A group of high school students sit in the school hallway cramming for a biology quiz. The bell rings, the students shove notes and textbooks into their bags and rush off to class. The quiz is on biological classification. Depending on the textbook, the teachers, and the state curriculum, these students learned to classify all live beings into three, or five, or six major groups, called either “kingdoms” or “domains.”

Taxonomy, the identification, naming, and classification of living things, is an indispensable unit in any biology curriculum and indeed, an integral part of biological science. Taxonomy catalogues life’s diversity and is an essential tool for communication. But it is more than that. Scientists endeavor to construct phylogenies, diagrams that, like family trees, show relationships among organisms through ancestral lineages. Thus modern classification systems are hypotheses about the genetic relationships among species and the evolutionary history of life.

Taxonomy is an especially dynamic field today. New molecular data, primarily DNA sequences, are available for an ever-increasing number of organisms. It appears that, as Emile Zuckerkandl and Linus Pauling predicted in 1965, molecules really are documents of evolutionary history. DNA sequences offer a way to quantify genetic similarity. Because DNA is universal, sequence data shed new light on evolutionary relationships, not only within esoteric groups of microbes but across the entire realm of life. The goal of a unified phylogeny appears within reach.

New Science, Old Standards

Where new data and interpretations outpace curricula, science teachers enjoy exciting opportunities to share cutting-edge research with students. But frustrating dilemmas arise: How should new information be incorporated into the framework of existing educational standards and materials? The committees that write state and national standards, authors of textbooks, and curriculum developers must also make decisions about how best to handle new developments.

The National Science Education Standards address taxonomy for grades 9-12 as follows:

*Biological classifications are based on how organisms are related. Organisms are classified into a hierarchy of groups and subgroups based on similarities which reflect their evolutionary relationships. Species is the most fundamental unit of classification.*

National Research Council, 1996

This standard describes the fundamental principles of biological classification without mentioning specific taxonomic systems. Many teachers, however, also answer to state or local standards.

Since 1996, I’ve observed several revisions in my state’s standards, the Massachusetts Curriculum Frameworks, which reflect the inherent difficulty in mandating what students should know in fields where methodologies and interpretations are controversial. Massachusetts has continually revised the expectations for student learning in biological classification, especially with regard to the number and kind of major categories of life. Presented below are the 2001 and 2006 high school life science learning standards for this topic.

In 2001, students were expected to be able to “describe how the taxonomic system classifies living things into domains (eubacteria, archaebacteria, and eukaryotes) and kingdoms (animals, plants, fungi, etc.).” The standard includes an additional note: “There is an ongoing scientific debate about the number of kingdoms and which organisms should be included in each. The following websites provide more information: Brave New Biosphere — whyfiles.org/022critters/phylogeny.html and The Tree of Life Project Root Page — phylogeny.arizona.edu/tree/tree.html.”

As of 2006, Massachusetts students are required to “use cellular evidence (e.g., cell structure, cell number, cell reproduction) and modes of nutrition to describe the six kingdoms (Archaebacteria, Eubacteria, Protista, Fungi, Plantae, Animalia).”

Massachusetts has high-stakes testing; passing a standardized test based on the Massachusetts Science and Technology/Engineering Curriculum Framework is a graduation requirement. The committee that revised the Frameworks in 2006 no doubt felt pressure to resolve the ambiguity of the earlier standard.

Biology textbooks also reflect the current taxonomic debate. For decades, most biologists accepted the classification of all life into five kingdoms: Bacteria (or Monera), Protocists (protists and their macroscopic relatives), Animals, Plants, and Fungi (Figure 1). Since the 1980s, a system that replaces the five kingdoms with three domains (Bacteria, Archaea, and Eucarya) has gained support in the research community and made its way into newer textbooks (Figure 2). The six-kingdom system described in the 2006 Massachusetts learning standard represents a merger between the five kingdoms and the three domains; this six-kingdom scheme dominates the most recent crop of high school biology texts. In my district, for example, a 1997 textbook I had been using in seventh grade life science presents five kingdoms; its 1999 update includes six; and our high school biology text, from 2004, uses the three-domain system.

