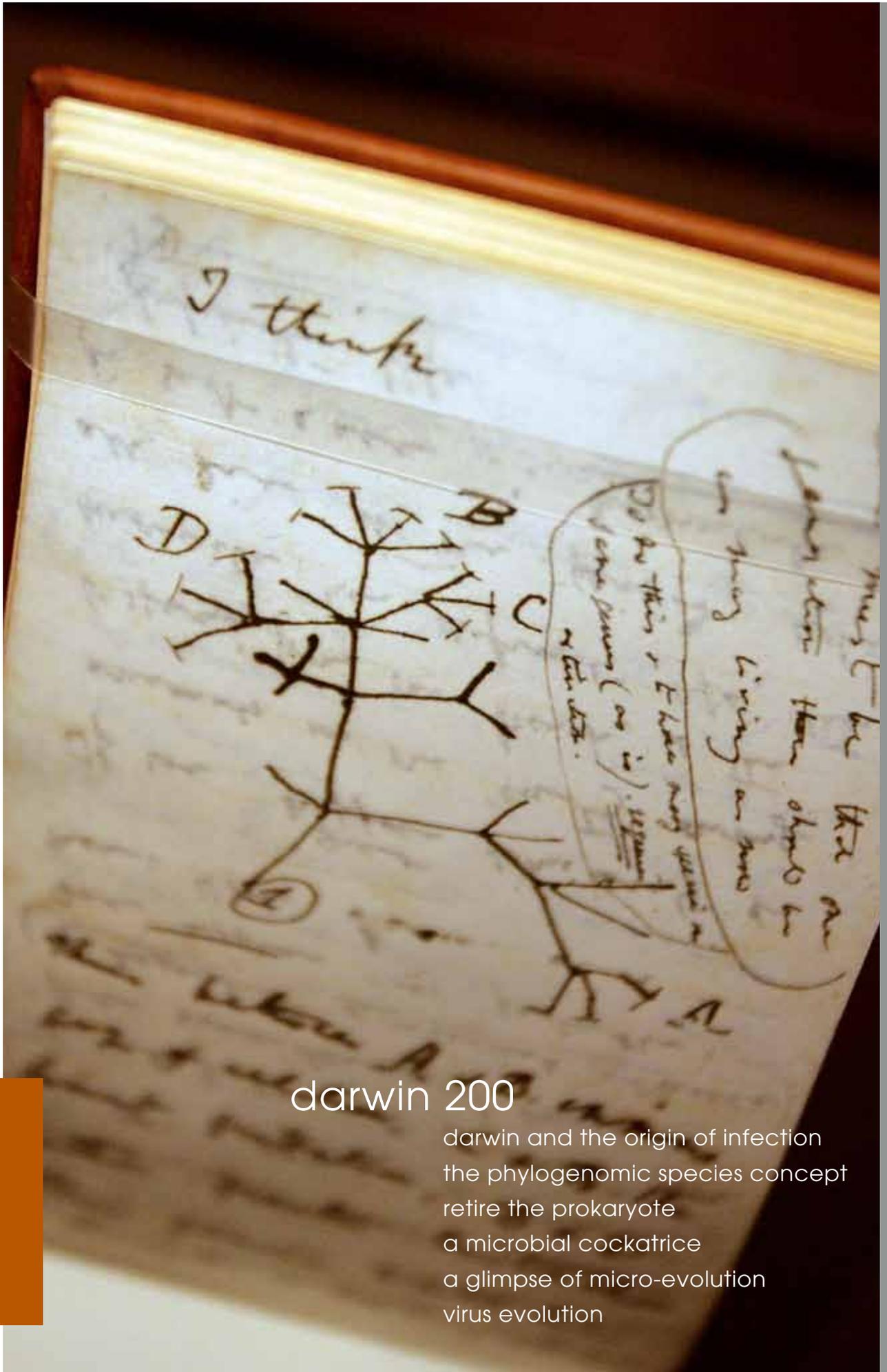


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darwin 200

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Experimental results rarely upset the common wisdom of a scientific discipline, but that happened to biology late in the 20th century. The common wisdom in deep evolution and how we classify organisms was rendered sorely in need of modernization. And that modernization is happening too slowly.

The anachronism here is the notion of 'prokaryote' and the model of biological organization and evolution that it elicits. This model, which I term the 'prokaryote-eukaryote' model, posits that fundamentally there are two kinds of organisms, prokaryotes and eukaryotes, defined by the presence or absence of a nucleus (more properly nuclear membrane). Additionally, the model proposes that prokaryotes gave rise to eukaryotes, as shown in the figure overleaf.

