CHAPTER 2

Robert Whittaker & the Classification of Kingdoms

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☐ INTRODUCTION

Imagine walking through a tropical rain forest in Central America. Above your head, a howler monkey roars in disapproval as it hangs from the limb of a *Cecropia* tree. A toucan with its outlandish yellow beak flies lazily above, visible through a small break in the forest canopy. With a brilliant flash of metallic blue an emperor butterfly flits in front of you. A column of leaf-cutter ants crosses the trail, each worker carrying a triangular piece of leaf like a parasol above its head. Unseen beneath your feet, billions of soil bacteria and fungi rapidly digest any leaf that falls from the canopy above, recycling the nutrients to the trees. These are just a few examples of the more than two million species of organisms recognized by biologists. Some taxonomists believe that perhaps thirty million more remain to be discovered. How are these multitudes of living things related? How do we create order out of this chaos of diversity? These are two of the most fundamental questions that biologists have always faced.

Traditionally, biologists divided all living things into two large groups: the plant and animal kingdoms. Many nonbiologists still see the living world this way. Yet, during the Renaissance, when the boundary between the living and nonliving worlds was less sharply drawn, it was common to place minerals into a third kingdom equivalent to the plant and animal kingdoms. Throughout history other three- and four-kingdom systems have occasionally been suggested. Today most biologists favor a five-kingdom system proposed about 25 years ago by the ecologist Robert H. Whittaker.

Despite its current popularity, the logic of this new system was not immediately obvious even to Whittaker himself when he began studying taxonomy in 1957. It took him over ten years to work out the details, and he continued to tinker with the system until his death in 1980. Why did our ideas about classification change so dramatically in response to Whittaker's research during the late 1950s and 1960s? Did the change to a five-kingdom system simply reflect our growing knowledge about the living world around us? If so, is the current system the correct way to classify organisms? Or, as some critics of taxonomy have charged, is classification merely glorified "stamp collecting," where the choice between alternative systems is simply a matter of taste?

Maybe there is another way to look at taxonomy. Perhaps classification systems are like other scientific theories that often change over time. If so, we might expect that at different points in history, biologists would favor different systems of classification. Their choices would partly reflect the state of knowledge about the living world but also reflect the current interests of biologists. As new areas of research emerged, ideas about classification would also change in response. This view of taxonomy as a creative, problem-solving activity is well illustrated by the development of Whittaker's five-kingdom system.

ROBERT WHITTAKER: AN EMINENT ECOLOGIST

When he died of cancer in 1980, Robert Whittaker was one of the most influential ecologists of his day. Aside from his development of the five-kingdom system of classification, he wrote nearly 150 books and articles on almost every important topic in plant ecology. In 1974 he was elected to the National Academy of Sciences, one of the greatest honors that an American scientist can achieve. Shortly before his death, Whittaker was named "Eminent Ecologist" by the Ecological Society of America, the highest recognition of success awarded by that professional association.

Despite his success, Whittaker's career started inauspiciously. Unimpressed by his undergraduate transcript, the Botany Department at the University of Illinois rejected Whittaker's application to graduate school. He was later admitted to the Zoology Department, where he completed a Ph.D. dissertation in community ecology. This study of the distribution of plant communities in the Smoky Mountains of Tennessee eventually became a classic paper in ecology. It is perhaps ironic that such an important study of plant communities (animals are not mentioned in the paper) was completed in a zoology department by a student who could not gain admittance to the graduate program in botany. This episode is instructive for two reasons. First, it shows that sometimes it may be difficult for teachers to recognize scientific potential in a student. Second, it highlights the artificiality of the boundary between zoology and botany. Like many other ecologists of his generation, Whittaker was interested in broad biological problems that did not fit the traditional distinction between plants and animals. His later work on the five-kingdom system of classification is a particularly good example of this broader view of the living world.

