

Haeckel's 1866 tree of life and the origin of eukaryotes

To the Editor — In their Letter describing an expanded version of the tree of life, Hug *et al.*¹ refer to a key publication of Carl Woese and co-workers², wherein a 16S rRNA-phylogenetic scheme of the domains Bacteria, Archaea and Eukarya is shown. However, the first three-kingdom tree of life that included microorganisms was depicted by Ernst Haeckel (pictured at around 26 years old) in his *General Morphology of Organisms*, a seminal book that was published one hundred and fifty years ago³.

In his *Origin of Species*, Charles Darwin refers to the Linnean two-kingdom system, with 'Animalia' and 'Vegetabilia' as the only two branches of the living world. Haeckel³, who was also known as the German Darwin⁴, introduced a three-kingdom scheme in which, as a supplement to the Linnean Animalia and Plantae (synonymous with Vegetabilia), the 'Protista' were added⁵. Haeckel's protists included all microscopic organisms known at that time (Amoebozoa, Myxomycetes etc.), and, as one of its eight divisions, the 'Monera'.

In several chapters of his *General Morphology*, Haeckel³ characterized the tiny Moneren as the "most simple organisms, without structure, homogeneous pieces of Plasma", and explicitly mentioned the bacterial genus *Vibrio* as an example. Hence, Haeckel's Monera included microorganisms that are today known as Bacteria (a term not yet coined in 1866).

Six years later, the German botanist Ferdinand Cohn published a monograph on the occurrence, cultivation, morphology, behaviour, reproduction, nutrition, and systematics of a group of microorganisms he called Bacteria. Cohn used the word 'bacteria' with reference to the genus-name



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Bacterium, and provided a definition of these tiny microorganisms that included their characteristic mode of propagation via binary fission⁶.

Despite Cohn's introduction of the term Bacteria in 1872, Haeckel's term Monera survived in the biomedical literature until 1969, when Robert H. Whittaker introduced his five-kingdom-system of classification. In this scheme, Monera refers to prokaryotic microorganisms (bacteria, cyanobacteria), that are juxtaposed to four eukaryotic kingdoms (Protista, Fungi, Animalia, Plantae)⁷. This taxonomic interpretation of extant biodiversity was replaced by the three-domains-system of Woese *et al.*², in which Monera are equated with the prokaryotic domains Bacteria and Archaea. The four remaining kingdoms

were summarized under the domain Eukarya, which includes all eukaryotic micro- and macroorganisms (from amoebae to humans).

In chapter 26 entitled 'Phylogenetic theses', Haeckel³ re-interpreted and supplemented Darwin's evolutionary deductions of 1859. With reference to the simplest protists (bacteria), which form the root of his 'oak tree' (see Fig. 6 in ref. 5), Haeckel³ concluded that "all organisms are the descendants of such autogenous Moneren". Hence, according to this Haeckelian interpretation of the phylogeny of life, the Monera (that is, Bacteria and Archaea)² are the progenitors of all more complex living beings on Earth.

This 150-year-old idea is consistent with recent discoveries and genomic analyses that support an archaeal origin of eukaryotes^{1,8}. A 'Lokiarchaea'-like host cell that had rudimentary phagocytotic capabilities for an uptake of bacteria may have been the most ancient, metabolically active, self-replicating protoplasmic unit from which all life on Earth evolved⁹. □

References

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