The problem, however, is that the prokaryote concept has been undermined critically by sequence-based phylogenetic results. Indeed, the notion of prokaryote was scientifically illogical from the beginning because the definition, an 'organism without a nucleus', is a negative definition. No

It's time to retire the prokaryote

Norman R. Pace

believes that the term 'prokaryote' is an anachronism in modern biology. Here he explains why and seeks the help of microbiologists in stopping its use.

one can tell you what a prokaryote is, they can only tell you what it is not. Yet, institutional biology embraced the notion of prokaryote and it came to dominate textbooks, journals and discourse in matters of deep evolution. But the hypothesis of the prokaryote was never tested.

Where it came from – the very short history of prokaryote

It is important to understand that the concept of prokaryote is not based on scientific results. Rather, it is based on historical conjecture. To simplify the history considerably, I think that prokaryote had its origins in evolutionary models of the late 1800s, with 'monera' at the origin of a tree of complex eukaryotes. Monera persists today at the base of the five-kingdom classification scheme, which was introduced in the 1960s and is popular in current textbooks. Also in the 1960s, the name 'monera' became

interchangeable in the textbooks with 'prokaryote'. It is curious that the nomenclature of 'monera' never caught on among earlier microbiologists, whereas 'prokaryote' was immediately incorporated into the lexicon. But in fact, prokaryote was never much more than a name-change from monera, a 19th century notion based on far more limited knowledge than is now available.

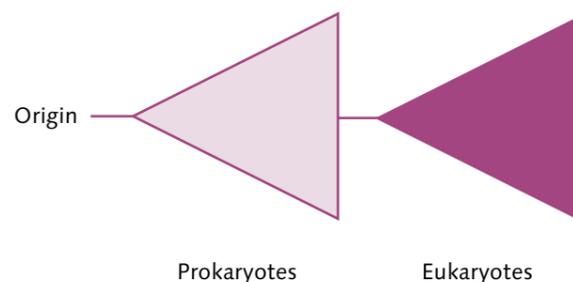
The disproof of prokaryote

The idea of prokaryote was disproved in 1977, with Carl Woese's discovery of archaea and the first articulation of a rudimentary molecular phylogenetic tree that related the most diverse forms of life. Woese saw through comparisons of ribosomal RNA (rRNA) sequences that life's diversity is composed not of two deeply related groups, prokaryote and eukaryote, but rather three such groups. These three phylogenetic 'domains' came to be called *Bacteria*, *Eukarya* (eukaryotes, which indeed proved monophyletic) and *Archaea*. Woese originally named the latter group *Archaeobacteria*, but this was changed to *Archaea* when it became clear they are fundamentally distinct from *Bacteria*.

◀ 'Prokaryotes' heading into the sunset. Medical R.F.Com / Science Photo Library (bacteria); Photos.com/Jupiter Images (sunset)

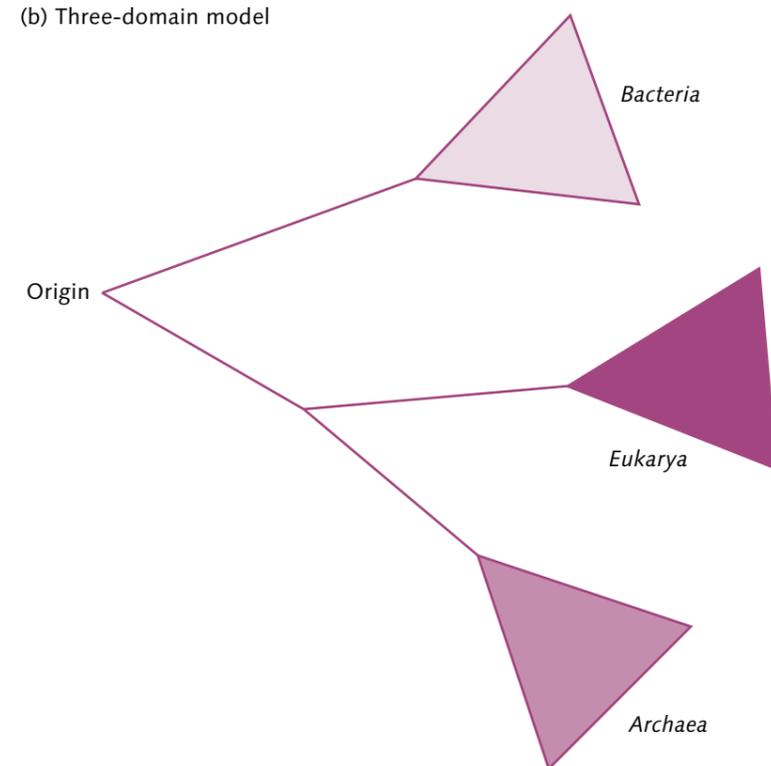


(a) Prokaryote–eukaryote model



▲ Prokaryote–eukaryote (a) versus three-domain (b) models for biological organization and the course of deep evolution. The wedges indicate radiations within the respective groups.

