

Zeitschrift: Bulletin de la Société Vaudoise des Sciences Naturelles
Band: 82 (1992-1993)
Heft: 2

Artikel: The polyphylectic nature of the urkaryote, the ancestral organelle-free eukaryote
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DOI: <https://doi.org/10.5169/seals-280172>

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The polyphyletic nature of the urkaryote, the ancestral organelle-free eukaryote

par

Claude-Alain Henri ROTEN^{1,2} and Dimitri KARAMATA¹

Résumé.-ROTEN C.-A. H. et KARAMATA D., 1992. De la nature polyphylétique de l'urkaryote, l'ancêtre de la cellule eucaryote. *Bull. Soc. vaud. Sc. nat.* 82.2: 151-153.

Les analyses de séquences macromoléculaires utilisées comme moyen de localisation phylogénétique de l'eucaryote ont engendré deux arbres évolutifs apparemment contradictoires: selon l'arbre archéobactérien, l'embranchement des eucaryotes se situe à la base de l'ensemble des archéobactéries, alors que, selon l'arbre éocyte, il se situe à la base des éocytes, un sous-groupe des archéobactéries. Nous proposons que les urkaryotes sont issus d'une ou de plusieurs endosymbioses indépendantes entre archéobactéries dépourvues de paroi, parmi lesquelles l'ancêtre de l'éocyte. Cette hypothèse postulant la nature polyphylétique de l'urkaryote permet non seulement de réconcilier les arbres archéobactérien et éocyte, mais d'expliquer de surcroît l'origine de la double membrane nucléaire des eucaryotes, ainsi que leur grande diversité, notamment parmi les protistes.

Summary.-ROTEN C.-A. H. and KARAMATA D., 1992. The polyphyletic nature of the urkaryote, the ancestral organelle-free eukaryote. *Bull. Soc. vaud. Sc. nat.* 82.2: 151-153.

Analyses of sequences of macromolecules aimed at positioning the eukaryotes on the phylogenetic tree have provided two apparently conflicting pictures: the archaeobacterial tree, with eukaryotes branching off at the root of all archaeobacteria, and the eocyte tree, according to which the eukaryotic branching point is situated at the root of eocytes, a subgroup of archaeobacteria. We propose that urkaryotes originate from one or several independent endosymbioses of wall-less archaeobacteria, including ancestral eocytes. The hypothesis of a polyphyletic nature of urkaryotes can reconcile the eocyte and the archaeobacterial trees and, in addition, provide explanations for the origin of the double-membrane surrounding the eukaryotic nucleus and the diversity of eukaryotes, in particular protista.

Key words: evolutionary tree, universal; archaeobacterial tree; eocyte tree; polyphyletic nature of eukaryotes; nuclear membrane, origin of; endosymbiosis; urkaryote.

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The living world is widely considered to harbour three major kingdoms, the bacteria, the archaeobacteria and the eukaryotes (WOESE 1987, RIVERA and LAKE 1992, fig. 1). Archaeobacteria, a relatively small kingdom, consists of subgroups adapted to highly specialized niches, the methanogens and the halophiles, grouped under the name of euryarchaeota, and the sulfur metabolizing thermophiles designated as eocytes or crenarchaeota. There is a general agreement that the most ancient branch point of the evolutionary tree is that separating bacteria from eukaryotes and archaeobacteria. However, two apparently conflicting views concerning the position of the branch point between eukaryotes and archaeobacteria have been proposed: the archaeobacterial and the eocyte trees (fig. 1). According to the former, euryarchaeota and eocytes are closer to each other than to eukaryotes, while, in the latter view, eukaryotes are most closely related to eocytes.

The argument favouring the archaeobacterial tree rests primarily on the amino acid sequence homologies of the elongation factor EF-2 (or EF-G) (CAMMARANO *et al.* 1992), while evidence favouring the eocyte tree are derived from the amino acid sequences of the elongation factor EF-Tu and of the tryptophan synthetase B gene (RIVERA and LAKE 1992), the morphology of the ribosomes (LAKE 1991), the organization of the rRNA operons (RIVERA and LAKE 1992), and the type of lysine biosynthetic pathway present, *i.e.* that containing the α -amino adipate intermediate being confined to eukaryotes and eocytes, while that of the diaminopimelate is present in prokaryotes, other than the eocytes, as well as in eukaryotic organelles (ROTEN and KARAMATA 1992). Finally, evidence derived from 16/18S RNA sequences have been interpreted in favour of both of the evolutionary trees (LAKE 1988, GOUY and LI 1989).

