

# New Concepts of Kingdoms of Organisms

Evolutionary relations are better represented by new classifications than by the traditional two kingdoms.

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There are those who consider questions in science which have no unequivocal, experimentally determined answer scarcely worth discussing. Such feeling, along with conservatism, may have been responsible for the long and almost unchallenged dominance of the system of two kingdoms—plants and animals—in the broad classification of organisms. The unchallenged position of these kingdoms has ended, however; alternative systems are being widely considered (1–18) and are appearing in many introductory biology texts (19–24). My purpose in this article is to discuss the merits of two classifications which depart from the traditional two kingdoms, the systems of Copeland (1–3) and Whittaker (4, 5).

## Two-Kingdom System

Man is terrestrial, and he sees around him two major groups of organisms of very different adaptation to nutrition on land—the photosynthetic, rooted, higher plants, and the food-ingesting, motile, higher animals. So distinct in way of life, direction of evolution, and kind of body organization are these groups that a concept of dichotomy—plants versus animals—is almost inescapable if they are considered by themselves. The two groups became the nuclei around which concepts of the plant and animal kingdoms were developed by early naturalists. The kingdoms have been part of the formal classification of living things since Linnaeus (25).

Mosses, liverworts, and macroscopic algae are clearly plants in their photosynthetic and nonmotile way of life, and (though the photosynthetic process itself was not understood by early naturalists) these forms were grouped

with the higher land plants. The higher fungi on land are nonmotile, and their apparently “rooted” manner of growth suggested the plants. It thus seemed reasonable to assign fungi to the plant kingdom, and some students believed that they had evolved from algae. The wealth of unicellular life discovered by microscopists offered greater difficulty. Some forms were motile and ingested food, however, and were naturally regarded as one-celled animals or protozoans. Others were nonmotile and photosynthetic, hence one-celled plants. There remained a wide range of unicellular forms in which nonmotility and flagellate or pseudopodial motility, and ingestive, photosynthetic, and absorptive nutrition, were combined in various ways which were neither clearly plant-like nor animal-like. In a number of cases plant-like and animal-like unicells were connected by a series of closely related intergrading forms within the same major taxon. There remained also the bacteria which, though few are photosynthetic and many are motile, seemed better treated as plants because of their walled cells. The plant and animal kingdoms are products of a process of concretion, by which groups of organisms which were aquatic, or fungal, or microscopic, or more than one of these, were added around the nuclear concepts of plant and animal derived from higher land organisms.

It was recognized that the two-kingdom system came into difficulties in treatment of the unicellular organisms, since some groups of these were claimed both for the plant kingdom by botanists and for the animal kingdom by zoologists. The system seemed, however, a reasonable treatment of the living world in terms of two kingdoms and evolu-

tionary directions (Fig. 1). In time the system seemed not reasonable but axiomatic; suggestions of other kingdoms were regarded as the idiosyncrasies of individuals. There were such suggestions, however, as the limitations of the two-kingdom system became more evident. I have reviewed proposals for other kingdoms in more detail elsewhere (5).

## Limitations of the Two-Kingdom System

The difficulties of the two-kingdom system may be summarized in relation to four points.

1) *The protists.* The most obvious difficulty is that for which we use *Euglena* and its relatives as the exemplar for students—the intergrading combinations of plant and animal characters, the fusion of the kingdoms, among unicellular organisms. Because of the impossibility of clear division of the unicells into plants and animals, a number of authors suggested third kingdoms of lower organisms (26–32). Hogg (26) observed the intergradation of plants and animals among lower forms and proposed for them the *Regnum Primi-genum* and the term “Protoctista.” Haeckel (29) proposed separating the lower organisms as the kingdom “Protista.” Haeckel included the sponges in this kingdom in one treatment (29), and the fungi in another (30); but the kingdom comprised primarily, and in later treatments (31, 32) only, the unicellular organisms.

Although content of the third kingdom of lower organisms and use of “Protoctista” and “Protista” have varied, two principal possibilities may be distinguished. The lower kingdom may either comprise only unicellular organisms (including those forming colonies of unicells), the kingdom Protista of Haeckel (29–32) and others (33, 20, 21, 5, 14), or the lower kingdom may comprise the unicells plus other organisms which lack the kind and degree of tissue differentiation characteristic of higher plants and animals, thus including fungi and most or all algae, the kingdom Protoctista of Hogg (26) and Copeland (3). (In either of these concepts bacteria and blue-green algae may be excluded as indicated below.)

