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

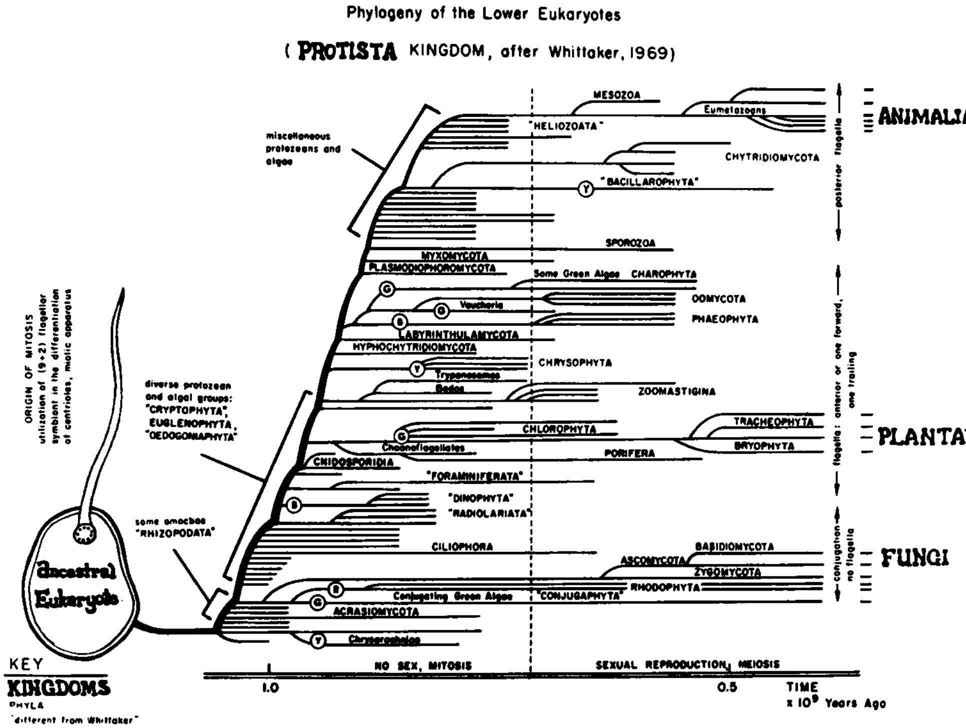

FIG. 1. Phylogeny of the Protista Kingdom (revised from Sagan, 1967 after Whittaker, 1969 with changes as noted in the text). Circle represent plastid homologies: Y = yellow, G = green, R = red or blue, B = brown (Margulis, 1970).

