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Multikingdom system of living organisms

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Summary. Analysis of present-day knowledge clearly indicates that the polyphyly of the traditional five kingdoms of the Whittaker-Margulis system, Plantae, Mycota, Animalia, Protoctista and Monera, is untenable. The multikingdom system of living organisms is proposed on the basis of the principle of cellular structures conservatism. This complex approach, based on an analysis of features on three levels, molecular, cytological and morphological, is needed for its construction.

Key words: cellular structure conservatism, living organisms, megasystematics, natural multikingdom system.

The system of the living organisms created by the father of biological systematics (or taxonomy) Karl Linnaeus comprised two kingdoms — Plantae and Animalia. Such division of living organisms in two main groups persisted for more than a century, until the introduction of Darwin's evolutionary theory initiated changes in the theory of systematics. Several attempts to create more natural systems with a larger number of seperate kingdoms were not accepted or were simply neglected at that time. Although two separate kingdoms, for fungi (Mycetoideum) and for protozoans (Protista or Protoctista), were proposed early in the 19th century, the majority of biologists continued to adhere to the two-kingdom system. Along with the description of a wide array of species, genera, families, and even orders, the major efforts of taxonomists in the second half of the 19th century and the first quarter of the 20th century were aimed at reorganization and gradual transformation of the existing, obviously artificial system into natural or phylogenetic one, which would be based on affinity rather than resemblance.

Chatton (1925, 1952, 1953) divided all cellular forms into Prokaryota, which are comprised of bacteria and blue-green algae without a nucleus, and Eukaryota for all other organisms which have a well-defined nucleus. The system of Whittaker was the most popular one in second half of the 20th century. He considered prokaryotes as separate kingdom Monera (Whittaker, 1969, 1977; Whittaker, Margulis, 1978), and divided eukaryotes into three higher kingdoms: plants, fungi, and animals. These three higher kingdoms originated in his scheme from the lower kingdom of Protista (Fig. 1). In that classification scheme, red and brown algae were placed near the base of the stock of plants, green algae were placed both in the protist kingdom (apparently, unicellular forms) and at the base of the plant kingdom, while myxomycetes were positioned near the base of the stock of fungi.

Further modification of Whittaker's system was proposed by Lynn Margulis (1974, 1981; Margulis & Schwartz, 1982, 1988), who introduced the scheme with five kingdoms. Margulis clearly delimitated the kingdom Protoctista from all three superior kingdoms. Algae were transferred to this kingdom, together with all flagellate forms of fungi and fungi-like organisms. By these changes she attempted presumably to obtain monophyletic kingdoms for plants, fungi, and animals, but the heterogeneity of the kingdom Protoctista only increased. Margulis frankly admitted herself that "the protoctist kingdom becomes looking as if it were a dump". In addition, retaining the algae in the plant kingdom and diploid water moulds in the kingdom of fungi, clearly indicated the "polyphyletic nature of the plant and animal kingdoms", what she also admitted. It is possible to conclude unambiguously from these words of Margulis, that all the schemes with few eukaryotic kingdoms (1 to 4) will err toward inadmissible

polyphyly, as it is confirmed by contemporary cytological and, especially, molecular biology data.

Whittaker's scheme was one of the last systems where adaptive features were interwoven with truly phylogenetic characteristics; that is, convergent similarity is claimed to be affinity. Being an ecologist, Whittaker himself pointed to the adaptive character of evolution of three higher kingdoms, which is connected with their feeding mode: plants are generally autotrophs, fungi feed by absorption, while animals are characterized by holozoic nutrition (digestion). Whittaker indicated this main trend in evolution with three arrows near each of the three higher kingdoms (Fig. 1). The progressive evolution of higher plants (development of the root, conductive system, orifices, reduction of gametophyte, and then loss of the flagellate stage, appearance of seed and fruit), true fungi (loss of flagella), and higher vertebrates (appearance of amnion, egg enclosed by membranes, or viviparity) was not related to feeding, but rather was connected to the adaptation for terrestrial life. Both the botanist Zernov (1972) and the ecologist Odum (1975, 1986) considered Whittaker's scheme to be a "functional" or ecological, rather than a taxonomic one, and Odum emphasized that its kingdoms, being "functional kingdoms", should not be confused with taxonomic ones, despite some level of coincidence. Trying to improve the principles under Whittaker's scheme, Margulis replaced arrows related to feeding habits with those indicating haplo-diploid nature of plants, diploid nature of animals, dikaryoid nature of fungi, and haploid nature of algae.