Every successful scientist has a distinctive approach to research. Those who knew Whittaker remember the intensity of his personality. He could immerse himself in a new area of research, master the literature of the subject, and create a novel theoretical explanation. The breadth of his biological interests was quite unusual, because most scientists focus on rather narrow lines of research. Many of Whittaker's most important papers involved blunt criticisms of well-accepted ideas and competing theories. This tactic could be intimidating, and some scientists accused him of being arrogant, dogmatic, and overly aggressive in his analyses of opposing views. Early in his career, his scientific style prevented him from publishing some of his research—it took eight years to convince an editor to publish his dissertation. It may also have cost him his first teaching position (he apparently criticized senior professors in his department—a dangerous move for an untenured instructor).

Personality can also influence a scientist's work. Whittaker had a reputation as a maverick in ecological theory, and he often had to defend unpopular ideas. His interest in broad biological problems meant that he sometimes moved out of his own specialty and argued with experts in other fields. Such a strategy involves professional risks, but Whittaker never shied from controversy. He actively pursued very broad, interdisciplinary problems. Perhaps if he had been less combative, his five-kingdom system would not have been successful.

A PRELIMINARY TAXONOMIC SCHEME

When Whittaker began his work, the reigning taxonomic system divided all organisms into the plant and animal kingdoms. Like other reformers before him, Whittaker criticized this system because it did not accurately reflect important biological relationships. Fungi, bacteria, and other distantly related organisms were lumped together in the plant kingdom (Figure 2.1). Animals, for the most part, were easily characterized, but what was to be done with curious creatures such as *Euglena viridis*, which shared characteristics of both plants and animals? Traditionally, both botanists and zoologists had claimed these unusual unicellular organisms that photosynthesize and also ingest food.

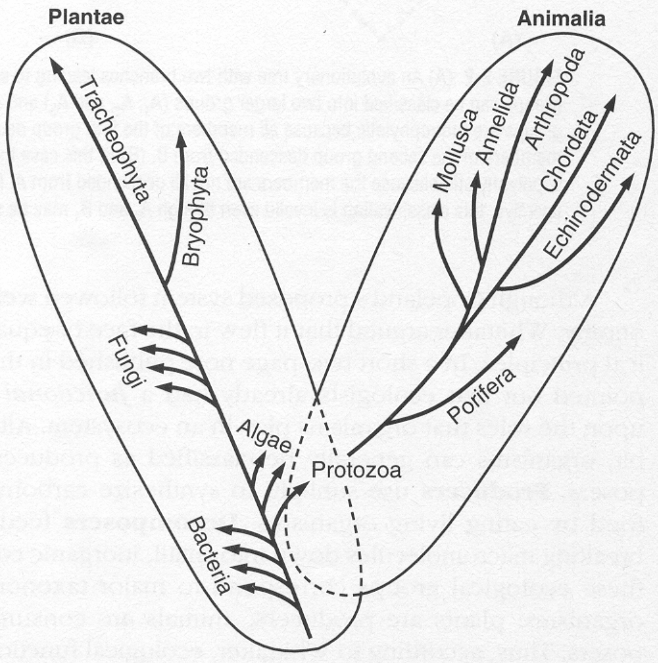

FIGURE 2.1 Whittaker's pictorial representation of the traditional two-kingdom system. Only some of the major phyla are included in this diagram.

Whittaker was equally critical of some earlier attempts to expand the number of kingdoms, particularly a four-kingdom system proposed by H. F. Copeland in 1956. Copeland recognized a new kingdom Monera (or Mychota) for all bacteria and a kingdom Protista (or Protoctista), which included various algae, protozoans, and fungi.

Copeland tried to represent as accurately as possible the important phylogenetic (evolutionary) relationships within these four fundamental groups of organisms. Each kingdom formed a major branch on the evolutionary tree, all members of which were descended from a common ancestor. In other words, all of the members of each kingdom were more closely related to one another than to any members of other kingdoms. The technical term for such a group is **monophyletic**. In a **polyphyletic** kingdom, by contrast, some organisms would be more closely related to some members of other kingdoms than to some members of their own (Figures 2.2(A) and 2.2(B)). By analogy, if you grouped two cousins together because they both have blue eyes but, in the process, separated a brother and a sister because one has blue eyes and one has brown, you would have created something similar to polyphyletic groups. Most taxonomists insist on monophyletic groups because they accurately reflect evolutionary relationships.