(b) Three-domain model



The three-domain model of relationships and evolution stands in stark contrast to the prokaryote–eukaryote model, as shown in the figure above. The three-domain pattern shows that eukaryotes constitute a phylogenetically coherent group, but there is no specific group to label ‘prokaryote’. Both archaea and bacteria would qualify through their lack of a nuclear membrane, but these two groups are not specific relatives. Indeed, archaea are more closely related to eukaryotes than archaea are to bacteria. This relationship is supported not only by molecular phylogeny, but also by many properties of archaeal and eukaryotic cells compared to bacterial cells.

Additionally, the phylogenetic model shows no specific group of organisms that preceded the eukaryotes. The textbook and common wisdom that eukaryotic cells arose late in the history of Earth by fusion of two prokaryotes is incorrect. Mitochondria and chloroplasts were derived from symbiotic bacteria, but the nucleus is far more ancient. The history of the nucleus is seen in the molecular phylogenetic tree as the eukaryal line of descent. The tree shows that the nuclear line is as old as the archaeal line and was derived from neither archaea nor bacteria. The molecular results say nothing at all about whether or not the earliest eukaryotes possessed nuclear membranes. In the light of the sequence comparisons, the presence or absence of the nuclear membrane or other morphological trait is irrelevant for classification or for deduction of the paths of deep evolution.

Some would argue

Some authors defend prokaryote as a useful classification. They argue, for instance, that bacteria and archaea are united by their very small size or their use of coupled transcription and translation. These arguments are not meaningful; rather, they are just other twists on the presence or absence of

the nuclear membrane. At the last resort, the proponents of prokaryote insist, ‘*You have to call them something!*’ But that’s the problem: there isn’t any ‘them’. The molecular phylogenetic results, bolstered by decades of biochemical corroboration, show that there is no natural grouping that would correspond to prokaryote.

Proponents of the concept of the prokaryote sometimes argue that the prokaryote terminology is a convenient classification and that historical usage justifies continued usage. But these rationalizations are scientifically inappropriate. A critical point here, one usually missed by proponents of the prokaryote concept, is that scientific classification is not a convenience. As scientists we must observe nature and classify accordingly, so as to promote scientific understanding. As Darwin insisted, ‘*Our classifications will come to be, as far as they can be so made, genealogies*’. ‘Prokaryote’ doesn’t fit the observed genealogy. It needs to be retired from the language of biology. It has become a distraction.

Why it matters

The legitimacy of prokaryote is more than an issue in terminology. It is also a matter of proper understanding of important biological concepts. Any scientific field rests essentially on two conceptual foundations. One foundation requires understanding of the order, the organization of the subjects of study. The other conceptual foundation is how the subjects of study change. Foundational issues for progress in biology, therefore, are proper perceptions of phylogenetic groups and relationships and, consequently, the path of evolution.

The prokaryote–eukaryote notion fails in both these regards. In contrast, the three-domain pattern of life’s organization and large-scale path of evolution is solidly grounded on scientific observations.

What to do about it and how microbiologists are critical

Institutional biology is now heavily invested in the prokaryote concept. The language permeates our literature and thereby distorts understanding of foundational issues. One hurdle that faces efforts to modernize this matter is that most students, biologists and authors of general textbooks don’t think very much about microbes. Their world is generally that of large organisms of limited diversity. They, unlike microbiologists, are not faced with trying to make sense of a vast diversity of life with comparatively little observable variation without resort to biochemistry and gene sequences. The three-domain phylogenetic model is beginning to appear in textbooks, but usually as just another method of classification, alongside the five-kingdom scheme. The evolutionary implications of the three-domain pattern of evolution are seldom broached, and the language of prokaryote perseveres. What to do about it?

The retirement of prokaryote from the lexicon of biology will be slow because it is now so deeply entrenched. Consequently, that retirement process needs to be catalysed. Microbiologists are in the best position to understand the issues and to participate in

modernization. This is because their organisms span the three domains, and the phylogenetic perspective is referentially necessary and an obvious utility. Modern treatment of issues in classification and evolution by microbiological journals and textbooks eventually will lead to upgraded general texts. One catalytic step that any microbiologist can contribute, however, is simply to stop using the term ‘prokaryote’. This may be hard to do because of long conditioning, but it is an important step for educators particularly.

How can teachers broach this issue in the face of the currently pervasive reference to prokaryotes in journals and textbooks? One way to do so is to use the discordance between recently emerging data and the textbooks as a prime example of how science, biology in this case, is an ongoing, living process, evolving in response to new experimental data. Dealing with the prokaryote issue is an opportunity to demonstrate the testing of specific hypotheses with experimental data, with results important for biology. Phylogenetic trees, maps of evolutionary relationships, are straightforward metaphors for the course of evolution and are not hard for students to understand in essence. The three-domain concept poses many questions,

to be sure, but it also provides a solid foundation for progress toward answering those questions.

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Further reading

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