

New views on the megaclassification of life*

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Summary

This paper provides a review of the existing literature about megaclassification of the living beings. Novel classification system is introduced, including 5 dominions and 17 kingdoms. In addition, a new nomenclature of higher taxa has been proposed with a premise that the dominion names end with a suffix “-biota”, subdominions with a suffix “-konta”, kingdoms with a suffix “-ida” and subkingdoms with a suffix “-ides”. Dominion Prionobiota comprises acellular organisms without nucleic acid, acellular organisms with nucleic acid have been classified in dominion Virusobiota, dominion Bacteriobiota consists of typical prokaryotic organisms, and dominion Archaeobiota comprises specific organisms of prokaryotic structure, whereas dominion Eukaryobiota entails all living beings with eukaryotic organization.

Key words: Bikonta, eukaryotes, nomenclature, priones, prokaryotes, Unikonta, viruses

Introduction

As humankind grew accustomed to a great variety of the living beings, a need arose to assort them. Principles of classification largely differ and three main schools of thought can be distinguished. Part of the authors follow Aristotle and acknowledge existence of not more than two kingdoms of the living beings (e.g. Dillon, 1962; Hadži, 1970), some advocate a small number of kingdoms (e.g. Fries, 1821; Hogg, 1860; Dobell, 1911; Copeland, 1956; Traub, 1963, 1964, 1971, 1975; Whittaker, 1969; Moore, 1971, 1974; Taylor, 1978; Cavalier-Smith,

1981, 1988, 1998; Parker, 1982; Shipunov, 2009), and certain authors perceive biodiversity through numerous kingdoms (e.g. Leedale, 1974; Drozdov, 2003). Nevertheless, none of the up-to-date classification systems assumes an existence of only two kingdoms. In addition, a taxonomic category beyond a level of kingdom – dominion or domain – is being used by some researchers (e.g. Moore, 1974; Traub, 1975; Woese et al., 1990).

History of megaclassification can be divided into four periods. The first period is characterized by the use of predominantly external morphological characteristics of the living beings. During this period, main instruments for the analysis of biological characteristics were binocular magnifier and light microscope. This period lasted until the invention of an electron microscope. In the course of the second period, by means of electron

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microscopy the common nature of the living beings progressively became more obvious on the cellular level. During the third period, biochemical and molecular characteristics of the living creatures were taken as basis for interpretation of evolutionary associations. At the beginning of the 21st century, the question of life definition was re-posed, starting the fourth period of megaclassification history. The landmark of this period is not only systematization and rather superficial interpretation of facts obtained by instrumental methods, but also an attempt to comprehend a multitude of discrete data in the most general fashion, taking on elements of philosophy.

Since Aristotle's time, the living beings have been traditionally divided into two groups – plants (Vegetalia) and animals (Animalia). This division is based on the plainly visible differences in the outer appearance and the structure of plants and animals (Ranković, 1994). Plants are autotrophic organisms, capable of synthesizing necessary “building blocks” of their cells from simpler inorganic compounds, using sunlight as a source of energy. Animals are heterotrophic organisms which, in order to satisfy their energy requirements, use the available chemical energy bound in organic compounds. Next to the mode of nutrition, other important differences have been elaborated, such as mobility – plants are immobile, whereas animals are mobile. Carl Linnaeus was the first to introduce taxonomic categories into the classification of the living beings and assign the status of a kingdom to plants (Vegetabilia) and animals (Animalia).

The word “Biology” in the sense of science that studied the living beings was independently mentioned in 1802 by two life researchers – Treviranus and Lamarck. Even though life scientists had been engaged in studying living organisms before that, botany and zoology enjoyed a status of two independent scientific disciplines.

Systematics reached its first peak upon publishing the work “Systema Naturae” by Linnaeus (1735). This work introduced order into the older systematics of the living organisms. Since then, describing the new species and determining resemblances between certain taxa as well as grouping them into systematic categories became the main task of systematics. After Darwin (1859) published his work “On the Origin of species...” the systematics achieved its second peak. Evolutionary biology gave the systematics a new task – interpreting the relationships between systematic categories. Shortly before the end of the 19th century, two international treaties (Candolle, 1867; Blanchard et al., 1905) settled the questions of biological nomenclature that had been giving the systematic biologists

considerable amount of trouble. After publication of these treaties, the interest for systematics began to decline. This period brought experimental biology (physiology, embryology and genetics) into focus, and the systematics remained in the shadow of these biological disciplines until the eighth decade of the 20th century.