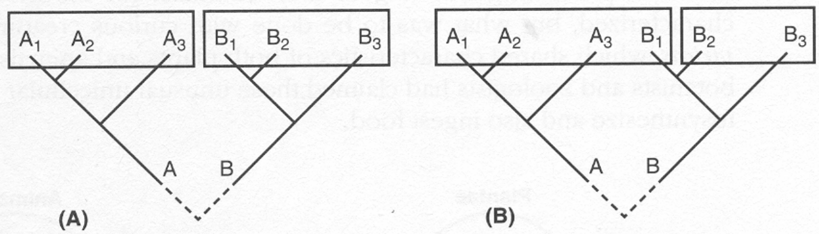

FIGURE 2.2 (A) An evolutionary tree with two branches leading to six present-day groups. These groups can be classified into two larger groups (A_1, A_2, and A_3) and (B_1, B_2, and B_3). These larger groups are monophyletic because all members of the first group descended from A, and all members of the second group descended from B. (B) In this case the group (A_1, A_2, A_3, and B_1) is polyphyletic because the members are not all descended from A. From an evolutionary perspective, this classification is invalid even though A_3 and B_1 may be superficially quite similar.

Although Copeland's proposed system followed well-accepted principles of taxonomy, Whittaker argued that it flew in the face of equally well-established ecological principles. In a short two-page note published in the journal *Ecology*, Whittaker pointed out that ecologists already had a *functional classification system* based upon the roles that organisms play in an ecosystem. Although the groups overlap a bit, organisms can generally be classified as producers, consumers, and decomposers. **Producers** use sunlight to synthesize carbohydrates. **Consumers** obtain food by eating living organisms. **Decomposers** feed on dead organic material, breaking macromolecules down into small, inorganic compounds. In a general way, these ecological groups correspond to major taxonomic groups of multicellular organisms: plants are producers, animals are consumers, and fungi are decomposers. Thus, according to Whittaker, ecological function provided a coherent basis for classifying most organisms that biologists study (Figure 2.3).

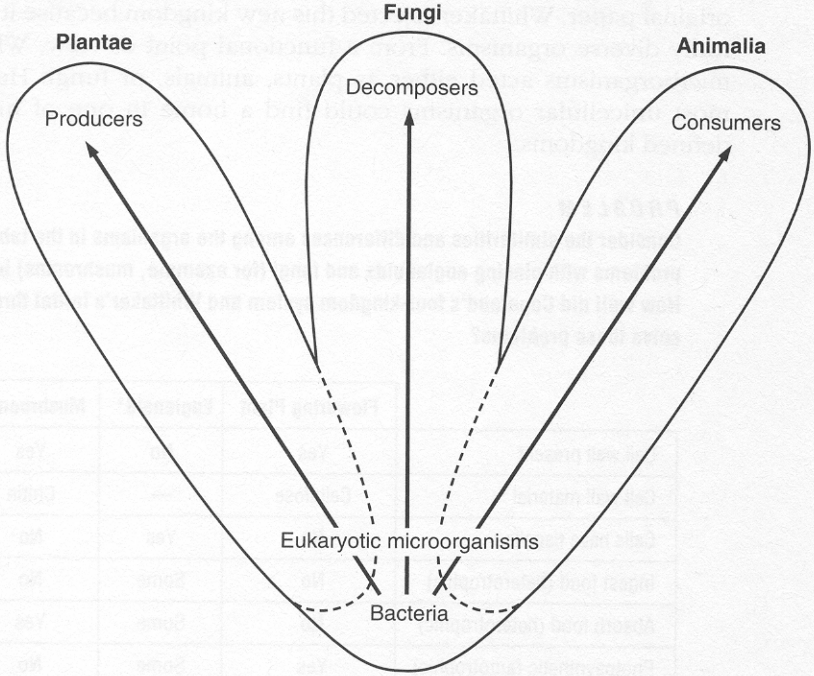

FIGURE 2.3 Whittaker's early three-kingdom system based upon ecological function.