Five Kingdoms or Three Domains

To better judge educational standards and textbook discussions of taxonomy, I turned to the scientific literature. There I found proposals for anywhere from three to eight domains or kingdoms. The crux of the debate lies in the criteria for classification, the methods used to construct phylog-
enies. The results have broad implications for understanding the origin and nature of cells. Here I examine the five-kingdom and three-domain systems, arguably the best-developed and most widely-accepted scientific hypotheses regarding the evolutionary history of life.

According to Lynn Margulis and Karlene V. Schwartz (1998), each of the five kingdoms “can be uniquely defined using all the features of the whole organism — molecular, morphological, and developmental.” Every fossil or living organism can be classified into one of the five kingdoms. Organisms within each kingdom share a common, and ancient, evolutionary history. Each kingdom belongs to one of two “superkingdoms”: prokaryotes (the bacteria), life composed of cells that lack membrane-bounded nuclei and protein-rich chromosomes, and eukaryotes, organisms with nucleated cells.

In 1990, Carl Woese and colleagues proposed the three-domain classification based on DNA sequence data. Woese’s analysis suggests all organisms can be assigned to one of three fundamental groups, or domains: Archaea, Bacteria, and Eucarya. The Archaea, of which relatively few have been studied, resemble bacteria; they are prokaryotes and are classified with bacteria in the five-kingdom scheme. The Eucarya (meaning “true nucleus”) include protoctists, animals, plants, and fungi.

The five-kingdom classification is based on no single criterion. Rather, it attempts to use all available evidence to infer evolutionary relationships. Paleontology, comparative anatomy, morphology, development, behavior, biochemistry, and molecular biology all come into play. By contrast, the division of life into three domains is based on the DNA sequence of one, extremely important gene. This DNA encodes part of ribosomes, cells’ protein-building organelles. Since no living thing can survive without ribosomes, the gene is universal. Because it is essential, the gene can only change in ways that still produce functional ribosomes. Thus the DNA sequence of the gene has been highly conserved through life’s history. Degree of similarity in this gene is therefore an excellent indicator of evolutionary relationships. DNA sequences from a few other genes, also highly conserved, are consistent with the three-domains tree of life.

The ribosomal RNA gene sequences that generated the three-domain system are used to identify organisms and relate them to others in phylogenetic trees. This method studies only molecular features of live organisms, but evolutionary relationships determined through traditional means, such as fossil analysis and comparative anatomy, can now be tested with this quantitative technique.

[Figure 1. The Five Kingdoms](http://www.nabt.org/sites/S1/File/pdf/070-08-fivekingdoms.pdf)
The five kingdoms (Bacteria, Protoctists, Animals, Fungi, and Plants) are shown here. The colored pathways show the acquisition of cell parts through symbiotic mergers (the nucleocytoplasm in red and yellow, the mitochondria in brown, and chloroplasts in green). In the third merger, photosynthetic cyanobacteria join with protoctist cells; they evolve into chloroplasts in plant cells.

[Figure 2. The Three Domains.](http://www.nabt.org/sites/S1/File/pdf/070-08-threedomains.pdf)
This tree divides life into three domains (Bacteria, Archaea, and Eucarya) based on sequence comparisons of a gene that encodes part of the ribosome. The tree does not show symbiotic mergers, such as those between bacteria and early protists that evolved into mitochondria and chloroplasts. From Woese, C.R. (2000). Interpreting the universal phylogenetic tree. Proceedings of the National Academy of Science, USA, 95, 8392-8396.

