Five Kingdoms, More or Less: Robert Whittaker and the Broad Classification of Organisms

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Robert Whittaker's five-kingdom system was a standard feature of biology textbooks during the last two decades of the twentieth century. Even as its popularity began to wane at the end of the century, vestiges of Whittaker's thinking continued to be found in most textbook accounts of biodiversity. Whittaker's early thinking about kingdoms was strongly shaped by his ecological research, but later versions were also heavily influenced by concepts in cell biology. This historical episode provides insights into important intellectual, institutional, and social changes in biology after World War II. Consideration of the history of Whittaker's contributions to the classification of kingdoms also sheds light on the impact of Cold War politics on science education and educational reforms that continue to shape the presentation of biological topics in introductory textbooks today.

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During the late twentieth century, Robert Whittaker's five-kingdom system was a standard feature of biology textbooks, serving as an important organizing scheme for discussing biodiversity. Even as its popularity waned at the end of the century, vestiges of Whittaker's thinking continued to be found in textbooks. Beginning with the germ of an idea in 1957, Whittaker significantly revised his concept in a series of articles published during the subsequent decade. He started with a three-kingdom system that challenged the traditional plant–animal dichotomy, quickly proposed an alternative four-kingdom system, and arrived at his well-known five-kingdom system only after a decade of critical reflection. At last, Whittaker had crafted a system that biologists and educators found attractive because it seemed to capture fundamental properties of living organisms. At its roots, the five-kingdom system was an ecological idea, but Whittaker increasingly relied on cell biology—particularly, the distinction between prokaryotes and eukaryotes—as a central organizing principle for later versions of his system. Thus, the five-kingdom system reflected important intellectual developments in biology during the post–World War II era. Equally important, the success of Whittaker's system owed much to changes in the institutional structure of biology and in science education during the Cold War. Although some of Whittaker's ideas eventually fell victim to molecular systematics, cladistics, and other recent biological developments, the persistence of his system testifies to its broad appeal.

Whittaker's classification of communities and kingdoms

Robert Whittaker (1920–1980) was one of the most influential modern ecologists and made important contributions to a wide range of fields (Westman and Peet 1985). Although the five-kingdom system was only a minor part of his work, it reflected two of Whittaker's fundamental interests. The first was the structure and function of communities and ecosystems. Whittaker's early research on biogeochemical cycles was focused on trophic levels, which provided the initial idea for his kingdom system. The second interest was what Whittaker referred to as "broad classification"—classifying communities and kingdoms in a rigorous way (Whittaker 1948, 1959, 1962, 1972, 1978).

Early in his career, Whittaker became known as one of the critics responsible for overthrowing Frederic Clements' idea that plant communities are highly organized systems comparable to organisms (Westman and Peet 1985, Nicolson and McIntosh 2002, Kohler 2008). Clements' organismic idea implied that the boundaries between communities were quite sharp and well defined, but Whittaker's dissertation on the vegetation of the Smoky Mountains demonstrated that populations and communities were independently scattered along environmental gradients (Whittaker 1948, 1956). Ecotones between communities were usually gradual and ill defined. In his dissertation, Whittaker struggled with his research's implications for classifying communities. The philosophical position that he took was a form of

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nominalism. Although he believed that populations and species were real, Whittaker argued that communities had only a "low degree of reality" (pp. 168–170); indeed, they were simply names applied by ecologists to areas with similar vegetation (Whittaker 1948). In the field, the ecologist was faced by a multitude of plant populations with broadly overlapping distributions. The task for the ecologist was to analyze these distributions and then impose subdivisions on what was, in fact, a continuum (Whittaker 1948).

The tension between the belief that species are distributed independently and the necessity of classifying vegetation into a coherent system provided a creative spark that drove much of Whittaker's later research (Whittaker 1962, 1972, 1978). Although he acknowledged that classifying vegetation always involved a large degree of subjectivity, he hoped that the methods employed by ecologists could be rigorously objective. Achieving this goal led Whittaker to develop mathematically sophisticated methods of ordination (Whittaker 1978) but also to develop simple graphical approaches illustrating how the broad pattern of plant communities could be explained in terms of a few climatic variables (figure 1). Although he was quick to point out that numerous exceptions occurred and that community boundaries could never be precisely predicted by temperature or rainfall, Whittaker claimed that his mosaic diagrams captured the "broad relations of natural communities" (Whittaker 1970, pp. 64–65; also see Whittaker 1948, 1956). Modified versions of these graphical representations became standard features in biology and ecology textbooks. Whittaker employed similar diagrams to represent the relationships among kingdoms. Using the two axes of mode of nutrition and cellular organization, Whittaker was able to present a conceptual map of the broad contours of the living world (figure 2). The important point that needs to be stressed is that although Whittaker was drawn into taxonomic controversies over kingdom classifications, his early and enduring ideas about classification were strongly shaped by his experiences studying plant communities as a graduate student.