Whittaker believed that this ecological classification system also reflected three major branches on the evolutionary tree. Each branch has evolved in response to a different type of nutrition. Leaves, roots, and conducting tissue in plants have evolved to optimize photosynthesis. Animals, as ecological consumers, have evolved various adaptations for catching and ingesting prey. Fungi, which often live on decaying organic material in the soil, have evolved bodies of ramifying filaments embedded directly in the food supply. Unlike animals, fungi absorb nutrients that they have digested externally.

The ecological and evolutionary justifications for this tripartite division were appealing, but Whittaker realized that the system also had some serious problems. In order to classify all organisms as producers, consumers, and decomposers, Whittaker would be forced to place most bacteria in kingdom Fungi. This made sense ecologically, because most bacteria are decomposers and like the fungi absorb nutrients from a food source that is externally digested. Combining the fungi and bacteria could not be justified on evolutionary grounds, however, because as Whittaker acknowledged, bacteria are no more closely related to fungi than to plants or animals.

Another problem involved more complex unicellular organisms such as algae and protozoans. These creatures are ecologically and phylogenetically diverse. Copeland had placed most unicellular organisms into kingdom Protista, but this kingdom also contained fungi and some other large, multicellular organisms. In his original paper, Whittaker rejected this new kingdom because it would unite ecologically diverse organisms. From a functional point of view, Whittaker believed, all microorganisms acted either as plants, animals, or fungi. He was confident that most unicellular organisms could find a home in one of his three ecologically defined kingdoms.

PROBLEM

Consider the similarities and differences among the organisms in the table. What are the problems with placing euglenoids and fungi (for example, mushrooms) in the plant kingdom? How well did Copeland's four-kingdom system and Whittaker's initial three-kingdom system solve these problems?

	Flowering Plant	Euglenoid*	Mushroom	Vertebrate Animal
Cell wall present	Yes	No	Yes	No
Cell wall material	Cellulose	—	Chitin	—
Cells have flagella	No	Yes	No	Some
Ingest food (heterotrophic)	No	Some	No	Yes
Absorb food (heterotrophic)	No	Some	Yes	No
Photosynthetic (autotrophic)	Yes	Some	No	No
Multicellular organisms	Yes	No	Yes	Yes
Sexual reproduction	Yes	No	Yes	Yes
Energy stored as starch	Yes	No	No	No

*Approximately 1,000 species, including the familiar green flagellate, *Euglena viridis*.

REFINING THE SYSTEM: AN ALTERNATIVE FOUR-KINGDOM PLAN

Whittaker had the germ of an important idea in 1957, but he had worked out few of the details. After his first article, Whittaker immersed himself in the taxonomic literature, particularly the classification of unicellular organisms, which he knew little about. Two years later he admitted that these organisms could not simply be distributed among the kingdoms Plantae, Animalia, and Fungi. A new kingdom Protista would need to be created, but it would be defined quite differently than Copeland's kingdom of the same name. According to Whittaker, all protists must be unicellular. He divided this new kingdom into two parts. The higher protists included all nucleated (**eukaryotic**) unicellular organisms: protozoans, diatoms, euglenoids, and many other microscopic organisms. Nonnucleated (**prokaryotic**) cells made up a lower subkingdom (Figure 2.4). This group included both the true bacteria and the cyanobacteria, an important group of photosynthetic prokaryotes often, but incorrectly, referred to as "blue-green algae." Unlike Copeland, Whittaker excluded all of the fungi, marine algae, and other multicellular organisms from kingdom Protista.