Bacteria
- Crenarchaeota
- Euryarchaeota

Archaea
- Crenarchaeota

Eucarya
- Animals
- Fungi
- Plants
Branches & Mergers on the Tree of Life

The methods used to analyze ribosomal RNA gene sequences produce monophyletic phylogenies. Monophyletic taxonomic groups include all organisms that stem from a single common ancestor and no others (Figure 3). Biologists seek monophyletic phylogenies because they represent unambiguous evolutionary lineage. Monophyly is an assumption built into the methods of DNA sequence analysis, but it has its limitations. Transfers of genes or entire sets of genes (genomes) between species have occurred throughout evolutionary history. Symbioses between different organisms can give rise to new species. These events confound the neatly diverging branches of monophyletic phylogenies.

Examine, for example, the symbiotic origin of chloroplasts. Chloroplasts are the organelles in which photosynthesis occurs in plants and algae. Evidence from many sources, including DNA sequences, confirms that chloroplasts were once free-living cyanobacteria that were engulfed, but not digested, by an early eukaryote. Figure 4 shows cells of a modern cyanobacterium and chloroplasts inside plant cells. Plants and cyanobacteria are vastly different; their structures, life histories, modes of reproduction, metabolic capabilities, and molecular sequences squarely support their placement in separate domains or kingdoms. Yet the evolution of plants and cyanobacteria are inextricably linked; ancient cyanobacteria are now part of plants. Note the positions of cyanobacteria and plants on the five-kingdom and three-domain phylogenies (Figures 1 and 2). The three-domain tree, faithful to monophyly, ignores symbiosis, plants and cyanobacteria lie on distant branches of separate domains. The five-kingdom scheme shows all plants have multiple ancestors; it depicts the merger between a cyanobacterium and a protist that became the algae from which plants evolved.

In the development of the three-domain scheme, Woese and his colleagues sought the most ancient branches of the tree of life. They focused only on the ribosomal RNA gene, disregarding genetic material that might have been acquired more recently by symbiosis or lateral gene transfer. Lateral gene transfer occurs when organisms acquire genes from other organisms in their environment, rather than inherit them. Ribosomal RNA gene analysis involves a tiny portion of the genome (less than 0.1%) that is much more likely to be inherited from ancestors than transferred between species. Woese’s idea is that this gene and a few others like it are the only way to trace parent-to-offspring inheritance, since so many other genes may undergo lateral gene transfer. In a few cases, however, even the ribosomal RNA gene has been laterally transferred.

Two Views of the Origin & Nature of Cells

One major conflict between the five-kingdom and three-domain classifications is the basis for classification, “whole organism” versus molecular DNA sequence of these few, highly conserved genes. Another divergence is the origin and nature of cells. Woese believes the three modern cell types (bacterial, archaeal, and eukaryotic cells) emerged very early in Earth history from a Last Universal Common Ancestor (LUCA) that is now extinct. In Woese’s speculative vision, LUCA was not a cell at all, it swapped genes so freely that it evolved communally and left no fossil, cellular, or molecular trace. The single trunk in Figure

![Figure 3. Monophyly.](image)
This hypothetical tree depicts a monophyletic group in the rectangle (A). This group includes all of the descendants from a single, common ancestor. Group B is not monophyletic because the members of the group have no single, common ancestor.

![Figure 4. Cyanobacteria and Chloroplasts.](image)
Cyanobacteria like the multicellular *Gomphosphaeria* sp. (left) are prokaryotes. Chloroplasts, shown at the right inside cells of the aquatic plant *Ceratophyllum*, were once free-living cyanobacteria that were engulfed but not digested by ancient protists. The scale in the images is close but not exact. *Gomphosphaeria* cells are similar in size to chloroplasts and the spherical colonies of *Gomphosphaeria* are slightly larger than typical plant cells. The table below compares the approximate sizes of the structures shown.