Some authors (10, 12, 15, 19, 22) prefer the more familiar term “Protista” for the second concept. Different inter-

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pretations of the Protista are possible from Haeckel's own treatments of the kingdom. Protists are conceived (29, 31) as unicellular and as organisms which form no tissues [in a later statement (32), "... organisms which as a rule remain unicellular throughout life (monobia), less frequently they form loose cell communities (coenobia) by repeated cleavage, but never real tissues."]. They are contrasted with the tissue-forming organisms of the kingdom Histonica, comprising the Metaphyta (including higher fungi, higher algae, and higher land plants) and Metazoa (multicellular animals).

From this contrast of unicellular and tissue-forming conditions, the difficulty has resulted. Kingdoms defined by the unicellular condition and by somatic tissue differentiation exclude a broad middle ground, occupied by organisms which lack evident somatic tissue differentiation but are clearly multicellular or multinucleate as organisms, as indicated by cell differentiation and interdependence (sponges), or somatic organ differentiation (higher algae, mosses), or differentiation of reproductive tissues and organs (higher fungi). I suggest in consequence that the Protista may best be defined not by lack of tissue differentiation but by lack of tissue formation—absence of integration of cells (or nuclei and cytoplasm) into the one or more tissues of a multicellular (or multinucleate) organism. Tissue differentiation in some lower multicellular and multinucleate organisms (some algae, fungi, and sponges) is limited to a single somatic tissue, plus reproductive cells, tissues, or organs distinct from it. For clarity and consistency terms and concepts for the lower kingdoms will be distinguished throughout this article. The kingdom Protista comprises organisms which are unicellular or unicellular-colonial and which form no tissues. The alternative kingdom, Protoctista, will be conceived, as by Copeland (3), as a broader kingdom of unicellular, multicellular, or multinucleate organisms which mostly lack somatic tissue differentiation, including higher algae and fungi.

2) *The monerans*. Haeckel (29-32) regarded the bacteria and blue-green algae as protists without nuclei and placed them in the group Moneres or Monera, subordinate to the kingdom Protista. Recent work has made more evident the profound differences of organization between bacterial cells and those of other organisms (19, 34). Cells of bacteria and blue-green algae lack

mitochondria and plastids, nuclear membranes and mitotic spindles, the endoplasmic reticulum and Golgi apparatus, vacuoles, and advanced (9+2-strand) flagella, among the organelles characteristic of the cells of other organisms. Nuclear material is probably a single strand of DNA without histones, dividing by means other than mitosis; sexual reproduction is apparently both infrequent and incomplete in the sense that only partial recombination of genetic material of cells may result from bacterial conjugation and other processes. Bacteria and blue-green algae also resemble one another and differ from other organisms in biochemical characteristics, including their method of ornithine synthesis, the apparently limited occurrence of sterols, sensitivity to antibiotics, and cell-wall composition (35, 36).

These contrasts between the procaryotic cells of bacteria and blue-green algae, and the eucaryotic cells of other organisms, define the clearest, most effectively discontinuous separation of levels of organization in the living world (19, 37, 38). The idea of ancient cellular symbioses, and the evolution of chloroplasts from blue-green algae and mitochondria from aerobic bacteria living

within other unicells, offers an attractive suggestion on the origin of part of this difference of organization (39). Margulis (38) has added a further, more striking hypothesis—origin of the (9+2-strand) flagellum and the centriole and spindle figure of the eucaryotes from a symbiotic, spirochaete-like organism—and on the basis of this hypothesis and other cytological and biochemical evidence considered the phylogenetic pattern of the living world. Symbiotic origin of the eucaryotic cell is accepted as a hypothesis here, but the difference between procaryotes and eucaryotes remains a line of division deserving recognition in a current system of broad classification. The bacteria are not plants in either way of life or evolutionary relation to other plants; and the blue-green algae, which are functional plants, are widely separated in their cell organization from all other plants. Most authors who consider alternatives to the two-kingdom system separate the bacteria and blue-green algae as either a subkingdom of the Protista (9, 5) or more commonly as the kingdom Monera (1, 7, 8, 10, 12-15, 22, 24) or Mychota (2, 3).

3) *The fungi*. Are the fungi plants, if the bacteria are not? There are reasons to judge that they are not (40-45). (i)