Numerous modifications of the general system of living organisms were published after the 1970s. More attention was paid in these systems to ultrastructural, cytological, and biochemical features. The majority of these systems were claimed by authors to follow the principle of monophyly for the taxa included. Detailed analysis of these systems was soon proposed (Kussakin & Drozdov, 1990, 1994), but it can be mentioned here that eukaryotes were usually subdivided into 6–18 kingdoms (Jeffrey, 1971, 1982; Leedale, 1974; Edwards, 1976; Ragan & Chapman, 1978; Starobogatov, 1985).

Vorontsov (1965) was the first who introduced into scientific usage a major taxonomic category with the rank higher than kingdom - empire. He recognized two empires: the first of precellular organisms in which he placed a single kingdom, that of viruses, and, second, the empire of cellular organisms with two subempires, that of prenucleate organisms comprising bacteria and blue-green algae and the subempire of nucleate organisms (or eukaryotes). The introduction of such high-level taxonomic category as the empire is considered as a highly important event in taxonomy. It was the second most important step after the introduction of the category phylum by Linnaeus.

As the development of the general classification of living organisms, Kussakin and Drozdov proposed the multikingdom system of organic world (1994, 1998). This system comprised of 11 kingdoms of prokaryotes and 15 kingdoms of eukaryotes and was based on the principle of conservatism of cellular structures formulated by Mashansky and Drozdov (1975, 1988). This principle was formulated in an attempt to solve a biological paradox: although at the molecular, cellular, organism, population or species levels, biological diversity is astonishing, the subcellular structures and organoids are extremely conservative. There are only two major ultrastructural variants of biological membranes and 7–8 variants of cell wall structure, 2–3 variants of ribosomes, 3–4 variants of organization of synthetic apparatus, and only six variants of ultrastructural plastid organization, 4–5 types of mitochondria, 3 variants of organization of nuclear apparatus, and 7–8 variants of organization of kinetic apparatus.

Mashansky and Drozdov postulated that living organisms belonging to the same kingdom are characterized by the same structure of cellular organelles and presumed that "kingdom" is as equally objective a taxonomic category as the "species". This system of living organisms is presented as a tree (Fig. 2).

Surely all proposed general systems of living organisms cannot be stable now just because of the unsatisfactory level of knowledge of ultrastructure for numerous groups of protists. Numerous and diverse organisms are still understudied so they cannot even be classified into the existing taxa of higher ranks. Still the degree of conservatism of cellular structures has to be elucidated and the methodology to demonstrate taxonomic relatedness of higher groups has to be improved. Thus, it is unsurprising that different authors recognize different numbers of kingdoms. Often, the authors themselves remake their systems too hastily. Thus, Cavalier-Smith (1981) delineates 7 kingdoms among the eukaryotes,