Even though during the mid-20th century it became clear that no sharp boundary existed between algae and protozoans, some biologists attempted to distinguish between these two groups. Unusual and uncomplicated systematization of the living world was proposed by Dillon (1962). According to this author, all single-celled organisms represented a part of the plant kingdom and the animal kingdom entailed only multicellular heterotrophic organisms. Within his phylogenetic tree, Dillon placed the animal kingdom between the green and brown algae, but still closer to the brown algae. According to his viewpoint, the animals were direct descendants of the brown algae.

In 1970, Hadži postulated a classification system of the living beings that acknowledged two kingdoms – plants and animals. Hadži believed that the differentiation between plants and animals occurred as a clean-cut bifurcation; therefore, the algae should be grouped within the plants and the protozoans within the animal kingdom. According to this school of thought, the term Protista would not be perceived as a systematic category. All the flagellates which are able to perform photosynthesis, as well as the closely related organisms that secondarily switched to the heterotrophic nutrition, ought to be considered as algae, i.e. plants. Accordingly, the slime molds should not be grouped among protozoans, but rather among fungi, which this author held for plants. Hadži thought that the attempts of a switch from typical autotrophic organism towards the typical heterotrophic had not conceived a typical animal life form. All of such changeovers would geologically be of a later date, occurring upon a former successful switch of the algae towards a protozoan state. According to this school of thought, development of the animals that lived to see the recent age and gave rise to multicellular animals occurred only once. So, animals are monophyletic; they originated not from fully developed plant predecessors, but rather from the predecessors of a lower organization. Those primitive predecessors of algae and protozoans (e.g. plants and animals) were named Probionta. According to such understanding, neither had animals developed from plants, nor plants from animals.

Aristotle's classification of the living world did not come into question until the 13th century, since Albert von Bolsted postulated that the fungi

were an intermediate group between plants and animals (von Bolsted, cited in Ranković, 1994). Nonetheless, it was only in 1821 that Fries put them into a separate kingdom. Reasons for classifying Fungi into an independent high-rank taxon are their specific characteristics. Fungi differ from the plants by their nutritional mode, composition of the cell wall, mechanism of their response to light, hormonal structure and numerous other features. Fungi are heterotrophs, and their cell wall contains chitin. They have pores in intercellular septa of their hyphae that enable cytoplasmic and nuclear communication and transfer. Intercellular nuclear migration is specific for fungi alone (Ingrouille and Eddie, 2006). In plants, morphogenetic processes are activated by light with a maximum wave length of 660 nm, whereas in fungi that maximum lies between 320 and 480 nm (Ranković, 1994). Developmental cycle of the fungi contains a haploid and a dikaryotic stage. Alternation of generations occurs extremely rare in fungi, whereas it is regular in plants. On the other hand, the fungi display similarities to animals. Presence of chitin, as well as pigment melanin and a common cytochrome system juxtapose them with animals. Despite numerous differences, fungi and plants share common features such as indefinite growth ability, cell wall, absorption through the enlarged outer surface, biosynthetic pathway for producing terpenes, and production of similar secondary metabolites. Early attempts to consider fungi as plants were based on the idea that fungi had evolved from algae (Martin, 1955).

Even though a third kingdom of life – Fungi – was separated from the other two kingdoms already in 1821, it was not widely accepted until 1969. Prior to discovery of microorganisms, kingdoms of plants and animals were clearly demarcated. Fungi fitted well into the plant kingdom despite many differences. As the microorganisms were first discovered, it seemed that they could be easily distributed between the initial two kingdoms based on the differences in mobility and nutritive mode.

Later on it appeared that the protozoans were difficult to perceive as unicellular animals. Whereas representatives characterized by phagotrophic nutrition and absence of cellular wall could easily fit within the definition of the animal kingdom, numerous other representatives could not. Detailed research of flagellated protozoans has revealed their specific nature, both plant- and animal-like. Namely, these organisms are actively motile due to their “whip-like tails”, flagella. Some of them feed phagotrophically or osmotrophically, others are capable of photosynthesis. Numerous resemblances between slime molds and certain animal groups have

been observed. During the vegetative phase of the life cycle, slime molds are amoeboid and phagotrophic, nevertheless they form fruiting bodies which shape and size are very similar to those of the true fungi (Vrbaški, 1993). It became clear that no straight borders could be drawn between protozoans and algae.