Biology during the Cold War

By coincidence, Whittaker (1957) published his first article on kingdoms just a few months before the launch of Sputnik 1, but the success of the five-kingdom system owed much to the Cold War context within which it was created. Biologists eagerly turned to large-scale funding from the National Science Foundation, the Atomic Energy Commission, and other post–World War II federal agencies to support new areas of research. Partly as a result, traditional taxonomy and natural history became marginalized. E. O. Wilson later noted that during the 1960s, "biology spun through a ninety-degree turn in its approaches to life" (p. 225) as many biologists turned away from studying whole organisms and biodiversity in order to focus on cells and molecules (Wilson 2006). This trend away from traditional botany and zoology was evident not only in the rise

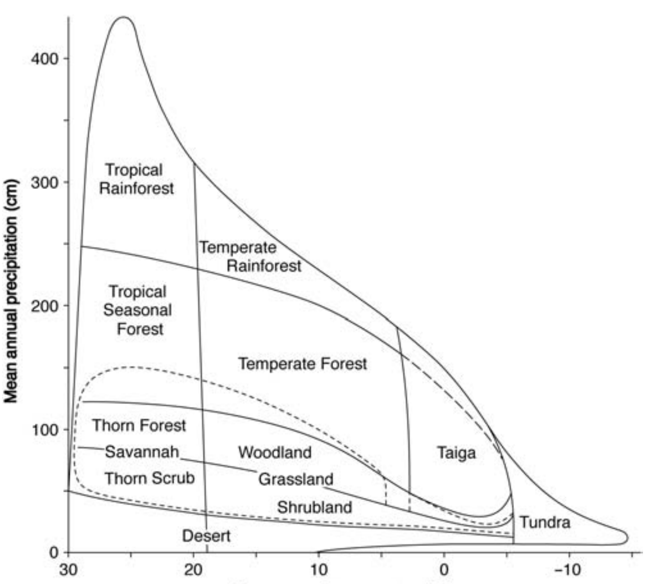

Figure 1. Diagram depicting major types of plant communities in relation to temperature and precipitation (in centimeters [cm]). The dotted lines enclose environments where several different community types might exist, depending on variables other than temperature and precipitation. Source: Figure illustrated by John Norton, adapted from Whittaker (1970).

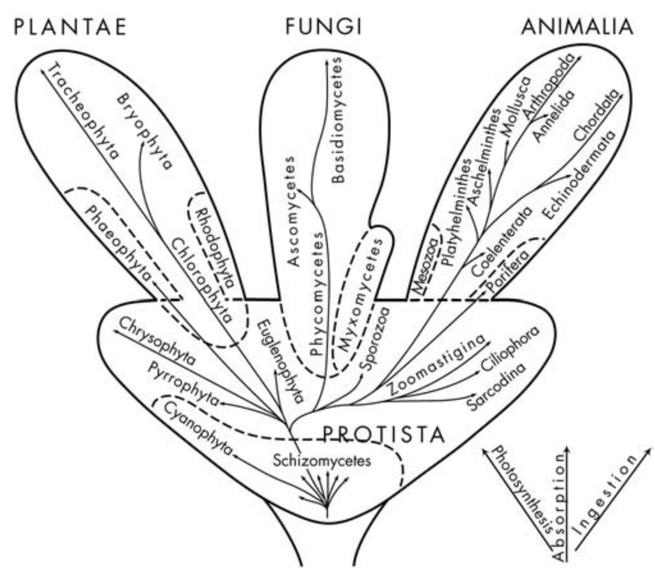

Figure 2. Whittaker's early four-kingdom system, based on three modes of nutrition and the distinction between unicellular and multicellular body plans. The dotted lines represent groups that include both unicellular and multicellular forms. Source: Reprinted from Robert Whittaker, "On the Broad Classification of Organisms," Quarterly Review of Biology 34 (1959): 210–226, with permission from University of Chicago Press.

of molecular biology but also in ecology. In his influential ecology textbook, Eugene Odum (1959) described biology as a layer cake: The slices represented taxonomic divisions such as entomology or ornithology, but the "more basic" and fundamental layers represented disciplines such as genetics, cell biology, and ecology. These broad intellectual changes were reflected institutionally, by traditional botany and zoology departments' increasing consolidation into biology departments or replacement by specialized departments along disciplinary lines that cut across taxonomic divisions. Whittaker's own career tracked these changes. Although much of his research fell within traditional plant ecology, he began his professional career in a research position in which he studied the biogeochemical cycling of radionuclides at the Hanford National Laboratory in central Washington. This ecosystem-level research—conducted within the immediate Cold War context of US nuclear weapons production—strongly focused Whittaker's sights on trophic levels (Whittaker 1961), which provided the intellectual foundation for his initial foray into the classification of kingdoms.