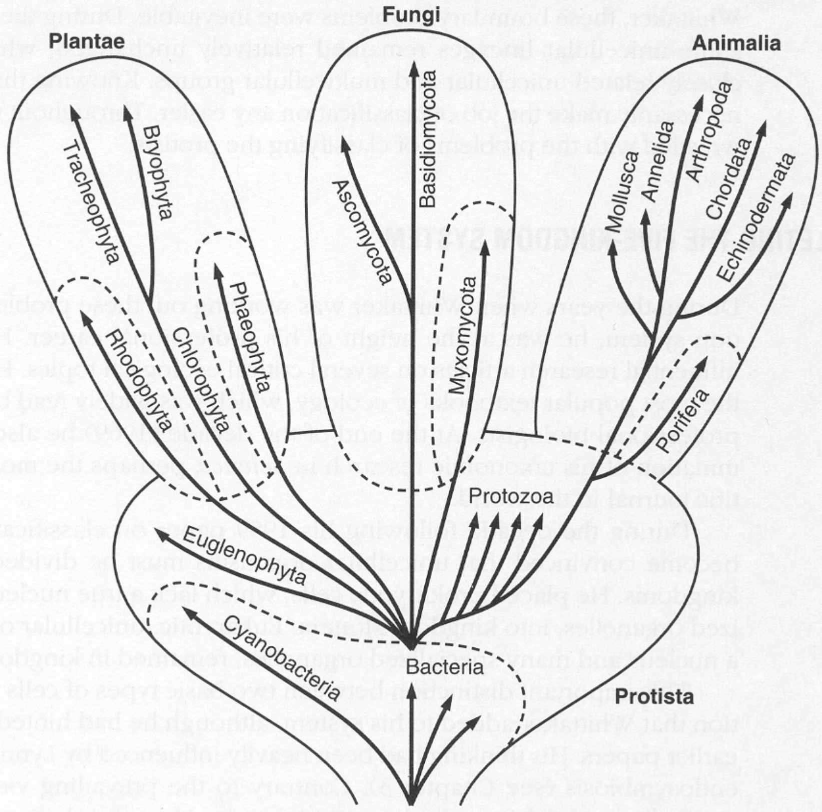

FIGURE 2.4 Whittaker's four-kingdom system. In this scheme, all unicellular organisms belong to kingdom Protista, which is divided into higher and lower subkingdoms.

Whittaker justified his new kingdom because he believed that unicellular organisms formed a distinct evolutionary level or grade. During the distant past, unicellular organisms filled all three fundamental ecological roles: producers, consumers, and decomposers. Some of the unicellular lines had evolved into complex, multicellular organisms, so today most ecosystems are dominated by plants, animals, and fungi. But modern protists—the direct descendants of early unicellular organisms—still carry out these ecological roles in some ecosystems.

Drawing the boundaries of kingdom Protista was troublesome. Whittaker admitted that bacteria were structurally much simpler than the higher protists. Why not place the two groups in separate kingdoms? Such a decision would undermine the ecological basis for defining his kingdoms. Perhaps also for simplicity's sake, Whittaker declined to recognize a separate kingdom Monera—at least in 1959. The upper boundaries of kingdom Protista were also quite fuzzy. Many unicellular protists were very closely related to multicellular plants, animals, or fungi. According to

Whittaker, these boundary problems were inevitable. During the course of evolution some unicellular lineages remained relatively unchanged, while others split into closely related unicellular and multicellular groups. Knowing this, however, did not necessarily make the job of classification any easier. Throughout the 1960s, Whittaker wrestled with the problems of classifying the protists.

COMPLETING THE FIVE-KINGDOM SYSTEM

During the years when Whittaker was working out these problems in his classification system, he was at the height of his professional career. He wrote a string of influential research articles on several critical ecological topics. He completed one of the most popular textbooks of ecology, which was widely read by both students and professional biologists. At the end of the decade (1969) he also presented the culmination of his taxonomic research in *Science*, perhaps the most prestigious scientific journal in the world.