Inspection of the available data reveals clearly that the choice of the evolutionary marker—a molecule or a given part of its sequence—, as well as that of the algorithm used for data analysis, can determine the evolutionary tree that is obtained. However, these apparent contradictions may represent a false dichotomy. The question of the relatedness of different phyla can be reframed by considering the eukaryote as being the result of endosymbiosis between two distinct prokaryotic members of the archaeobacterial kingdom. For instance, the urkaryote (eukaryote endowed with the nuclear membrane, but devoid of organelles) could have originated from endocytosis of an eocyte by another wall-free cell, distant from contemporary archaeobacteria, which we will name the proto-urkaryote. Such an event could have generated an eocyte surrounded by a double membrane, the ancestor of the nucleus, and, subsequently, through translocation of the proto-urkaryotic genome into this nucleus (ROTEN and KARAMATA 1992) and recombination, a polyphyletic cell. This would mean that individual components of the eukaryotic cell are most closely related to the organisms from which they have been acquired through endosymbiotic and recombination events. Present eukaryotes could be all derived from a unique endosymbiont or, alternatively, could have arisen from several different and independent endocytotic events. The polyphyletic nature of eukaryotes, possibly a different one for different phyla, implies inevitably that determination of their position on the phylogenetic tree of the living world will depend upon the choice of the evolutionary tracer.

In conclusion, our hypothesis may not only allow the archaeobacterial and the eocyte trees to be reconciled, but could also account for the origin of the nuclear membrane.

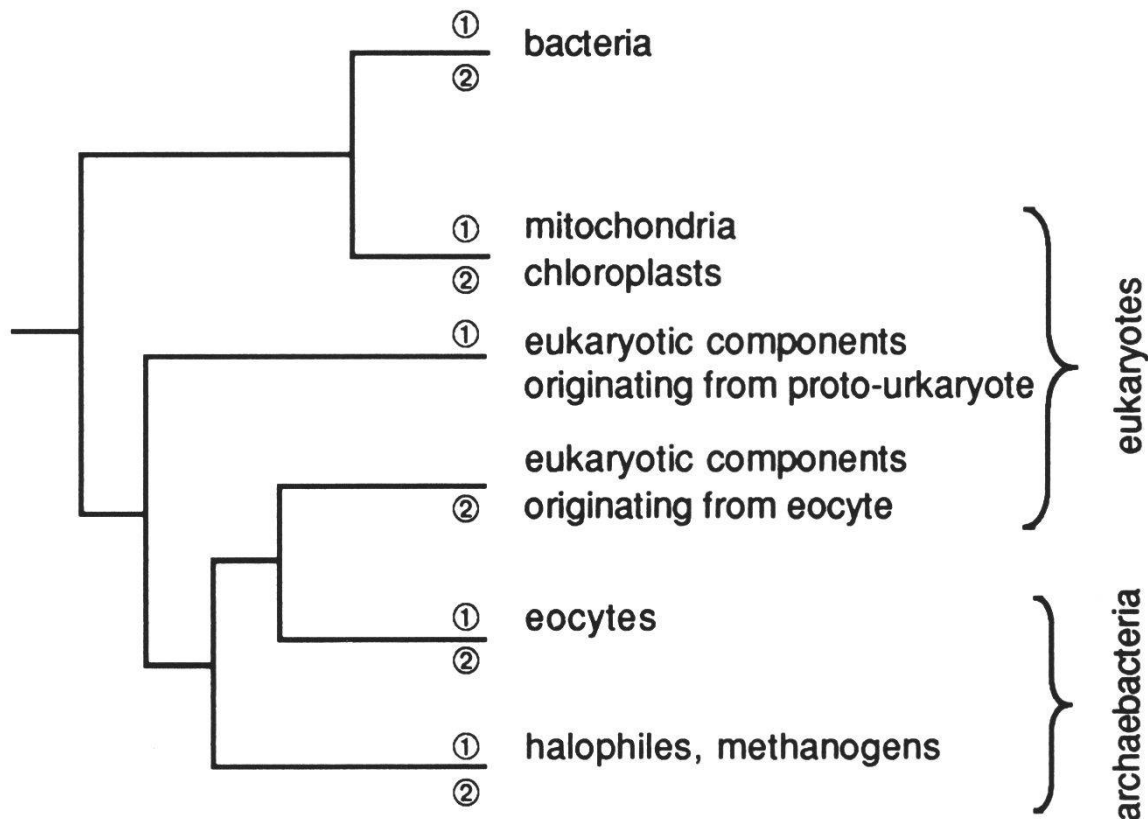


Figure 1.—A universal evolutionary tree which accounts for so far available treeing experiments obtained with different evolutionary tracers.

Depending on the eukaryotic tracer, either the archaeobacterial ① (WOESE 1987) or the eocyte ② (RIVERA and LAKE 1992) tree is obtained.

Eukaryotes are represented as polyphyletic organisms whose genomes can contain genetic determinants from a variety of different origins.

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