the older sister of biology, at the level of the electromagnetic field theory. In contrast to Maxwell's book, Darwin's grand design was expressed in simple sentences comprehensible to a lay audience. Understandably, his theory became a scientific and philosophical revolution.

Interestingly, the only non-verbal information in Darwin's book was a single figure with a hypothetical tree of descent for organisms. In the late nineteenth century, Ernst Haeckel quickly popularized the tree by putting names on the branches. Darwin's tree has been grown into a veritable forest. From the very concept Darwin's tree was daring: not only extant, but also all extinct organisms found, in principle, a place on this tree. It was from the very beginning designed as a universal tree.

This intuitive insight has been vindicated by the 150 years of biological research performed since Darwin first put forward his theory. Organisms so small that they were mere specks in the microscope of the nineteenth century biologists have now found a place on this tree of life. Darwin lacked any knowledge about the physical basis of heredity. Nevertheless, when the genetics, molecular biology and genomics revolutions successively rolled over biology, his theory stood the test of time and could incorporate the new discoveries (Padian 2008). Understandably, the tree became quite complex and modern depictions resemble now a rather impenetrable thicket (Doolittle 1999). The complexity of modern tree displays does not only reflect increasing knowledge and mere numbers of species. When analysing prokaryotic genomes, microbiologists actually questioned the linear descent concept of vertical evolution, a basic tenet of Darwin's concept (Doolittle & Bapteste 2007). Pictorially, many branches of the tree became interconnected. The transition of the tree of

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