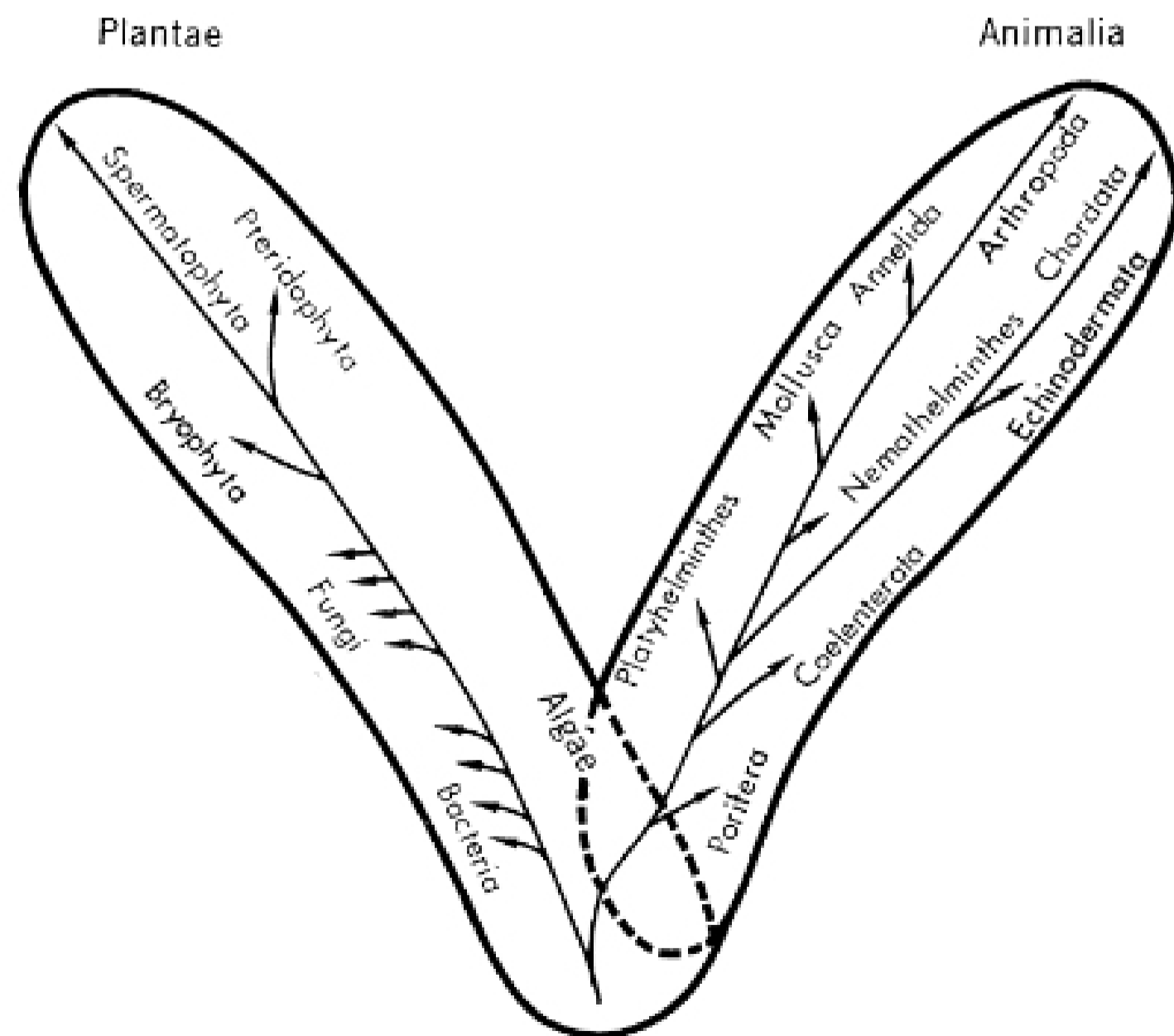


Fig. 1. A simplified evolutionary scheme of the two-kingdom system as it might have appeared early in the century. The plant kingdom comprised four divisions—Thallophyta (algae, bacteria, fungi), Bryophyta, Pteridophyta, and Spermatophyta. Only major animal phyla are indicated.

They were separately derived from the unicells. Although earlier authors speculated on derivation of fungi from algae (46, 47), it now seems likely that the lower fungi (chytrids and others) include a number of groups polyphyletically derived from different colorless flagellate ancestors, and that the higher fungi (Ascomycetes, Basidiomycetes) were derived from one of these groups of lower fungi (40, 43, 48-50, 36). (ii) Their organization is very different from, and nonhomologous with, that of the plants (44, 45, 4, 5). The characteristic somatic organization of the higher fungi, the syncytial mycelium with protoplasm flowing in a system of tubes, could hardly be less like that of the true plants. Reproductive structures and the dicaryotic condition (combining nuclei of different individuals in the same syncytial or multinucleate tissue without nuclear fusion) are different from, and nonhomologous with, the reproductive structures and diploid condition of the higher plants. Many lower fungi are not mycelial but have a different organization of the chytrid type—a globular spore-case with (in many species) slender protoplasmic rhizoids extending into the food source. The spore-case is at first unicellular, then becomes multinucleate, and finally many-celled as the flagellated zoospores or reproductive swimmers are formed and released. It is probable that only convergences relate the structures and life cycles of the fungi to the algae on the one hand, and to the mycelial bacteria (actinomycetes) on the other. (iii) The nutritive mode and way of life of the fungi differ from those of the plants. So far as is known the fungi have been wholly nonphotosynthetic from their origin from unicells to their present diversity of forms. Fungi characteristically live embedded in a food source or medium, in many cases excreting enzymes for external digestion, but in all cases feeding by absorption of organic food from the medium. Their organization, whether mycelial, chytrid, or the unicellular of yeasts, is adapted to this mode of nutrition.