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

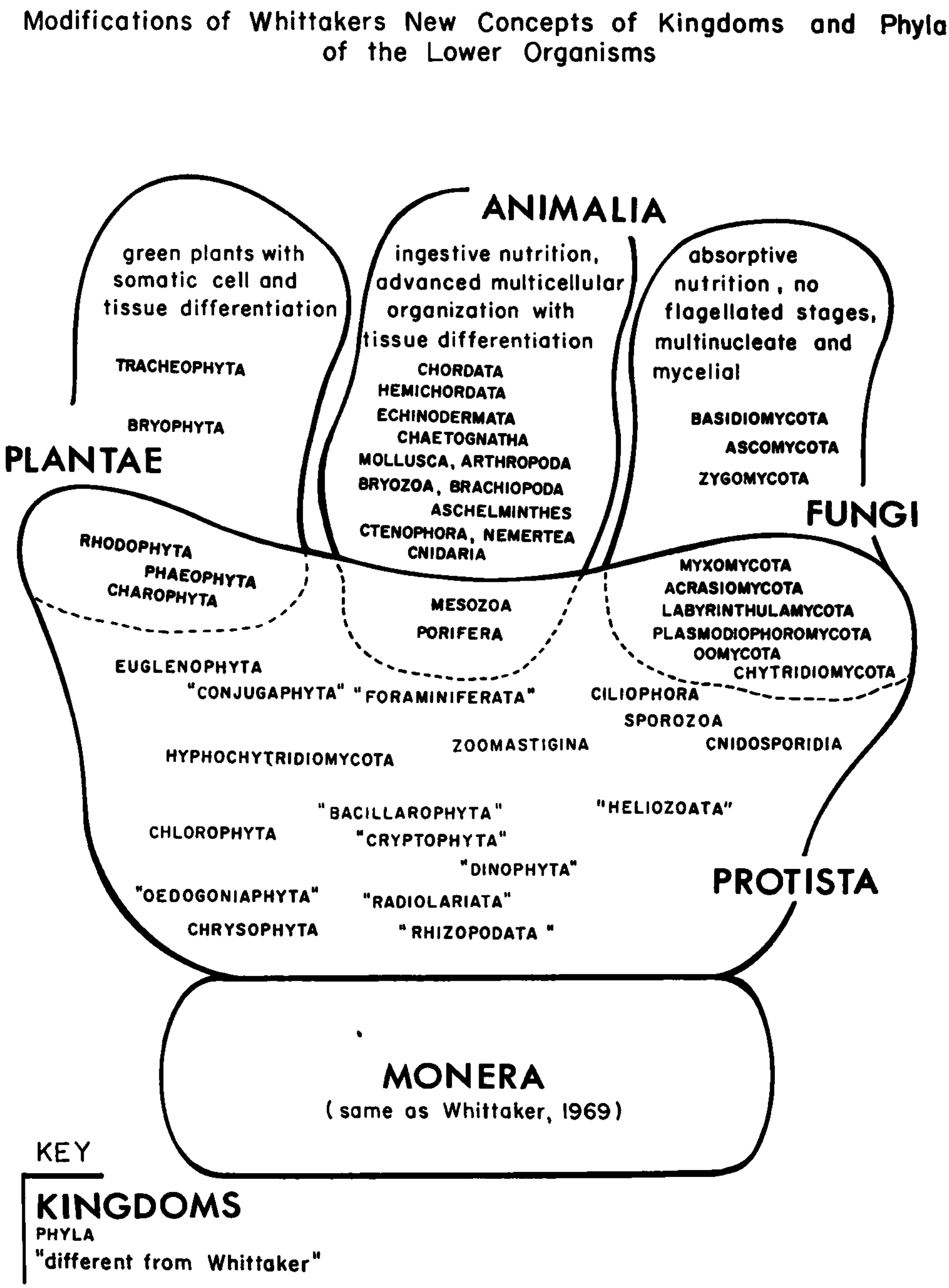

FIG. 2. Modifications of Whittaker's (1969, his Fig. 3) Five Kingdom Scheme based on protist phylogeny.

(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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LITERATURE CITED

BONNER, J. 1970. Personal communication.

COPELAND, H. F. 1956. Classification of the Lower Organisms. Pacific Books, Palo Alto.

DANIELS, W. E., AND E. P. BREYER. 1967. "Ultrastructure of the Giant Amoeba, *Pelomyxa palustris*." J. Protozool., 14:167–179.

GRELL, K. 1967. "The Protozoan Nucleus" *in* The Cell, J. Brachet and A. Mirsky (eds.), (Academic Press, New York) 6:1–79.

KUBAI, D. F., AND H. RIS. 1969. "Division in the Dinoflagellate *Gyrodinium cohnii* (Schiller). A New Type of Reproduction." J. Cell Biol. 40:508–528.

MARGULIS, L. 1968. "Evolutionary Criteria in Thallophytes: A Radical Alternative." Science, 161:1020–1022.

——. 1970. Origin of Eukaryotic Cells. Yale University Press, New Haven.

OLIVE, L. S. 1969. "Reassignment of Gymnomycota." Science, 164:357.

SAGAN, L. 1967. (Margulis) "Origin of Mitosing Cells." J. Theor. Biol. 14:225–275.

STANIER, R. Y., M. DOUDEROFF, E. A. ADELBERG. 1970. "The Microbial World." Prentice-Hall, Englewood Cliffs, N. J., ed. 3.

WHITTAKER, R. H. 1969. "New Concepts of Kingdoms of Organisms." Science, 163:150–159.

ON REVERSIONS TO FORMER ANCESTRAL CONDITIONS IN MEGADRILE OLIGOCHAETES

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This statement, "another instance of a return to a long lost ancestral condition," in a recent manuscript, provoked a referee to deny categorically that any such thing is possible. The various instances, long known to earthworm specialists, are buried in systematic literature rarely if ever consulted by other zoologists. A discussion of the subject should then be of general interest especially if the above-mentioned denial is representative of current thought.

Some knowledge of oligochaete phylogeny is essential for understanding the reversions. All specialists have agreed that a major trend in megadrile evolution has been reduction in number of genital organs, especially the following:

1) Gonads. Gamete production in polychaetes is diffuse. Early in evolution of the oligochaetes, gamete producing tissue was restricted to paired gonads. Those organs today are located, with but few modifications, on posterior faces of intersegmental septa near the ventral parietes and the central nerve cord. Male gonads always are anterior to the female. Opposite each gonad, on the anterior face of the next septum is a funnel from which a gonoduct grows back more or less directly to an external gonopore. The ancestral battery of gonads, in the past, usually was thought to have comprised four pairs, with testes in segments *x* and *xi*, ovaries in segments *xii* and *xiii*. Stephenson (1930, p. 698) for reasons now known