During the decade following his 1959 paper on classification, Whittaker had become convinced that unicellular organisms must be divided into two separate kingdoms. He placed prokaryotic cells, which lack a true nucleus and most specialized organelles, into kingdom Monera. Eukaryotic, unicellular organisms, each with a nucleus and many specialized organelles, remained in kingdom Protista.

This important distinction between two basic types of cells was the last innovation that Whittaker added to his system, although he had hinted at the possibility in earlier papers. His thinking had been heavily influenced by Lynn Margulis's theory of endosymbiosis (see Chapter 3). Contrary to the prevailing view that protists had gradually evolved from prokaryotic bacteria, Margulis claimed that all eukaryotic cells were derived from multiple symbiotic partnerships among prokaryotic cells. According to this theory, some of the specialized organelles of eukaryotic cells had originated as free-living bacteria. If this explanation of cellular evolution was true, then the transition from prokaryotic cells to eukaryotic cells must have occurred relatively quickly. There should be few intermediate forms between the types of cells, and, therefore, the boundary between kingdoms Monera and Protista should be sharply defined (Figure 2.5).

Endosymbiosis was only a provisional theory in 1969, but it certainly strengthened Whittaker's five-kingdom system. All organisms could now be arranged hierarchically into three well-defined evolutionary levels: prokaryotic organisms (kingdom Monera); eukaryotic, unicellular organisms (kingdom Protista); and eukaryotic, multicellular organisms (kingdoms Plantae, Animalia, and Fungi). Upon this evolutionary hierarchy, Whittaker superimposed his original ecological classification based on nutrition: producers, consumers, and decomposers. These ecological distinctions can be seen in the horizontal arrangement of the multicellular kingdoms and in the various evolutionary lines within kingdom Protista (Figure 2.5).

By 1969 the broad outlines of a successful taxonomic system emerged. Because Whittaker used a variety of criteria—evolutionary, ecological, cellular, and molecular—his system appealed to a broad audience of biologists. Compared to the traditional two-kingdom system and Copeland's four-kingdom system, Whittaker's five