The development of Whittaker's five-kingdom system

Shortly after leaving Hanford, Whittaker published a brief note in *Ecology*, arguing that the traditional dichotomy between plants and animals was artificial (Whittaker 1957). According to Whittaker, a better classification would recognize three broad kingdoms based on ecological trophic levels: producers (plants), consumers (animals), and decomposers (fungi and bacteria). He acknowledged that these kingdoms did not correspond very closely with taxonomic groupings in the traditional two kingdoms or with alternative three- and four-kingdom revisions that had been proposed earlier by some taxonomists. Instead, he appealed to a combined ecological and evolutionary justification: All ecological communities, past and present, included producers, consumers, and decomposers. Although these groups were heterogeneous, the three nutritional modes that characterized the trophic levels were conceptually clear cut and represented three "major directions of evolution." Whittaker argued that recognizing kingdoms by ecological function provided an intellectual coherence that was lacking in systems based on morphological characteristics or speculative phylogenetic relationships.

Not only did Whittaker intend to replace the traditional two-kingdom system, but he also intended to forestall several competing three- and four-kingdom alternatives. In particular, Whittaker took aim at a four-kingdom proposal published a year earlier by Herbert Copeland (1956). Copeland also criticized the traditional plant–animal dichotomy, but both his approach and his solution were strikingly different from Whittaker's. Primarily interested in "lower organisms," Copeland proposed a new kingdom, Mychota, to include all prokaryotic organisms and another kingdom, Protoctista, for all eukaryotic organisms that were not plants or animals. The appeal of this system rested on making the plant and animal kingdoms monophyletic and solving the problem of intermediates like *Euglena* that had been claimed by both botanists and zoologists. Combining the fungi, various algae, protozoans, slime molds, and other organisms that lacked true tissues made the kingdom Protoctista very heterogeneous. Nonetheless, Copeland claimed that this new kingdom was monophyletic because in the distant past, all of its diverse members shared a common ancestor. Copeland placed bacteria, which had traditionally also been included in the plant kingdom, into the kingdom Mychota on the basis of their unique prokaryotic cell structure.

In his book *The Classification of Lower Organisms*, Copeland (1956) provided a detailed taxonomic system subdividing his new kingdoms into phyla, classes, and orders. He paid considerable attention to important taxonomic issues of nomenclature, priority, stability, and phylogenetic relationships. For example, he provided a long historical account of various taxonomic revisions and group names that led to his new kingdom, Protoctista. Whittaker had little use for these technical taxonomic considerations and argued that kingdoms should correspond primarily to clear-cut ecological distinctions and should serve only secondarily as taxonomic units. Whittaker was particularly critical of Copeland's decision to include the fungi, red and brown algae, and numerous groups of microscopic eukaryotes in kingdom Protoctista. According to Whittaker, "The kingdom Protoctista seems more a product of taxonomic definitions than a grouping of organisms with coherent meaning or common evolutionary theme" (Whittaker 1957, p. 536). From Whittaker's perspective, fungi and algae were two very different types of organisms, and it made no sense—ecologically or evolutionarily—to place them in the same kingdom. Imposing order on a complex and chaotic nature required conceptual clarity. From Whittaker's perspective, Copeland's kingdom Protoctista badly failed this criterion.

It would be tempting to portray Copeland as Whittaker's unsuccessful competitor, and, indeed, Whittaker effectively used the taxonomist as a target for criticism. At a time when taxonomy was being marginalized in American biology, Copeland's elaborate taxonomic scheme provided an easy foil for Whittaker's conceptually simpler approach. However, Copeland played at least two important positive roles in the subsequent development of Whittaker's approach to kingdoms. In the late 1950s, Whittaker was relatively unfamiliar with microorganisms, and Copeland's detailed system acted as an important spur to developing Whittaker's later ideas about unicellular life. Second, Copeland's distinction between prokaryotic and eukaryotic cells eventually became a critical part of Whittaker's final five-kingdom system, even though he resisted it for over a decade.