In order to overcome the difficulties of fitting microorganisms into the system of the living world, Hogg (1860) proposed the third kingdom, named Primigenum (formal name) or Protoctista (vernacular name), which included all microorganisms. Haeckel (1866) acknowledged the third kingdom and named it Protista, classifying microorganisms within this kingdom. The kingdom consisted mainly of four groups: algae, protozoans, fungi, and bacteria. Despite numerous differences among the representatives of the kingdom, it was observed that the majority of species belonged to the category of unicellular organisms, whereas the fewer multicellular representatives of the kingdom had very simple body structure. In 1911, Dobell introduced the term “Protistology” and redefined the concept of unicellularity. By doing so, he reinterpreted the definition of Protista as “acellular” instead of “unicellular” organisms.

Ivanovsky found the viruses in 1892, however nothing was known about their structure during the following nearly half-century, until the elucidation of viral nucleoprotein properties (Bawden and Pirie, 1937). Two years later, the first virus particle was observed by means of electron microscopy (Kausche et al., 1939). Martin (1922) described an unusual potato pest that turned out to be caused by organisms of even more simple organization than viruses, later named viroids. Yet, it was only much later that Diener and Raymer (1967) defined the nature of viroids. Two other groups of acellular organisms were discovered at the beginning of the eighth decade of the 20th century. Randles and co-authors (1981) found one of those two groups and named them virusoids. Although the diseases caused by the other group – the prions – were known before 1982, it was only then that Prusiner (1982) characterized the nature of these organisms and gave them the name.

The third boom of systematics took place in the mid-20th century as a result of the notable accumulation of ultrastructural data from electron microscopic studies that helped to recognize the remarkable similarities of all cellular organisms on a cytological level. During this period of time, a discipline that dealt with the understanding of phylogenetic relations between higher taxa of the living beings developed abruptly. This discipline was

named megaclassification. It provided a new motive to gather all the biological disciplines into a single integrative science: biology. In 1952, Hadži wrote: “With pleasure, we can assert that nowadays a much needed balance between different areas of biology has been reached, hereby attaining peer disposition for all of them”.

Along with the improvement of microscopic methods, knowledge on microorganisms became more complete. Further efforts of putting such classification systems together that would reflect evolutionary trends resulted in grouping the living beings into two categories: Prokaryotes and Eukaryotes. This division was made by Chatton (1925); however, it was only in 1971 that Moore grasped these two categories as superkingdoms. In 1938, Copeland was the first to understand that the Bacteria should be classified into a separate kingdom. Copeland (1956) demarcated the following four kingdoms: Monera (prokaryotic organisms), Protocista (eukaryotic microorganisms and fungi), Metaphyta (plants) and Metazoa (animals). The five-kingdom system was proposed by Whittaker in 1969, separating Fungi as a stand-alone kingdom. This classification system has remained widely acknowledged until the last decade of the 20th century.

Traub (1963, 1964, 1971) found it the most acceptable to classify the living beings into two superkingdoms: Cellularae and Acellularae. This author divided the Cellularae superkingdom into two kingdoms – Procaryotae (with subkingdoms Autobacae and Heterobacae) and Eucaryotae (with subkingdoms Plantae, Heteroplantae and Animalia). Moore (1974) distinguished three large groups of living organisms and gave them a dominion rank: Virus, Prokaryota and Eukaryota. After Moore had introduced the dominion rank into classification, Traub (1975) revised his system by raising the level of superkingdom to that of dominion, kingdom to superkingdom and subkingdom to kingdom. Obviously, this author did not form the Protista group, but rather observed Algae in the frame of the Plantae kingdom and protozoans within the Animalia kingdom. Traub separated the kingdom Animalia into two subkingdoms: Protozoae and Metazoae. It is worth noticing that the viruses were included in the classification systems of the sixties and seventies in the 20th century, whereas later on they were completely ignored.

Schimper (1883) noticed the similarity between Cyanobacteria and plant chloroplasts and concluded that the chloroplasts stemmed from endosymbiotic bacteria. However, this hypothesis was not acknowledged until the publications of

Mereschkowski (1905, 1909), who worked it out in more detail. Subsequently, Wallin (1923) postulated that the mitochondria stemmed from the endosymbiotic bacteria as well. These hypotheses could not develop any further without gaining a profound understanding of a detailed structure of these organelles, which was achievable only by the means of electron microscopy. Only L. Margulis (Sagan, 1967; Margulis, 1981) interpreted the available at that time data which offered strong evidence to corroborate the endosymbiotic theory. According to her, other organelles (flagella, cilia and peroxisomes, etc.) had also been incorporated into the cells through endosymbiosis. The importance of this theory for the megaclassification of the living world lies in the fact that the eukaryotes came into consideration as organisms built from well integrated groups of prokaryotic cells.