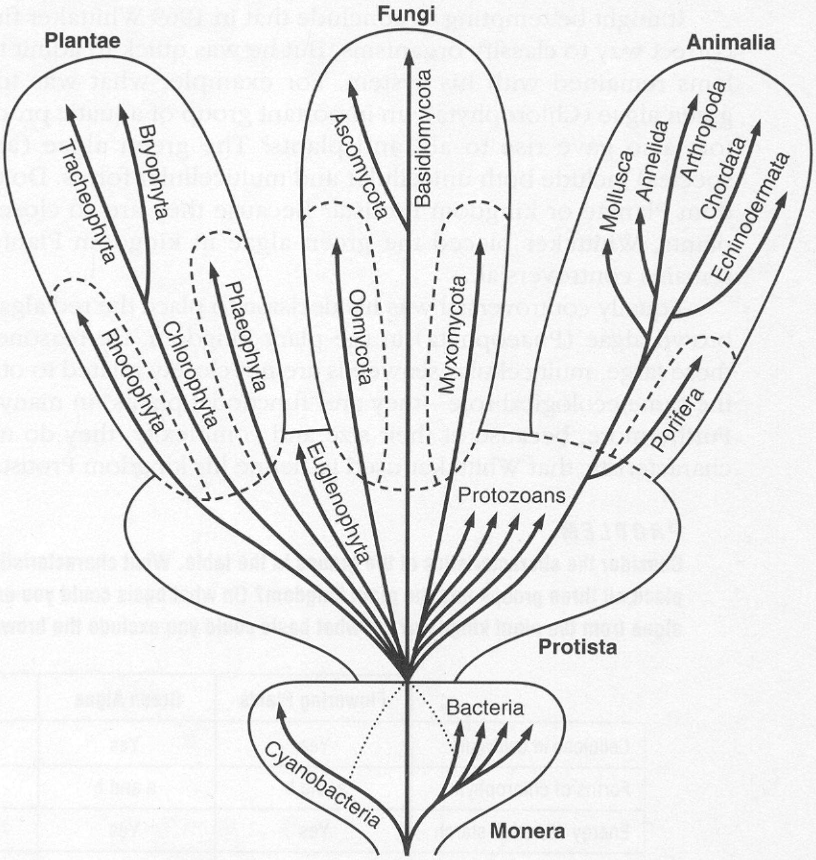

FIGURE 2.5 Whittaker's five-kingdom system. Notice the dotted lines in kingdom Monera indicating the endosymbiotic origin of eukaryotic cells. Also notice that the boundary between kingdoms Monera and Protista is very narrow, because according to the endosymbiotic theory there are few intermediaries between prokaryotic and eukaryotic cells. Ambiguous "problem groups" included in plants, fungi, and animals make each of these multicellular kingdoms polyphyletic in Whittaker's scheme.

kingdoms seemed to be based upon fundamental natural relationships. Whittaker emphasized the differences between his system and its two competitors. By aggressively presenting his argument in a prestigious scientific journal, Whittaker ensured that his critical comparison of taxonomic systems reached a broad audience.

In contrast, neither of the other competing systems had vocal supporters. Few biologists in the later 1960s would strongly defend the outmoded two-kingdom system. Copeland never responded to Whittaker's early criticisms of his ideas, and he died in 1968, a year before Whittaker unveiled the final version of the five-kingdom system. Many biologists initially sympathetic to the four-kingdom system switched allegiance to Whittaker's plan. Within a few years, therefore, the five-kingdom system was almost universally adopted by biologists.

It might be tempting to conclude that in 1969 Whittaker finally discovered the correct way to classify organisms. But he was quick to admit that important problems remained with his system. For example, what was to be done with the green algae (Chlorophyta), an important group of aquatic producers whose ancestors also gave rise to all land plants? The green algae (approximately 7,000 species) include both unicellular and multicellular forms. Do they belong in kingdom Plantae or kingdom Protista? Because they are so closely related to higher plants, Whittaker placed the green algae in kingdom Plantae—a decision that remains controversial.

Equally controversial was his decision to place the red algae (Rhodophyta) and brown algae (Phaeophyta) in the plant kingdom. He reasoned that even though these large, multicellular seaweeds are not closely related to other plants, they play the same ecological role—they are "functional plants" in many marine ecosystems. Furthermore, because of their size and complexity, they do not fit the unicellular characteristic that Whittaker used to define his kingdom Protista.

PROBLEM

Consider the characteristics of the groups in the table. What characteristics could be used to place all three groups into the plant kingdom? On what basis could you exclude the green algae from the plant kingdom? On what basis could you exclude the brown algae?

	Flowering Plants	Green Algae	Brown Algae
Cellulose in cell wall	Yes	Yes	Yes
Forms of chlorophyll	a and b	a and b	a and c
Energy stored in starch	Yes	Yes	No
Vascular tissue	Yes	No	Yes
Multicellular	Yes	Some	Yes
Cells with flagella	No	Some	Reproductive cells
Habitat	Mostly terrestrial	Mostly freshwater	Mostly marine

Whittaker realized that a plant kingdom including the seaweeds would be polyphyletic. The shared similarity in ecological roles between land plants and seaweeds seemed too compelling to ignore, however. As an ecologist, Whittaker was willing to accept a polyphyletic plant kingdom, but most taxonomists found this unacceptable. They modified Whittaker's system by placing the red and brown algae into kingdom Protista—a decision that makes this kingdom a hodgepodge of unicellular and multicellular organisms.

