CLASSICS

Whittaker's Five Kingdoms of Organisms: Minor Revisions Suggested by Considerations of the Origin of Mitosis*

From 4th century BC to 17th century AD, a simple classification of living organisms into plants and animals, introduced by the Greek philosopher Aristotle, was in use. Carolus Linnaeus introduced the binomial nomenclature of plants and animals but continued with the two kingdom classification. Ernst Haeckel observed single-celled organisms in the 19th century and placed them in a new kingdom called Protista in 1866. Herbert Copeland recognized that Protista comprised both prokaryotes and eukaryotes. He placed eubacteria and blue-green algae into a fourth kingdom called Monera (prokaryotes). Robert Whittaker assigned fungi into their own kingdom, thus creating a five-kingdom classification of living organisms. Although Lynn Margulis was a champion of the five-kingdom classification, she also recognized that the Protista in Whittaker's classification consisted of organisms that were not phylogenetically related. She applied the principle that all eukaryotes originated from prokaryotes via endosymbiosis of protomitochondrion and protoplastids (for alga and plants). She proposed that Monera that arose in the early Precambrian era (1–3 billion years ago) were ancestral to Protista that arose in the late Precambrian. She proposed that unicellular eukaryotes in the modified Protista kingdom were ancestral to plants, animals, and fungi, respectively.

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NOTES AND COMMENTS

WHITTAKER'S FIVE KINGDOMS OF ORGANISMS: MINOR REVISIONS SUGGESTED BY CONSIDERATIONS OF THE ORIGIN OF MITOSIS

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Whittaker's (1969) new system of classification into five kingdoms (Monera, Protista, Animalia, Plantae and Fungi) has made a fundamental contribution to the clarification of relationships among lower organisms. Although it was constructed without consideration of any particular concept of the relationships between prokaryotes and eukaryotes it reflects remarkably well the evolutionary concepts of the symbiotic theory (Sagan, 1967; Margulis, 1970). Since Copeland's (1956; discussed by Whittaker, 1969) was the only sufficiently detailed taxonomic work recognizing the biological discontinuity between prokaryotic and eukaryotic microbes (Stanier et al., 1970) available to me at the time of my discussion of modern evolutionary criteria in "Thallophytes" (Margulis, 1968) I adopted Copeland's four kingdom system. Whittaker's excellent new

TABLE 1. *The Five Kingdom Classification modified after Whittaker (1969).*

Kingdom	Examples of organisms	Approximate time of evolution (millions of years ago)	Major traits that environmental selection pressures acted on to produce	Major significant selective factor in the environment
Monera	All prokaryotes: bacteria, blue green algae, mycelial bacteria, gliding bacteria, and so forth	Early-Middle Precambrian (3000–1000)	uv photoprotection, photosynthesis and aerobiosis	solar radiation, increasing atmospheric oxygen concentration
Protista	All eukaryotic algae: green, yellow-green, red and brown, and golden-yellow; all protozoans, flagellated fungi, slime molds and so forth	Late Precambrian Early Paleozoic (1500–500)	classical mitosis and meiosis: obligate recombination each generation; more efficient nutrition	depletion of organic nutrients
Animalia	Metazoa: all animals developing from blastulas	Phanerozoic (700 on)	tissue development for heterotrophic specializations: ingestive nutrition	transions from aquatic to terrestrial and aerial environments
Plantae	Metaphyta: all green plants (above green algae)	Phanerozoic (700 on)	tissue development for autotrophic specializations: photosynthetic nutrition	transitions from aquatic to terrestrial environments
Fungi	Amastigomycota: conjugation fungi, sac fungi, club fungi, yeasts	Phanerozoic (700 on)	tissue development, dikaryotic, advanced mycelial development: absorptive nutrition	nature of nutrient source, transitions from aquatic to terrestrial environments