The clash of ideas between Whittaker and Copeland was evident in a long review article published two years later (Whittaker 1959). Analyzing the history of kingdom classification, Whittaker presented a clear overview of several alternative systems. At the same time, he argued forcefully for his own ideas. This didactic approach was one that Whittaker also effectively used in his writing about community classification (Whittaker 1962, Westman and Peet 1985). In both cases, Whittaker argued that there were no absolute criteria for choosing among competing classification systems but only relative criteria, which included important practical, theoretical, and aesthetic considerations. A successful system needed to be useful and biologically coherent but also needed to provide the "subjective satisfaction" of a well-organized set of categories (Whittaker 1962). Weighing the advantages and disadvantages of alternative systems, Whittaker argued cogently for a new four-kingdom system that he had devised, which included plants, animals, fungi, and a new kingdom that Whittaker called *Protista* (figure 2).

Throughout the 1959 article, Whittaker contrasted his ecological approach with the taxonomic approach used by Copeland and other biologists who classified kingdoms. First, he continued to argue for "functional" kingdoms that were primarily ecological and only secondarily taxonomic groupings. The idea that kingdoms should be defined in terms of ecological function was the origin of Whittaker's approach to the subject, and in his 1959 article, he tied this idea more explicitly to the ecosystem theory that had rapidly developed during the 1950s (Hagen 1992, Golley 1993, Kingsland 2005). Second, Whittaker argued for a classification system that was broadly evolutionary, although not necessarily phylogenetic. Phylogenetic relationships were important but, according to Whittaker, monophyletic grouping needed to be balanced with other important criteria, such as ecological function and cellular organization. In addition, Whittaker resisted a purely phylogenetic basis for classification because he considered many of the phylogenetic claims made by Copeland and other taxonomists to be highly speculative. Before the widespread acceptance of cladistics, which did not occur until the 1970s, Whittaker's views on phylogeny were held by many biologists.

The differences between Whittaker's ecological approach and Copeland's traditional taxonomic approach are evident in the way they treated several important groups of organisms. Both Whittaker and Copeland argued that the fungi should be removed from the plant kingdom, but for very different reasons. Copeland chose to group the fungi with other "lower" eukaryotic organisms that lacked tissues in his kingdom Protoctista. Although Copeland claimed that the kingdom was monophyletic, Whittaker challenged this view and also argued that the Protoctista were biologically "incoherent" because the kingdom was a hodgepodge of unicellular and multicellular organisms with very different modes of nutrition. Whittaker created a separate kingdom for the fungi, not because the group was monophyletic, but because the fungi were united by their ecological role as multicellular decomposers in ecosystems. This emphasis on decomposition as an ecological process worthy of defining a kingdom reflected Whittaker's own work with biogeochemical cycling and also the growing prominence of biogeochemistry in ecosystem ecology (Hagen 1992). To further support a separate kingdom for the fungi, Whittaker pointed to recent research that cast doubt on the belief that modern fungi had descended from photosynthetic ancestors similar to filamentous algae. According to Whittaker, the evidence against this earlier claim undercut both the traditional grouping of fungi within the plant kingdom and Copeland's decision to combine the fungi with various algae in his kingdom Protoctista.

In place of the Protoctista, Whittaker (1959) now proposed a purely unicellular kingdom, Protista—an idea that he attributed to Ernst Haeckel. Although he acknowledged that many groups such as Chlorophyta had both unicellular and multicellular members, Whittaker argued that the distinction between unicellular and multicellular body plans was conceptually clear cut and biologically meaningful. Furthermore, Whittaker pointed to the symmetry between the multicellular kingdoms of animals, plants, and fungi and the various subgroups within the Protista. In both cases, one could find the three major directions of evolution and ecological functions: producers, consumers, and decomposers. Therefore, by using two fundamental characteristics—mode of nutrition and cellular organization—Whittaker created a system of classification that was both simple and conceptually coherent (figure 2).

The addition of kingdom Protista to Whittaker's original three-kingdom scheme highlighted another major difference between his ecological approach and Copeland's taxonomic approach. Copeland restricted his plant kingdom to a monophyletic group of vascular plants and their close relatives. Whittaker originally wanted to include all producers in the plant kingdom. He was now willing to relegate unicellular algae and cyanobacteria to his new kingdom Protista, but Whittaker continued to place all multicellular producers in kingdom Plantae. Whittaker's functional plant kingdom was an admittedly polyphyletic group of land plants, brown algae, and red algae. He justified this grouping on the grounds of both ecological function and cellular structure. The brown and red algae included large, complex, multicellular organisms that played the same ecological role in marine ecosystems that plants played in terrestrial ecosystems: They were, indeed, "functional plants."