<table>
<thead>
<tr>
<th>STRUCTURE</th>
<th>DIAMETER IN MICRONS</th>
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<tbody>
<tr>
<td><em>Gomphosphaeria</em> colony</td>
<td>50</td>
</tr>
<tr>
<td><em>Gomphosphaeria</em> cell</td>
<td>1-6</td>
</tr>
<tr>
<td>chloroplast</td>
<td>5</td>
</tr>
<tr>
<td>plant cell</td>
<td>30</td>
</tr>
</tbody>
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Right photo by Charles Delwiche; left photo and composite courtesy of Lynn Margulis.
2 represents LUCA. In the three-domain scheme, which separates bacteria and archaea into two distinct lineages that arose independently, the term "prokaryote" is not informative. Woese advocates abandoning this term; he points out that prokaryotes are defined by traits they lack rather than characters they share. Further, the ribosomal gene sequence data indicate that archaeans are more closely related to eukaryotes than to bacteria.

Proponents of the five-kingdom system maintain that DNA sequences are only one among many tools that should be used to classify organisms. In the five-kingdom system, DNA sequence data are the basis for the subkingdoms Archaea and Eubacteria in kingdom Bacteria. But the five-kingdom classification maintains that prokaryotes evolved from a common, cellular origin, well before the appearance of the first eukaryotes. Cell structure, gene organization, reproduction, and metabolism are far more similar in the two groups of prokaryotes than they are between any prokaryote (bacterial or archean) and any eukaryote.

The origin of life, in the five-kingdom system, was the origin of bacteria. Support for this hypothesis is found in both the fossil record and analysis of modern life. The earliest eukaryotes evolved from symbioses between different prokaryotic cells, according to Margulis and others. Symbiosis is a physical association between members of separate species for a significant portion of their life histories (For a discussion of the evolutionary implications of symbiosis, see Case, 2003.) Molecular and morphological evidence clearly point to a symbiotic origin of two classes of eukaryotic organelles: mitochondria and chloroplasts. Margulis and her colleagues also suggest that the nucleus and the eukaryotic motility organelles (cilia and flagella) emerged from an earlier symbiosis that generated the first eukaryotic cell (Margulis & Sagan, 2002). One line of evidence that supports this hypothesis is the connection between mitosis (the division of the nucleus) and motility.

Implications for Educators

Debate about classification systems and techniques unearths fundamental hypotheses about the origin and evolution of life and stimulates discussion about the philosophical underpinnings of taxonomy. Was the earliest life on Earth bacterial, or something wholly different from anything alive today? Did eukaryotes arise independently or as a result of symbiotic mergers? Should phylogenies show only the lineage of highly conserved genes or the history of genetic mergers and acquisitions as well? Imagine a high school biology class equipped with information to discuss these questions. Imagine those students rushing off to the quiz, the ones who were just cramming in the hallway, being asked to evaluate classification systems rather than recite them. It is unlikely that they are even aware of the questions and controversy that characterize biological classification today.

These students may understand characteristics that are used for classification but probably do not realize that the "correct" scheme on the test is a hypothesis about evolution. Chances are, they will be expected only to identify and describe the three domains, five kingdoms, or six kingdoms they have been taught.

An increasing number of biology textbooks and other curricular materials present the six kingdoms of Monera (or Bacteria), Archaea, Protists, Animals, Plants, and Fungi as the fundamental categories of living things. These texts explain that Archaea used to be classified with the Bacteria until molecular evidence indicated that they belong in their own group.

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Reading the scientific literature, I see widespread acceptance of Woese’s three domains, continued practical use of the five kingdoms, and a few pockets of intense debate (see, for example, the paper by Ernst Mayr [1998] and a response from Carl Woese [1998] in *Proceedings of the National Academy of Science*). Absent from scientific discourse is mention of the six kingdoms that high school biology students today are learning about. This six-kingdom classification is not a scientific hypothesis; it is a compromise.

Though reluctant to abandon the five-kingdom system that dominated high school biology textbooks from the 1950s until now, authors and publishers are eager to appear up-to-date. Six kingdoms is a compromise that leaves the five kingdoms largely intact while recognizing the molecular data that establish archaea as a distinct group. It is a tidy solution – expedient and cheap – because it requires revision only to sections of text about taxonomy and bacteria.

