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# Time for a change

Prokaryote: gene-sequence comparisons show the tree of life consists of bacteria, eukarya and archaea. The use of the term 'prokaryote' fails to recognize that an idea about life's origins has been proved wrong.

**Norman R. Pace**

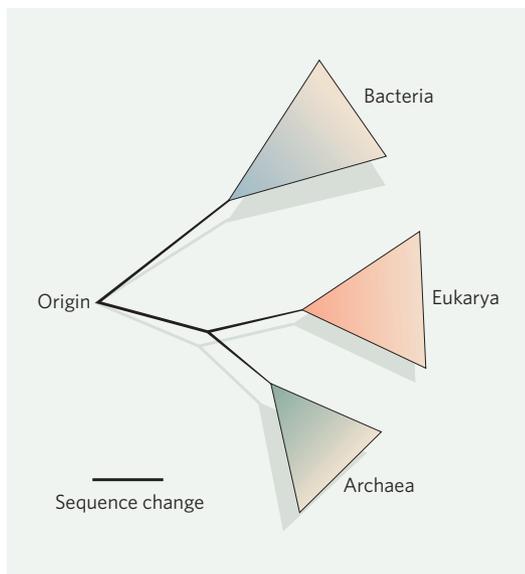
The explosive accumulation of gene sequences over the past few decades has brought a new perspective on life and its history. Some of the results indicate that we need to reassess our understanding of the course of evolution at the most fundamental level.

The current textbook paradigm for biological diversity and evolution is based on what I will call the prokaryote/eukaryote model. This posits that there are two kinds of cells: prokaryotic, those without nuclei (specifically, without nuclear membranes) and eukaryotic, those with a classical membrane-bounded nucleus. The model further posits that the former gave rise to the latter. The historical antecedents of this model are complex and rooted in the nineteenth century; for example, German biologist Ernst Haeckel positioned 'monera' (masses of protoplasm without a nucleus, later termed 'prokaryotes') at the base of his four-kingdoms phylogenetic tree.

The recognition that the main eukaryotic organelles, mitochondria and chloroplasts, were derived from bacteria by symbiosis between the bacteria and an ancestral eukaryotic cell prompted speculation on a similar origin for the eukaryotic nucleus. And the discovery of archaea — microbes that in many molecular ways resemble eukaryotes more than bacteria — resulted in proposals for archaeal origins for nuclear and cytoplasmic components of eukaryotic cells. Such proposals have sustained the concept that prokaryotes evolved into eukaryotes — an evolutionary model invoked by the terms themselves.

Molecular-sequence comparisons, first of ribosomal RNA genes in the late 1970s and of many other genes since, replaced analyses based on morphological subjectivities (such as the presence or absence of a nuclear membrane) with credible maps of evolutionary relationships between genes. These sequence comparisons have rendered the prokaryote/eukaryote model obsolete.

Ribosomal RNA, because of its ubiquity and slow rate of evolution, provides the most reliable view of the earliest evolutionary events. Comparisons of ribosomal RNA sequences show a three-domain tree of life (see figure). The diagram in essence is an experimentally derived map of biological organization and the course of evolution at the largest scale.



**Comparisons of ribosomal RNA sequences reveal a three-domains tree of life, rendering the term 'prokaryote' obsolete.**

Although some details of ribosomal RNA-based trees remain controversial, the basic three-domains structure and the relationships between the domains are generally accepted and are supported by observed biochemical variation. Phylogenetic trees based on all genes encoding the information-processing machinery needed to express genetic sequences are congruent with the three-domains tree. So the tree represents the evolutionary course of the genetic machinery, the functional core of genomes.

The lessons of the three-domains tree are profound. Instead of two kinds of organism, prokaryotes and eukaryotes, there are three: bacteria, eukarya (eukaryotes) and archaea. The root, or origin, of this universal tree, cannot be determined from ribosomal RNA sequences, but other phylogenetic results and biochemical correlates show that the genetic lines of eukarya and archaea have a common ancestral branch that is independent of that giving rise to the bacteria (see figure). That is, eukaryotes and archaea are more closely related to one another than either is to bacteria.

There is not a single (monophyletic) phylogenetic group upon which to hang the tag prokaryote. The major eukaryotic organelles, mitochondria and chloroplasts, are definitely bacterial in origin, but the nucleus is not. The nuclear line of descent is as ancient as the archaeal line

and not derived from either archaea or bacteria. Thus, the prokaryote/eukaryote model for biological diversity and evolution is invalid.

Some have asserted that 'prokaryote' has utility, as a term for non-eukaryotes. However, this is a negative and therefore scientifically invalid description; no one can define what is a prokaryote, only what it is not. Lumping bacteria and archaea conceptually discounts fundamental differences between those two kinds of organism and reinforces an incorrect understanding of biological organization and evolution.

But if we can't call them prokaryotes, what should we call them? That, of course, depends on what is meant by 'them'. If what is meant is 'the little stuff out there', then try microbes or microbial.

Other things may need more precision. For instance, references in textbooks and in the literature to 'prokaryotic transcription' — meaning a transfer of information from DNA to RNA that relies on sigma transcription factors — overlook a deeper complexity. Archaea do transcription differently from bacteria, with TATA-binding proteins, much like those used by eukaryotes. Bacterial transcription is the correct term to use in this case. Another such oxymoron is 'prokaryotic protein synthesis', when the bacterial version is meant.

I believe it is critical to shake loose from the prokaryote/eukaryote concept. It is outdated, a guesswork solution to an articulation of biological diversity and an incorrect model for the course of evolution. Because it has long been used by all texts of biology, it is hard to stop using the word, prokaryote. But the next time you are inclined to do so, think what you teach your students: a wrong idea. ■

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#### FURTHER READING

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