Whittaker was aware of the problems facing his five-kingdom proposal, and he continued to debate the issues until his death in 1980. He struggled with the conflicting demands of a system that would reflect important ecological principles while still accurately portraying evolutionary relationships. Just as important was the demand that the system be convenient to use, both by students and professional biologists. One critic, for example, claimed that a truly monophyletic classification of protists would require 20 separate kingdoms. Such a system might accurately reflect evolutionary history, but Whittaker pointed out that it would be needlessly cumbersome. A five-kingdom system was more reasonable, but it meant compromising some well-established taxonomic principles and accepting many ambiguities.

☐ EPILOGUE

According to Whittaker, the uncritical acceptance of the two-kingdom system before 1969 was largely due to a distinction that humans make between the large organisms they most often encounter: plants and animals. This common-sense dichotomy became enshrined in the organizational structure of biology. Most biologists identified themselves either as botanists or zoologists, and many university departments were organized along these lines. The newer five-kingdom system called into question the logic of the plant-animal dichotomy. Although many universities still have botany and zoology departments, most biologists now recognize that this distinction is artificial and does not reflect the most important boundaries in the natural world.

In Whittaker's five-kingdom system a new dichotomy was recognized. The distinction between prokaryotes and eukaryotes became the most important boundary in the living world. All organisms seemed to fit neatly into one of these two categories, and Lynn Margulis's endosymbiotic theory explained why this should be the case. What were the consequences of this change? Some biologists have emphasized the positive influence that Whittaker and Margulis had on directing research toward previously little-studied groups of unicellular organisms. Better understanding the prokaryote-eukaryote boundary became an important biological problem. But other biologists claim that this distinction became a "new dogma" and that the biology of prokaryotes was taken for granted by biologists who were primarily interested in eukaryotic cells and how they evolved.

Carl Woese has spent his career studying several unusual groups of prokaryotes referred to as the archaebacteria. These organisms have fundamentally different molecular, biochemical, and ecological characteristics than other bacteria. The archaebacteria are intriguing because they often exist in extreme habitats characterized by high temperatures, high salinity, and high acidity. Some (methane producers) are of vital human importance. Largely due to the work of Woese and his colleagues, most biologists now recognize the archaebacteria as a separate subkingdom. Woese, however, believes that a more radical restructuring is in order. According to Woese, archaebacteria are so different from all other organisms that they should be placed in a separate taxonomic group. He would erect a new system with three superkingdoms or "domains": Archae (archaebacteria), Bacteria (all other bacteria), and Eucarya (all eukaryotic organisms). Although most biology textbooks ignore this proposal, a few now place the archaebacteria into a sixth kingdom. The ongoing debate over the status of these unusual prokaryotes serves to warn us that systems of classification, like all scientific theories, are open to revision.

QUESTIONS AND ACTIVITIES

1. What does this case show about the following aspects of doing biology?
   — revision of scientific theories
   — role of assumptions in creating new theories
   — interrelationships among scientific disciplines
   — the role of personality in scientific creativity
2. The two-kingdom system was accepted by most biologists and naturalists for hundreds of years. Why do you think this way of classifying the living world was so popular?
3. Why do you think fungi and bacteria were originally classified as plants rather than animals? What changes in biology made this classification unsatisfactory?
4. Many evolutionary biologists reject the use of comparative terms such as *higher* and *lower*, or *primitive* and *advanced*, when describing groups. Such comparisons are value laden and may mislead readers into believing that evolution is progressive, always leading to greater complexity. Does Whittaker's five-kingdom diagram have such evolutionary implications? Could the diagram be drawn in a way that does not imply progressive evolution? Would such a diagram be an improvement over Whittaker's originals? *Note:* many different five-kingdom diagrams exist. Compare Figure 2.5 with several different diagrams that you find in biology textbooks.
5. There continues to be disagreement about where to draw the boundaries dividing the five kingdoms. Compare the classification scheme presented in your textbook with others that you find in the library. Do the authors justify their placement of "problem groups" in one kingdom or another? Discuss the advantages and disadvantages of each classification scheme.

SUGGESTED READING

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