But the six-kingdom compromise misrepresents science. It obscures important questions about how life evolves and masks the dynamism of scientific inquiry. Science teachers, curriculum developers, and standards-writers would do better to focus on the logic and evidence of real taxonomy to bring students face-to-face with scientific questions, hypotheses, debates, and the unsolved mysteries of life.

### Criteria for Evaluation of Textbook Discussions of Classification

Some textbooks do a superior job conveying information about the shifting ground of biological classification. Here is a simple guide to evaluate textbook discussions of taxonomy. Textbook discussions of taxonomy should:

- **Provide historical background about the science of taxonomy.**
  
  History is one of the best ways to present science as a human endeavor, and convey a sense that scientific understanding evolves. One textbook that has a lively approach to the history of taxonomy is *Prentice Hall Biology: Exploring Life* (2004). This text discuss the taxonomic systems that each author learned in school; the oldest learned Linnaeus’ two-kingdom system, another learned a three-kingdom model, and the youngest learned the five-kingdom system. The text goes on to discuss the three domains and speculates that “it is quite possible that if you continue your study of biology in the coming years, you may learn about new and different taxonomic systems.”

- **Present modern classification systems as hypotheses about the evolutionary history of life.**
  
  A fundamental principle that underlies modern taxonomy was introduced by Charles Darwin, who wrote in *On the Origin of Species by Means of Natural Selection* (1859), “Our classifications will come to be, as far as they can be so made, genealogies...” Taxonomy should reflect the evolutionary history of life. This principle is essential to understanding how classification systems are developed, revised, and evaluated.

- **Emphasize the process, rather than the results, of classification.**
  
  Textbooks, like teachers, should take every opportunity to portray science as a process. Classification schemes are not merely information retrieval systems, they are hypotheses and, in accordance with Darwin’s mandate, they are hypotheses about the evolutionary relationships among living things. How can these hypotheses be tested? What evidence should be used? At what point does a hypothesis reach the status of a theory? All these questions, which may be posed to rather than answered for students, bring to life the process of reconstructing life’s history, doing the science of taxonomy.

- **Discuss classification systems in the context of the evidence that supports them.**
  
  The results of doing taxonomy, modern classification systems, should be discussed in the context of the evidence that supports them, rather than as mere descriptive categories. Analysis of the differences among classification schemes and unresolved questions will enrich students’ ability to understand and evaluate taxonomic systems. I advocate including both the five-kingdom and the three-domain systems in textbook discussions, but not the six-kingdom compromise, which lacks evidence and discussion in the scientific literature and conceals questions and controversy about the origin and nature of modern cells.

### Acknowledgments

I extend my appreciation to Dr. Lynn Margulis, Micah Dunthorn, Dr. Michael Dolan, and Hannah Melnitsky for valuable feedback on this manuscript, as well as to Dr. W.J. Trewbella of the Virtual School of Biodiversity for providing a copy of the “Five Kingdoms or Three Domains” courseware tutorial for me to evaluate.

### Some Useful Resources For Teaching Taxonomy


An invaluable resource for biology teachers, this book describes and illustrates the defining characteristics of the five kingdoms and the phyla within each. It is the only reference book ever published that includes descriptions, photographs, and analytical drawings of all phyla in the professional literature.


The *Five Kingdoms* CD-ROM follows the same organization as the book but many additional pictures and video clips have been added. It is an excellent resource for classroom presentations or student research.


Students and teachers can explore the definition and history of taxonomy, use identification keys, and learn about tools and methods used in biological classification.

University of California, Berkeley Museum of Paleontology: [http://www.ucmp.berkeley.edu/](http://www.ucmp.berkeley.edu/).

Visit the phylology “wing” of this virtual museum for information about evolution, classification, and specific descriptions of
organisms from diverse groups. The Web site is organized by the three-domain system.

Virtual School of Biodiversity

Five Kingdoms or Three Domains?
Module: For information, see http://vsb.nott.ac.uk/vsb/.

This interactive course is available from the Virtual School of Biodiversity. The module describes the criteria for classification in each system and the characteristics of major groups.

References