Whittaker's delineation of the kingdoms Plantae and Protista was later rejected even by some of his strongest supporters (Margulis 1971, 1974), but it highlights the distinction between his functional kingdoms and traditional taxonomic kingdoms. It also illustrates the philosophical underpinnings of Whittaker's approach to classifying both kingdoms and communities. Just as one could not always use environmental variables to precisely determine whether an area would be forest or grassland, so one could not neatly place groups such as the Chlorophyta into one or another kingdom on the basis of cellularity (figures 1 and 2). Despite the ambiguity, Whittaker (1959) argued that his system provided the better alternative because it was conceptually more coherent than Copeland's system. Interestingly, later biologists tended to define kingdom Protista using a combination of criteria borrowed from both the Whittaker and the Copeland systems.

A decade later, Whittaker published his definitive five-kingdom system in the high-profile journal *Science*, ensuring that his ideas would reach a broad audience (Whittaker 1969). Although the article repeated much of the line of reasoning that Whittaker employed in 1959, there were several substantive differences in both content and style. Most importantly, Whittaker now accepted Copeland's earlier decision to place all prokaryotic organisms into their own kingdom. Although he had considered this possibility in 1959, Whittaker made the more conservative decision to include the bacteria as a subkingdom of the Protista. The prokaryotic kingdom Monera now joined kingdoms Protista, Fungi, Plantae, and Animalia in the final version of Whittaker's system.

Whittaker justified adding the new kingdom Monera to his system for several reasons. By the end of the 1960s, the prokaryote–eukaryote distinction was a mainstream idea accepted by leading microbiologists (Sapp 2005, 2006, 2009). Citing the still-controversial endosymbiotic theory being championed by Lynn Margulis as an attractive explanation for the evolution of eukaryotic cells, Whittaker now claimed that the prokaryote–eukaryote boundary represented the most fundamental division in the living world. Finally, Whittaker argued that the absorptive nutritional mode that characterized most Monerans was the original method of gaining energy. Photosynthesis had evolved in a few Monerans, but the three nutritional modes became well established only after the first eukaryotic protists evolved through endosymbiosis. Therefore, organisms could be placed into one of three structural grades: prokaryotes, unicellular eukaryotes, and multicellular eukaryotes. Within the two higher grades, various lineages of producers, consumers, and decomposers could be clearly identified, although only producers and decomposers were found at the prokaryotic grade.

Stylistically, Whittaker departed from the broad review of competing systems that he had used in 1959 and presented classification as a choice between two alternatives: Copeland's four-kingdom system and Whittaker's new five-kingdom system. Both the importance of the choice and the rationale for making it were also new. Whittaker now emphasized the pedagogical importance of revising the traditional two-kingdom system with one that better represented the broad contours of the living world. Noting that several introductory biology textbooks questioned the plant–animal dichotomy, Whittaker had an obvious motivation for highlighting the differences between the two alternative replacements. Compared with Copeland's elaborate taxonomic system, Whittaker claimed that his functional kingdoms rested on two criteria that biologists considered important and that students could easily understand.

The five-kingdom system and Cold War educational reforms

The Soviet launch of Sputnik 1 in 1957 served as a potent catalyst for educational change (Grobman 1969, Sundberg et al. 1992, Rudolph 2002). Exploiting fears that the United States was falling behind the Soviet Union in science, educational reformers pushed for revamping the nation's outdated approach to biology. Critics complained that existing textbooks were little more than dry surveys of plant and animal phyla, emphasizing anatomical description rather than unifying principles (Grobman 1969, Rudolph 2002). Drawing on expanded federal funding, new organizations such as the Biological Sciences Curriculum Study (BSCS) and the Commission on Undergraduate Education in the Biological Sciences (CUEBS) designed innovative curricula, textbooks, and laboratory exercises (Sundberg et al. 1992, Engleman 2001). Highlighting how difficult this was, BSCS published three different high school textbooks because of disagreements over fundamental biological principles. Two of these textbooks (the "blue" and "green" versions) departed radically from earlier textbooks by emphasizing evolution, the process of science, and unifying principles of cell and molecular biology (blue version) and ecology (green version). Students were exposed to a variety of organisms but in the context of discussing these broader biological concepts, rather than as a taxonomic survey.