In 1978, Taylor introduced utilization of mitochondrial cristae as a leading character in classification of Eukaryotes. Eukaryotes with plate-like cristae were listed within the kingdom of Lamellicristata, whereas those with tubular cristae ended up in the kingdom of Tubulicristata. Shortly, Cavalier-Smith (1981) suggested a classification system that was primarily based on the characteristics of mitochondrial cristae. This system separated Eukaryotes into nine kingdoms: Eufungi, Ciliofungi, Animalia, Biliphyta, Viridiplantae, Euglenozoa, Cryptophyta, Chromophyta and Protozoa. Cavalier-Smith (1988, 1989a, 1993) formed the Archezoa group, which included all the protists that did not display mitochondria. According to this author, the Archezoa affiliates the primary eukaryotes that had appeared earlier than the process of mitochondrial formation started. Patterson (1999a) considered the Archezoa as a paraphyletic group within the taxon Excavata.

In the eighth decade of the 20th century, an intensive consideration of biochemical and molecular biological traits made its way into the classification of the living world. Introduction of such attributes into the megaclassification has led to an understanding that the living world is far more diverse than previously believed. Due to that, most authors postulated the existence of more than five kingdoms. Nevertheless, some biologists proposed systems with fewer kingdoms, in attempt to decrease the chaos in megaclassification.

Parker (1982) divided all living beings into two superkingdoms: Prokaryotae and Eukaryotae. He integrated viruses (Virus) and bacteria (Monera) as kingdoms of the first superkingdom. Within the second superkingdom, Parker also introduced two kingdoms: Plantae (algae, fungi and plants) and

Animalia (protozoa and animals). Clearly, this author did not recognize protists as formal taxon; nevertheless, he considered viruses as the living beings.

Cavalier-Smith (1988) published a classification system consisting of two large taxa with an empire status – Bacteria and Eukaryota. Within the Bacteria, two kingdoms were proposed – Eubacteria and Archaeobacteria, whereas the empire Eukaryota was divided into two superkingdoms – Archezoa (comprising only the Archezoa as a kingdom) and Metakaryota (composed of five kingdoms: Protozoa, Plantae, Animalia, Fungi and Chromista). In 1998, Cavalier-Smith proposed a six-kingdom classification system of the living beings – Animalia, Protozoa, Fungi, Plantae, Chromista and Bacteria. According to Shipunov (2009), the living beings were grouped into four kingdoms – Monera, Protista, Vegetabilia and Animalia. These authors acknowledged the existence of paraphyletic groups.

Leedale (1974) made an exceptional, revolutionary step by demarcating 19 kingdoms. However, this system had never been widely acknowledged, since Whittaker's system was a lot more pragmatic. Namely, Leedale (1974) segregated a large number of insufficiently studied groups of microorganisms, whereas Whittaker (1969) integrated all eukaryotic microorganisms into a single kingdom. Within the coming thirty years, large number of classification systems turned up, assuming a large number of kingdoms. For example, Drozdov (2003) published the system encompassing 26 kingdoms.

Woese and Fox (1977) concluded their research of prokaryotic organisms by denying the phylogenetic base of division into Prokaryotes and Eukaryotes. These authors acknowledged three groups of the living beings: Archae, Bacteria and Eucarya (Woese et al., 1990). As it had already been clear that the living beings were extremely diverse, introducing less than three kingdoms was not seen as pragmatic, since such system would require large number of subsidiary categories between a kingdom and division. Therefore, Woese with co-authors (1990) introduced the term “domain”. The division of the living beings into three domains became nearly commonly adopted at the end of the 20th century: Bacteria, Archaea and Eukaryota.

At the beginning of the 21st century, the question of life definition was again put forward in the center of scientific discussions. In particular, this question relates to the dilemma: whether viruses exist as the living beings, or they are representing forms of inorganic matter. Novel discoveries in the area of virology challenged the opinions of most authors that had for more than two decades ignored viruses

while composing classification systems of the living world.

La Scola with co-authors (2003) described a gigantic DNA virus named Mimivirus, with the capsid diameter reaching 400 nm. This virus was the largest known virus of that time, and it was presumed that Mimivirus harbored an enormously large genome. This presumption was confirmed as the genome length of 1,182 kb had been ascertained (Raoult et al., 2004). It is of interest that the Mimivirus genome contained three genes for aminoacyl-tRNA-synthetase (Raoult and Forterre, 2008).