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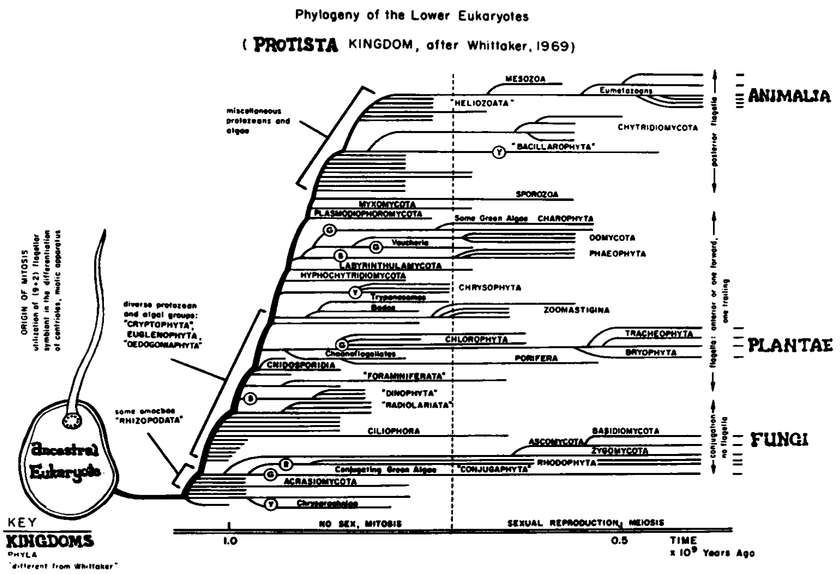

FIG. 1. Phylogeny of the Protista Kingdom (revised from Sagan, 1967 after Whittaker, 1969 with changes as noted in the text). Circle represent plastid homologies: Y = yellow, G = green, R = red or blue, B = brown (Margulis, 1970).

system, which I hope will ultimately prove generally acceptable to biologists, incorporated into it the most attractive aspects of Copeland's earlier contribution. Whittaker's systematics is most consistent with the theory of the evolution of prokaryote microbes in the early Precambrian, their subsequent adaptation to increasing ambient oxygen concentrations due to blue green algal photosynthesis, followed by the origin of the eukaryotic cell by serial symbioses in the Late Precambrian (Margulis, 1969, 1970). Whittaker's work suggests modifications of my Table 1 (Margulis, 1968) and eukaryote phylogeny (Sagan, 1967). Accordingly the revisions are presented here (Table 1, Figure 1).

Although the overall taxonomic scheme of Whittaker is extremely consistent with the theory (Margulis, 1970) recent work, (for example on the unique primitive mitotic cytology of dinoflagellates, Kubai and Ris, 1969) suggests that some of Whittaker's protist phyla notably the "Chlorophyta," "Pyrophyta" and "Sarcodina" arbitrarily contain vastly different organisms. His phylum Sarcodina admittedly places together asexual multinucleate amoebae (*Pelomyxa palustris* probably does not even contain mitochondria, Daniels and Breyer, 1967) with the much more advanced heliozoan rhizopods and specialized radiolarians (Grell, 1967). Figure 2 shows my suggested modifications of Whittaker's system that takes into account a concept not stressed by him: the protozoans and nucleate algae represent a large group of organisms with flagellated heterotrophic eukaryote ancestors that diverged from each other during the Precambrian evolution of mitosis (Margulis, 1970). The genetic entity responsible for the basal body of the (9 + 2) flagellum differentiated to form the centrioles and centromeres of mitosis; these evolutionary steps were prerequisite for the subsequent development of meiosis. Eukaryote protists therefore comprise distinct widely divergent groups of microbes (recognized by Copeland, 1956, as heterogeneous and only distantly related to each other). These heterogeneous protists represent polyphyletic evolutionary "experiments" leading toward the ultimate establishment of mitosis and regular meiosis. Presumably the three major (probably) monophyletic and regularly sexual kingdoms (green plant; eumetazoan animal; amastigote true fungi) evolved independently from eukaryotic protist ancestors. The "phyla" in quotes in Figure 2 show deviations from Whittaker's scheme based on these concepts. The removal of all but the higher plants

Modifications of Whittakers New Concepts of Kingdoms and Phyla of the Lower Organisms