CUEBS never produced comparable products at the college level, but its recommendations influenced the writing of new college textbooks that were profoundly different from their predecessors (Sundberg et al. 1992). Popular pre-Sputnik textbooks were based on the pedagogical assumption that understanding topics such as genetics or ecology required a thorough familiarity with plant and animal taxa (Johnson et al. 1956). Therefore, chapters on heredity and ecology were tucked at the end of the book, where critics complained they were rarely read (Rudolph 2002). Conscious of the educational reforms proposed by CUEBS, later editions of these established textbooks added more chapters on cell biology, genetics, and ecology (Johnson et al. 1966) but retained the pedagogical premise that familiarity with biodiversity was a prerequisite for understanding the unity of life. By contrast, a new generation of post-Sputnik textbooks emphatically rejected this traditional pedagogical approach. Rather than detailed taxonomic and anatomical surveys, these books shifted much greater attention to cell biology, genetics, development, animal behavior, and ecology (figure 3). These topics were organized around three overarching themes: evolution, the molecular and cellular basis of life, and energetics.

The new design adopted by the authors of post-Sputnik textbooks posed serious challenges for discussing biodiversity. The emphasis on unifying principles, combined with a much-reduced taxonomic survey, demanded a more compelling way to describe the broad classification of organisms than the traditional plant–animal dichotomy. By emphasizing the importance of both ecological trophic levels and cellular structure, Whittaker's five-kingdom system organized biological diversity using the very themes that new biology textbooks stressed so heavily. Still, the two most popular post-Sputnik textbooks did not immediately adopt Whittaker's system but only gradually came to embrace it in

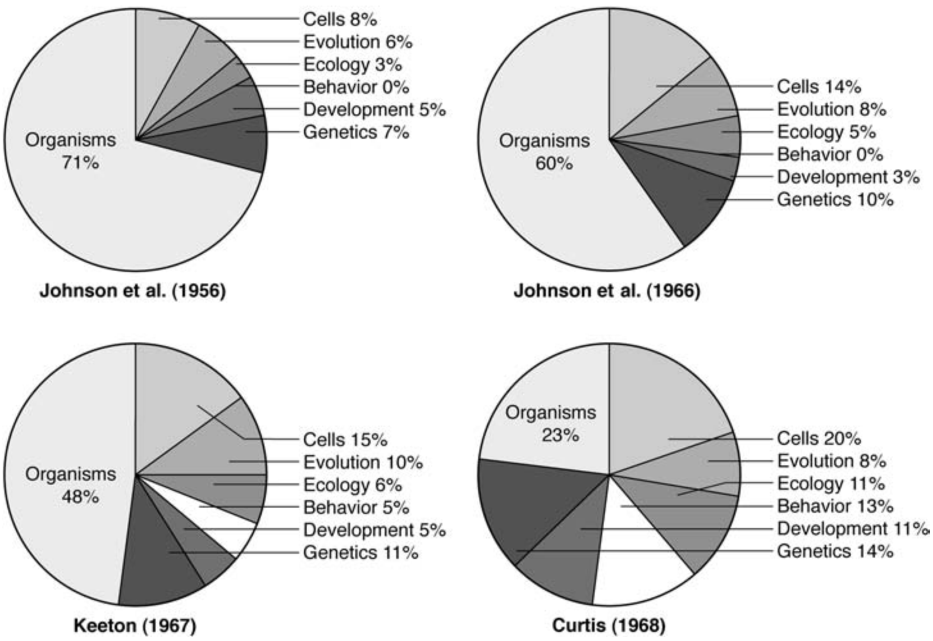

Figure 3. A comparison of coverage of topics in pre- and post-Sputnik introductory biology textbooks.

later editions. Examining this transition sheds light on the difficulties of presenting biodiversity in the context of a new biology that deemphasized traditional taxonomy and the study of organisms.

William Keeton was an invertebrate taxonomist, but he also turned a boyhood interest in training homing pigeons into a successful research career in avian orientation and navigation at Cornell University (Emlen 1981). When the life sciences were reorganized at Cornell, Keeton moved from the Department of Entomology to a newly established program in Neurobiology and Behavior. During this period, he designed and taught an extremely popular introductory biology course and spent five years writing his highly successful textbook (Keeton 1967, Emlen 1981).