Häring with co-authors (2008) described a novel virus with a hyperthermophilic prokaryotic organism of the Archaea group as a host. This species lives in acidic hot springs. The lemon-shaped virus that infects this species develops a filament at each of the two virion endings once it exits the host cell, which means that the virion is not necessarily inactive functionally all the time, as previously believed.

Arslan with co-authors (2011) described a DNA virus akin to Mimivirus and named it Megavirus. The Megavirus virion reaches 520 nm in diameter; its genome size is 1,259 kb, and it contains four genes for aminoacyl-tRNA synthetase. Lately, other authors also hold viruses for the living beings (La Scola et al., 2008; Pearson, 2008; Claverie and Ogata, 2009). Certain authors (Koonin et al., 2006; Forterre, 2010; Koonin, 2010) even communicated that the complex DNA viruses (giant viruses) should be seceded into a separate domain. Yet, none of them have made a clear standpoint or in a customary way suggested any novel classification system, considering such action as premature. Boyer with co-authors (2010) separated giant viruses into a discrete domain, named Nucleocytoplasmic Large DNA Viruses (NCLDV); however, these authors did not give a Latin name to the fourth domain either.

General considerations

The above introductory part is a brief overview of the history of research in the field of classification of life. Clearly, considerable confusion does exist in this research area. In the further section, a novel view on the classification and nomenclature of the living world will be proposed.

In order to set up a classification system, one first of all needs to define life as a term. The nature of life, however, is yet insufficiently grasped to generate a common direct and adequate definition. Nowadays, we are aware that life represents the highest form of mobility of matter and that it is an essential feature

of the living beings. Unlike abiogenic matter, the living beings are subjects to the evolution, and they are capable of reproducing. Still, the majority of contemporary authors regard the cell as a common structural and functional unit of all living beings. Does the cell represent a sole, basic structural unit of the living beings, or it is the most complex elementary structural corpuscle of the living beings? This dilemma puts forward a question of structure as the criteria for determining the notion of life.

Status of viruses is certainly the most questionable issue in the classification of the living world. Many authors do not consider the viruses as living beings at all and for those reasons do not deal with them within the classification systems. Two strongest arguments underpin the hypothesis according to which viruses are regarded as non-living entities: the viral ability to form mineral-like crystals and their inability to self-sufficiently divide and grow. Other authors consider viruses alive because they contain nucleic acids.

Today, three groups of theories exist that deal with the origin of viruses. One says that there is no doubt about certain organelles coming into living organism as intracellular symbionts. Namely, predecessors of contemporary eukaryotic cells had once ingested free-living prokaryotes, which became adapted to survival and proliferation inside the hosts cell over time. Secondary plastids and other complex structures originated in a similar way through successive rounds of endosymbiosis. Such way of life inevitably leads to structural simplification of what were to become the organelles. Some authors suggest that the acellular organisms appeared in much similar manner. *Chlamydia*, a rather simplified intracellular parasite, is commonly presented as the evidence for such theory. Moreover, structure and metabolism of acellular organisms and *Chlamydia* largely differ, making it difficult to assume the mechanism of acellular organisms evolving from cells. This theory cannot explain the origin of RNA viruses, since both eukaryotic and prokaryotic cells have DNA-based genome. The regressive viral origin theory is able to explain the origin of the DNA genome and the intracellular life of viruses; however, it fails to clarify the next step – appearance of the viral envelope. This theory of the viral origin leaves numerous questions unanswered.

According to another group of hypotheses, viruses represent acellular organisms labeled as protobionts. Authors that are advocating this view regard viruses as offsprings of the primal organisms that appeared on Earth in its ancient past. This theory cannot explain the origin of the cell from a virion.

Third group of theories about viral origin claims

that a part of the cellular genetic information or its informational RNA, as a copy of the cellular DNA molecule, acquired a self-reproducing ability and began its development independently of the cell. Presumably, viruses originated from plasmids (naked, cyclic DNA molecules, which are transferable between cells) or transposones (parts of DNA molecule capable of commuting within a cell genome). According to this theory, transposones as mobile genetic elements could be the predecessors of today's viruses.

Upon the discovery of viruses and electron microscopy, even tinier acellular organisms were observed and considered as sub-viral particles in literature. Viroids, virusoids and prions have been assorted within this group of organisms. Currently, the commonly accepted classification system divides the acellular organisms into six groups. Viruses represent the first five groups, and the sixth one consists of subviral particles.