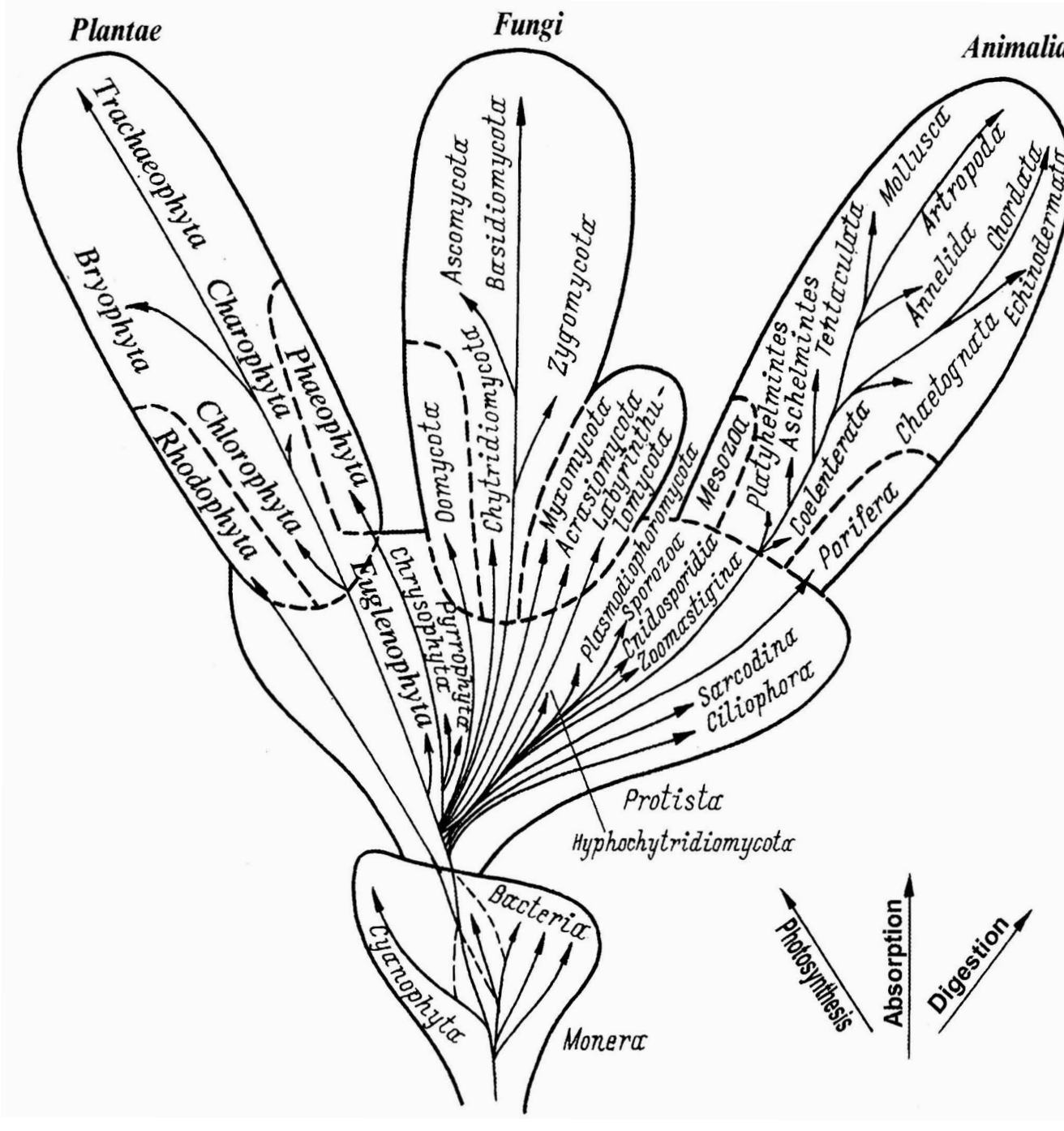

Fig. 1. The five kingdom system of organisms (Whittaker, 1969).