In some ways, Keeton's (1967) *Biological Science* was a major departure from older textbooks, but it initially retained the traditional focus on plants and animals. Indeed, Keeton's teaching innovation was combining botany and zoology into a single course (Emlen 1981), and this was reflected in the textbook that he wrote. Although he briefly discussed the kingdom Monera, Keeton stuck closely to the traditional taxonomic system of plants and animals. He acknowledged the weaknesses of the plant–animal dichotomy but justified his choice in two ways: First, organisms familiar to students tended to be either plants or animals, so the traditional two-kingdom system provided a commonsense way to organize biodiversity. Most of the examples used by Keeton to illustrate unifying biological principles were drawn from multicellular plants and animals. Second, Keeton argued that phylogenetic relationships among protists and fungi were highly speculative and provided little support for newer classification systems. Although he briefly presented several alternative systems in a table, it was not until the third edition, in 1979, that Keeton adopted Whittaker's five-kingdom system. By this time, Whittaker, who was Keeton's colleague at Cornell, was acting as a consultant on the textbook. Not only did Keeton now use Whittaker's system to reorganize the five chapters on biodiversity, but he also devoted a page of the introductory chapter to discussing the logic of Whittaker's system in relation to the other major themes of the textbook. Thus, the five-kingdom system joined natural selection, energetics, and cell theory as broad explanatory principles that provided the foundation for discussing all of the other topics in the book. This approach was widely copied by later biology textbooks.

Helena Curtis's (1968) *Biology* was an even greater departure from traditional textbooks, because less than 25% of the book was devoted to organisms (figure 3). Curtis was a highly successful science writer, who made up for a lack of professional training in biology by enlisting a lineup of distinguished scientists as consultants. The result of this collaboration was a textbook widely acclaimed for its engaging style (Luria 1969, Villager 2005). Curtis initially dismissed the choice of kingdom classification as a technical matter of interest only to professional taxonomists (Curtis 1968). Like Keeton, she emphasized that phylogenetic relationships—particularly among the protists—were highly speculative. Because there was little compelling support for any of the competing systems, Curtis was ambivalent about her choice of adding a third kingdom of microorganisms to the traditional plant and animal kingdoms. Despite her initial reluctance to strongly endorse any system of kingdom classification, Curtis's approach to introducing biological concepts harmonized well with the logic of Whittaker's approach. Like Keeton, Curtis emphasized energetics at both the cellular and ecological levels, and she presented the distinction between autotrophs and heterotrophs as fundamental. Similarly, her emphasis on cellular evolution (including endosymbiosis) and the prokaryote–eukaryote dichotomy for understanding cell structure provided another rationale for eventually accepting the five-kingdom system.

Curtis significantly reorganized the chapters of her textbook for the third edition, published in 1979, using two broad thematic divisions: the unity of life and the diversity of life. Despite misgivings about Whittaker's kingdom Protista, Curtis now endorsed the five-kingdom system as the best alternative for understanding the general contours of biodiversity. Just as Darwinian evolution, cell theory, and energetics served as fundamental principles for understanding the unity of life, Curtis now used the five-kingdom system as a basic principle underlying the section of her book devoted to the diversity of life. Both the "unity and diversity of life" themes and the use of Whittaker's system for organizing diversity were widely copied by later textbooks that tried to compete with the textbooks of Curtis and Keeton during the final two decades of the twentieth century.

Why Keeton and Curtis did not more quickly adopt Whittaker's five-kingdom system is an intriguing historical question. Whittaker suggested that the continued use of the two-kingdom system by biologists was largely attributable to intellectual conservatism and that acceptance of the five-kingdom system required a kind of cultural evolution in biological thinking (Whittaker 1969, Whittaker and Margulis 1978). The two-kingdom system had long been criticized, and several alternatives had been suggested, beginning in the late nineteenth century. In the first two editions of his textbook, Keeton acknowledged these alternatives without strongly endorsing any of them. His continued use of the plant–animal dichotomy for organizing biodiversity until the late 1970s was a conservative element in an otherwise highly innovative textbook. When Keeton and Curtis finally adopted the five-kingdom system in the third editions of their textbooks, both of them justified the switch on the basis of a gradual shift among biologists toward supporting Whittaker's system. Several reasons can be suggested for the gradualness of this change. The decline of traditional botany and zoology—as disciplines, departments, and introductory courses—made the plant–animal dichotomy less attractive, but this shift occurred in a piecemeal way during the Cold War era. Conversely, the increasing prominence of ecology in the biology curriculum—partly in response to popular environmental movements—reached a peak during the 1970s. This, in addition to new developments in cell biology, contributed importantly to the success of Whittaker's system. Perhaps most significantly, an alliance between Whittaker and Lynn Margulis closely linked the five-kingdom system with the controversial but increasingly influential theory of endosymbiosis (Margulis 1970, 1971, 1974, Whittaker and Margulis 1978). Margulis quickly embraced the five-kingdom system, focused considerable scientific attention on unicellular organisms, and played a major role in refining Whittaker's problematic kingdom Protista. The growing linkage between endosymbiosis and the five-kingdom system appears to have been important for both Curtis and Keeton, who each placed the topics back to back in the third editions of their textbooks. All of these changes took time, but a decade after Whittaker introduced his system, the tide had turned decisively toward the acceptance of five kingdoms. Suffice it to say that during the final two decades of the twentieth century, all major biology textbooks followed Keeton and Curtis in using some version of Whittaker's five-kingdom system to organize discussions of biodiversity.