Understanding that the postulate about cells being the only elementary structural units had no substantial ground brought about the nucleic acids as criteria for differentiating the living creatures from the non-living matter. Nevertheless, the prions as protein particles with no nucleic acid content are capable of changing and reproducing. No other natural body without nucleic acid is able to evolve or reproduce. Due to these features, prions may be considered as the living beings. It is obvious that the viroids, virusoids and viruses share a number of common characteristics, whereas the prions reproduce in an entirely different fashion. Additionally, prion structure is uncommon to that of other acellular organisms that contain nucleic acid. It can therefore be assumed that the evolutionary origin of prions is not connected with the origin of other acellular organisms.

Acellular organisms manage to maintain their elementary traits at minimum energy requirement as a pre-requisite to survival and reproduction. I believe that it is important to alter the definition of life according to novel discoveries of the extreme life diversity, but not reassess the life diversity according to life's definition. For this reason, I propose the following definition: the living beings are natural entities that have the ability of reproduction.

Since the current literature does not offer clearly define rules for the nomenclature of the higher taxa, I am hereby proposing a simple system of rules to classify the tree of life. I suggest that the domain names for the living beings end with a suffix “-biota”, subdomains with “-konta”, kingdoms with “-ida” and subkingdoms with “-ides”. In addition, I share the views of Dubois (2007) and Shipunov (2009),

who consider the name of the author upon the name of the higher taxa unnecessary, since it would only make the contemporary megaclassification even more complicated.

It is important to stress that the term “domain”, suggested by Woese with co-authors (1990), in fact represents a synonym for the category of dominion (lat. *dominium*), introduced earlier by Moore (1974). Unlike Moore, Woese with co-authors (1990) did not suggest a Latin term for this category, which represents a further argument supporting the accurately introduced term dominion.

Overall, the current classification system of the living beings requires modification. Differences between prions and the rest of acellular organisms are comparable to those between the nucleic-acid-containing acellular organisms and the cellular life forms. Namely, three large groups of the living beings exist: acellular organisms without nucleic acid, acellular organisms with nucleic acid, and cellular organisms. Regarding these three groups as dominions would be logical; however, since the cellular organisms comprise an immense number of species, practical reasons speak in favour of the five-dominion classification of the living beings: Prionobiota (acellular organisms without nucleic acid), Virusobiota (acellular organisms with nucleic acid), Archaeobiota (organisms with prokaryotic structure that show many differences in their biochemistry and in genome from all other forms of life), Bacteriobiota (typical prokaryotic organisms), and Eukaryobiota (eukaryotic organisms). Dominion names have been modified according to the aforementioned nomenclature rules.

Dominium Prionobiota

The living beings without nucleic acid are ranked within this dominion. Until now, they have been insufficiently studied, and only a modest number of species is known. Since majority of biologists do not regard prions as the living beings, their classification has remained unedited. I have grouped all prions into a single kingdom – Prionida.

Regnum Prionida. Prions are infective protein particles with an ability to multiply/replicate and evolve. They live exclusively in eukaryotic cells and consist entirely of proteins without nucleic acids. Prions are hereby deprived of any genetic information in its classical sense. Genes necessary for prion replication are provided by the very host cell, named PrP (Prion Protein) genes (Prusiner, 2004). Healthy organisms comprise prions, which are regarded as normal. They are located on the outer

cellular membrane of neuronal and glial cells. Innate structure of prions does not cause any disorders. The exact function of this protein is still unknown; it has been assumed that it plays a role in maintenance of the cellular membrane integrity and in transmission of neural impulses (Prusiner, 2004). Primary structure of a pathogenic prion protein is identical to the nonpathogenic form. They differ in their tertiary structure. Namely, pathogenic prion protein contains a higher percentage of the β -sheet on account of a lower frequency of its α -helix. Pathogenic prion protein can occur via two routes – consequential to a mutation of the prion-coding gene or upon digestion of infected meat. Once in the cell, pathogenic prion protein binds the nonpathogenic protein forming a heterodimer, which causes a conformational change of the nonpathogenic protein. Upon the conformational change, a homodimer is formed, giving raise to two molecules of pathogenic protein. Two newly formed pathogenic prion proteins bind the other two nonpathogenic prion proteins, hereby increasing the ratio of pathogenic over the nonpathogenic prion proteins in the cell. Once the prions reach the critical concentration in the cell, they begin forming rod-shaped aggregations, which accumulate in the infected tissue, causing tissue damage and host cell death (Prusiner, 2004).

Dominium Virusobiota

The dominion of Virusobiota encompasses acellular organisms with nucleic acid content. Traditionally, viruses, viroids and viral satellites are known as the acellular organisms with nucleic acid (Hull, 2009). I attributed a kingdom status to these groups, integrating all viral satellites within a common name virusoids. The names for these three kingdoms have been assigned as aforementioned – Virusoida, Viroida and Virusida.