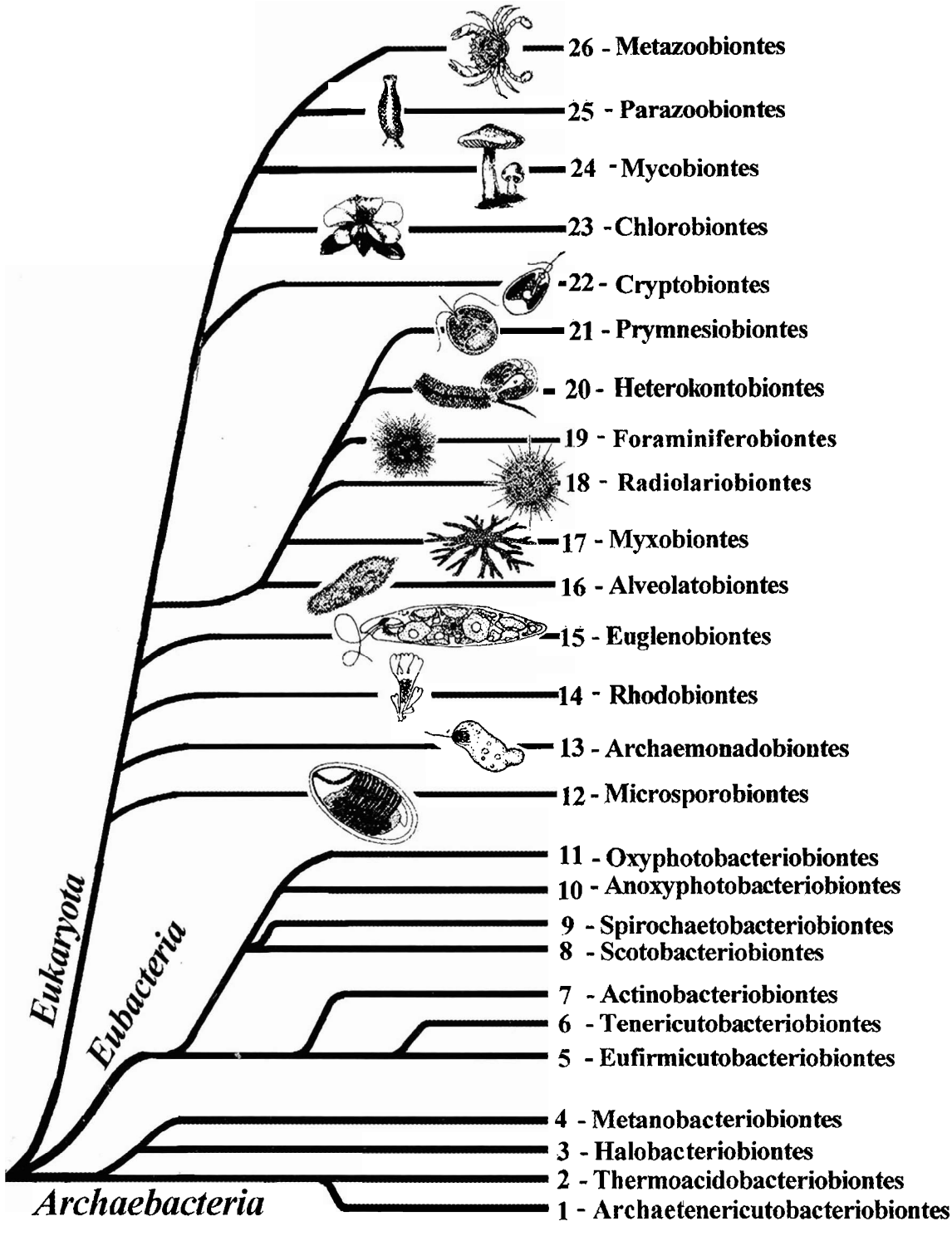

Fig. 2. Proposed multikingdom system of organisms.

three years later he already recognized 9 kingdoms, and later he reduced the number of kingdoms to 6 (Cavalier-Smith, 1983, 1993 a,b, 1995, 1998, 2002 a,b).

It can be mentioned that the system similar to that presented above was proposed recently by Leontiev and Akulov (2002). This latter system was exclusively based on ribosomal DNA data, unlike system as above which was created on the basis of combined evidence of cytological features.

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Резюме. Анализ современных молекулярных и цитологических данных однозначно свидетельствует о полифилетичности традиционных пяти царств общепринятой системы Виттекера-Маргулис: Plantae, Mycota, Animalia, Protoctista and Monera. Предлагается многоцарственная система живых организмов, в основе которой лежит принцип консерватизма клеточных структур. Для ее построения необходим комплексный подход, основывающийся на анализе признаков трех уровней — молекулярных, цитологических и морфологических.