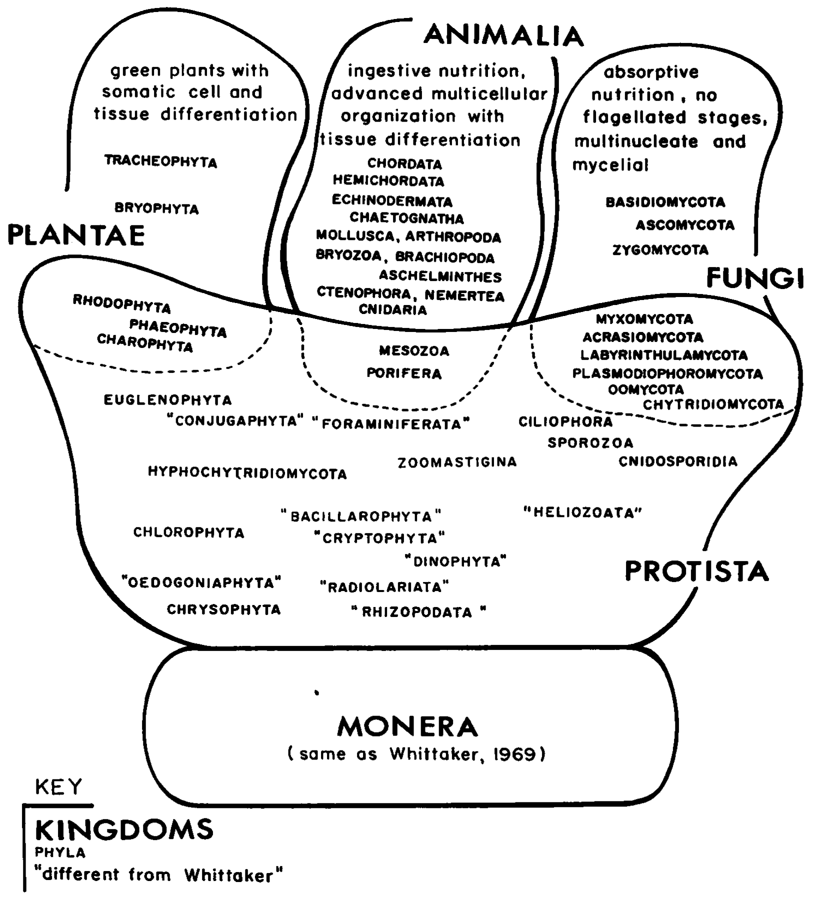

FIG. 2. Modifications of Whittaker's (1969, his Fig. 3) Five Kingdom Scheme based on protist phylogeny.

(mosses, liverworts and vascular plants) from Plantae follows from the realization that the nucleated algae like the protozoans represent examples of these evolutionary "experiments." The exclusion of all phyla except the three generally agreed to consist of a homologous series (Amastigomycota: Zygomycota, Ascomycota and Basidiomycota, Whittaker, 1969) from the Fungi Kingdom, a manifestation of the same principle, is consistent with recent results showing some species of *Phycomyces* and *Neurospora* lack nucleohistones (Bonner, 1970). These changes also incorporate the suggestion of Olive (1969) to put the slime molds (Myxomycota, Acrasiomycota) and the slime net amoebae (Labyrinthulamycota) back into the Kingdom Protista (or Protoctista). This reorganization of Whittaker's lower eukaryotes simultaneously solves the difficulties he notes in defining the Protist Kingdom. It is ancestral to the three higher kingdoms, comprising eukaryotes that branched from each other in the origin of mitotic-meiotic sexuality. Selection on populations of Late Precambrian protists resulted in life cycles providing Mendelian inheritance and eventually obligate recombination each generation. In the course of the evolution of the three highest kingdoms particular patterns assuring regular alternations of haploidy and diploidy were stabilized. This laid the substratum upon which eventually developed the complex multicellular tissue organization for which advanced organisms of the three higher kingdoms are so well known in living populations and the fossil record.

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