Regnum Virusoida. In the course of researching viroids, novel acellular organisms were discovered, named viral satellites. A group of such organisms has been named virusoides; therefore, I am proposing a derivative name of the kingdom based on the group name. They are different from viroids by structure and replication mode. Unlike viroid RNA molecules, virusoid ones are smaller, single-stranded and circular. Both virusoids and viroids lack a protein capsid (Strauss and Strauss, 2008). These organisms take part in pathogenesis of certain plant diseases. Viroids use innate cellular mechanisms to replicate, whereas virusoids replicate in the cytoplasm using cellular RNA-dependent RNA-polymerase or RNA-polymerase coded by a

helper virus. Therefore, their replication depends on a co-infection with a helper virus (Strauss and Strauss, 2008).

Regnum Viroida. Viroids are subviral particles, smaller than viruses and characterized by a simpler structure (Hadidi et al., 2003). These organisms are built solely of a single-strain RNA with molecular weight of 50,000 – 200,000 Da. RNA molecules can be linear or circular. Although the viroid RNA is single-stranded, complementary base matching may occur between certain segments, hereby forming a double-strain secondary structure (Hadidi et al., 2003). This gives the viroid molecule a hairpin shape. It contains 250–400 bases with high guanine–cytosine content. Viroids are sensitive to ribonuclease activity and resistant to organic solvents, high temperature, deoxyribonucleases and proteases. Since such a few nucleotides cannot carry substantial genetic information, replication of the viroid RNA remained elusive for quite a long time. Namely, in order to replicate, acellular organisms need a virus-specific polymerase – an enzyme which requires RNA of roughly 300,000 Da, or at least 1000 nucleotides in length (Hadidi et al., 2003). Viroid RNA composed of several hundred nucleotides is unable to synthesize the polymerase, and a helper virus assisting viroid reproduction has not been observed. Therefore, it was assumed that viroids used a DNA-dependant RNA polymerase to replicate and that their genome did not function as mRNA. However, it has currently been determined that viroids replicate in the host cell nucleus by means of the host RNA polymerase II, using viroid RNA as a template (Hadidi et al., 2003). Pathogenic mechanism of these organisms remains unclear. It has been assumed that viroids interfere with regulation of the host cell's gene expression or that they prevent correct intron excision and subsequent splicing. Terminal consequence of the viroid presence in the cell is inability to express genes required for normal cellular functions. The way of their release from the cell is insufficiently conceived, as well as their transmission paths and mechanisms of the host cell infection (Hadidi et al., 2003).

Regnum Virusida. Viruses are basically built of two components – nucleic acid and protein sheath. Infective viral particle outside the cell is called virion. The dimensions of a virion vary within 28–200 nm range. Virions are said to be filterable, since they are capable of passing through bacteriological filters. Size of a viral particle can be measured by electron microscopy, ultracentrifugation in gradients, ultrafiltration, and by means of ionizing irradiation. The inner structure and symmetry of viruses can be explored by electron microscopy or X-ray structural analysis. Nucleic acids, contained

by virions as carriers of genetic information, can be DNA or RNA, but both types never occur within the same virion. Certain viruses contain both DNA and RNA, however never synchronously, but exclusively in separate phases of their life cycle (Hull, 2009).

Dominium Bacteriobiota

Traditionally, bacteria are divided into Gram-positive and Gram-negative. The division has been based on staining techniques and reaction of the cell wall to this procedure. Gram-negative bacteria have an additional outer cell membrane containing lipopolysaccharides in its outer leaflet and phospholipids in the inner leaflet. Gram-positive bacteria lack such a membrane, but have a thicker peptidoglycan layer. This layer is responsible for ability of Gram-positive bacteria to retain crystal violet dye in Gram staining protocol. In contrast, Gram-negative bacteria can not retain this stain; instead they take up the red counterstain. This is not the only difference between these two groups of bacteria, but it is certainly the most important one. It has been found that Gram-positive bacteria are more susceptible to antibiotics than Gram-negative bacteria. Classification system proposed by Margulis and Schwartz (1988) relies directly on this demarcation, except for naming Gram-positive bacteria Firmicutes and Gram-negative bacteria Gracilicutes. However, the first classification system based on these criteria was proposed by Gibbons and Murray (1978). They divided the kingdom Procaryotae into three divisions: Gracilicutes (“cells that have a rigid or semirigid cell wall, containing peptidoglycan, and in which the Gram reaction is negative”), Firmicutes (“cells that have a rigid or semirigid cell wall containing peptidoglycan and in which the Gram reaction is positive”), and Mollicutes (“cells that do not have a rigid or semirigid cell wall”). Margulis and Schwartz (1998) proposed classification of bacteria comprised of nine groups; Tudge (2000), Garrity with co-authors (2001, 2003) and Black (2002) suggested later some modifications to this system. For example, in the internationally recognized manual on systematic bacteriology (Garrity et al., 2001) as many as 23 bacterial groups (“phyla”) have been recognized. Since 2001, the number of clades has increased up to 70 including possible candidates with unculturable representatives (e.g. Rappé and Giovannoni, 2003; Pace, 2009). The phylogenetic analysis of bacteria is very specific. Horizontal gene transfer represents the biggest problem, and many authors (e.g. Gupta, 2001; Gupta and Griffiths, 2002; Ciccarelli et al.,