Convenience still places the fungi in the plant kingdom in many textbooks. It may be fair, however, to observe the extent to which this is a position of convenience; for the fungi are a separate, major group of organisms of different origin, different direction of evolution, and different organization in adaptation to a different primary nutrition from that of the plants. The fungi are separated from the plants in most

recent proposals on broad classification and are placed either in the kingdom Protoctista (3, 9, 13, 19, 22) or in a separate kingdom Fungi (5, 8, 14).

4) *Nutritional modes.* When the significance of bacteria and fungi in natural communities was unrecognized, it seemed reasonable to think of two major modes of nutrition for the kingdoms—ingestive in the animals, and in the plants primarily photosynthetic (and secondarily absorptive). There are, however, not two principal modes of nutrition but three—the photosynthetic, absorptive, and ingestive. The three modes largely correspond to three major functional groupings in natural communities, the producers (plants), reducers (saprobes, that is, bacteria and fungi), and consumers (animals) (4, 5, 51). The importance of the reducers in the cycling of materials in ecosystems appears to exceed that of the consumers. In evolution ingestive nutrition was a development secondary to the absorptive nutrition of most monerans and many eucaryotic unicells. Both protozoans with food vacuoles and metazoans with digestive tracts have probably evolved from absorptive flagellates, and in this evolution internalized the process of food absorption and added to it the process of ingestion. One may consider that the eucaryotic plants also have internalized the absorption of food through a membrane, that surrounding the chloroplast as symbiont and organelle. The three modes of nutrition imply different logics on which the evolution of structure in higher organisms was based (44, 4, 5).

Photosynthesis has implied evolution among higher plants of: (i) nonmotile life with structure based on walled cells differentiated into organs including (ii) blades or leaves as organs for concentration of chloroplast-containing cells and photosynthetic activity, and (iii) stipes or stems as organs to support these in favorable light conditions, with (iv) holdfasts to hold the plant in its place or roots to hold the plant and provide access to soil water and nutrients, and, (v) in the latter case, vascular tissue to conduct materials between roots and leaves by way of the stem, hence (vi) an intermediate level of somatic tissue differentiation (higher than fungi, lower than animals). The direction as stated has been realized to different degrees in a number of independent evolutionary lines of plants including higher green algae, red algae, brown algae, mosses, and vascular plants.

Ingestion in animals has implied evo-

lution of: (i) a motile, food-seeking life in most cases, requiring evolution of both (ii) the sensory-neuro-motor complex of tissues, organs, and organ systems which make possible perception of and response to food and (iii) the digestive-circulatory-excretory complex for food and waste processing and transport, and in larger forms a system of external respiration; these systems implying, and serving to support (iv) a complexly differentiated structure of diverse, highly specialized tissues of wall-less cells, functioning at high metabolic levels in support of active life, the complex structure requiring in turn (v) highly developed mechanisms of integration and internal regulation through the nervous, circulatory, and endocrine systems. The logic has led to levels of structural and functional complexity among animals which are without parallel among other organisms, and ultimately toward complexity of inherited behavior or toward intelligence. It has led also to a diversification of structural designs without clear relation to one another, recognized by systematists in the large number of animal phyla, which is without parallel in other groups of organisms. (There are 20 phyla listed for the Eumetazoa in Table 1, and some authors recognize 25 to 30.)

In adaptation to absorption higher fungi have evolved: (i) nonmotile life embedded in the food supply, with (ii) mycelial organization combining maximum surface of contact with food with free movement of food and protoplasm through the mycelial system, while (iii) only the reproductive organs emerge from the food supply to release spores. The low level of somatic tissue differentiation in the fungi is as much a correlate of their way of life as the high level in the animals is of theirs. Diversification of the higher fungi is expressed, rather, in reproductive structures; and their classification is largely based on these.

These logics based on nutrition are the central meaning of the plant and animal kingdoms as long recognized, and of the fungi as a third major direction of evolution. The same nutritive modes necessarily appear among the unicells. Absorption is the principal nutritive mode among the bacteria; but blue-green algae and certain bacteria are photosynthetic or chemosynthetic, while *Bdellovibrio* and some of the myxobacteria are motile (but absorptive) predators on other unicells. All three modes and all possible transitions and