Domains and kingdoms

Ironically, as the five-kingdom system became a prominent and well-established feature of introductory textbooks, the rationale for Whittaker's approach was being undermined in a number of important ways. Molecular systematists rejected the earlier belief that phylogenetic relationships among protists and bacteria were inherently speculative and perhaps unknowable (Sapp 2009). As molecular sequences rapidly accumulated, along with advanced computational techniques to analyze them, confidence grew among biologists that monophyletic classification of formerly problematic groups was within reach. This undercut the logic of Whittaker's system, which was broadly evolutionary but not phylogenetic. Whittaker's belief that phylogeny was only one of several equally valid criteria for classification had also been widely shared when he began writing about kingdoms, but with the rapid rise of cladistics during the 1970s, biologists increasingly rejected this view. The seemingly fundamental distinction between prokaryotes and eukaryotes was also challenged by the discovery of the archaea (initially referred to as *archaebacteria*) and Carl Woese's claim that all living organisms belonged to one of three broad domains: archaea, bacteria, and eukarya (Woese et al. 1990, Sapp 2009). Woese was highly critical of the prokaryote–eukaryote dichotomy, both as a basis for classification and as a supposedly useful distinction between types of cells (Sapp 2006, 2009). Woese claimed that the dichotomy was based on a false distinction that was phylogenetically misleading; he opposed defining the kingdom Monera negatively, on the basis of the lack of a structure (i.e., the nucleus); and he argued that the dichotomy was incompatible with the three-domain system that he championed. In short, he wanted to eliminate the terms *prokaryote* and *eukaryote* from the biological vocabulary (Sapp 2006).

Textbooks quickly adopted Woese's idea of three domains, but his critique of the prokaryote–eukaryote dichotomy was ignored. Therefore, Woese's three domains and the remnants of Whittaker's five kingdoms rest somewhat uncomfortably in modern textbook discussions of biodiversity. Many textbooks recognize a new kingdom for the archaea, but both the archaea and bacteria are typically discussed in the chapter devoted to prokaryotic life. Similarly, although most textbook authors have abandoned the polyphyletic kingdom Protista, they continue to devote a chapter to "protists." The persistence of Whittaker's ideas about kingdoms cannot be explained entirely by intellectual inertia but rather by genuine ambiguities in the broad classification of organisms. This ambiguity is reflected in the spirited debate over the implications of recognizing Woese's three domains and the controversy over Woese's critique of the prokaryote–eukaryote dichotomy (Mayr 1998, Woese 1998, Sapp 2006, 2009). Despite the popularity of Woese's domains, most educators find the distinction between prokaryotes and eukaryotes to be useful, and textbooks continue to highlight the significance of the two cell types. The strong support that some prominent biologists continue to voice for the five- (or six-) kingdom system—albeit in modified form—is another reason that textbooks have not completely abandoned Whittaker's approach. For example, Margulis and Chapman (2009) criticized Woese's domains for being based exclusively on molecular data and ignoring other important biological characteristics of organisms. As a result, Margulis and Chapman continued to argue for maintaining a prokaryotic superkingdom that includes both bacteria and archaea. Margulis and Chapman also pointed out that a completely monophyletic classification would have so many kingdoms that it would lose any pedagogical value for students' understanding of biodiversity. This pedagogical point highlights the tension between basing a kingdom system strictly on phylogeny while still "providing a synoptic view of the living world" (Whittaker and Margulis 1978, p. 11). The need for this "synoptic view" reinforces the major strengths of Whittaker's system: its simplicity and close ties to easily understandable ecological and cellular principles. Whittaker's grouping of organisms according to cellular structure and ecological function constituted a manageable and conceptually pleasing scheme—one that seems difficult to completely abandon, despite its acknowledged shortcomings.

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