2006) have been investigating this issue.

Later, Cavalier-Smith (2006) proposed the division of the prokaryotic kingdom into two subkingdoms – Negibacteria and Unibacteria. Within the subkingdom Negibacteria, three clades were distinguished – Glidobacteria (Chlorobacteria, Hadobacteria and Cyanobacteria), Gracilicutes (Spirochaetae, Sphingobacteria, Proteobacteria and Planctobacteria) and Eurybacteria (Selenobacteria, Fusobacteria and Togobacteria). Within this partition, Chlorobacteria, Hadobacteria, Planctobacteria, Spirochaetae, Sphingobacteria, Proteobacteria, Planctobacteria and Eurybacteria have been granted the level of phylum within the subkingdom Negibacteria. Subkingdom Unibacteria is comprised of two clades – Posibacteria (Endobacteria and Actinobacteria) and Archaeobacteria (Euryarchaeota and Crenarchaeota), both given the status of a phylum.

This paper essentially supports the classification proposed by Battistuzzi and Hedges (2009). According to these authors, the clade Bacteria encloses the following five clades: Terrabacteria, Hydrobacteria, Fusobacteria, Aquificae and Thermotogae. In the proposed megaclassification system these clades are granted the status of a kingdom within the dominion Bacteriobiota.

Regnum Terrabacterida. This prokaryotic kingdom comprises more than 6100 species (Battistuzzi and Hedges, 2009). They have been given this name since the majority of them are terrestrial. In the course of evolution, they have adapted to varying environmental stresses of the land habitats – atmospheric impacts, ultraviolet radiation, etc. Some species among these organisms are capable of oxidative photosynthesis. Both Gram-positive and Gram-negative representatives have been found within this kingdom (Battistuzzi and Hedges, 2009).

Regnum Hydrobacterida. This bacterial kingdom contains over 3200 species (Battistuzzi and Hedges, 2009). Hydrobacterida are the exceptionally ancient and divergent prokaryotic group, difficult for any common characterization. The Spirochaetes clade is also classified within this group, characterized by long, spiral cellular shape. Many of the species are free-living, some are commensals, and a large number of spirochaetes are parasites (Battistuzzi and Hedges, 2009).

Regnum Aquificida. This kingdom encompasses 22 species of extremophilic bacteria (Battistuzzi and Hedges, 2009). So far, they have been found in

hot springs, sulphur basins, thermal ocean cavities, and similar extreme habitats (Inc Icon Group International, 2008). These bacteria are dominant in many terrestrial neutral-to-basal hot springs with water temperature exceeding 60°C. Aquificida are autotrophic organisms, representing the primary carbon fixators in their habitats (Inc Icon Group International, 2008).

Regnum Fusobacterida. Only 32 species belong to this kingdom (Battistuzzi and Hedges, 2009). These bacteria are anaerobic, sessile and spindle-shaped. Frequently, cells have a swelling in the middle part (Samaranayake, 2006).

Regnum Thermotogida. Thirty species belong to this kingdom (Battistuzzi and Hedges, 2009), representing a small, coherent group both in morphological and physiological sense. All the representatives are extreme thermophiles and inhabit exclusively the anaerobic niches. An outer sheath-like membrane (“toga”) is specific for Thermotogida (Oren and Papke, 2010).

Dominium Archaebiota

Woese with co-authors (1990) postulated two genetically clearly separated kingdoms within the domain Archaea – Crenarchaeota and Euryarchaeota. Upon that, a third, clearly separated evolutionary line was discerned within this dominion – Korarchaeota (Barns et al., 1996). Huber with co-authors (2002) discovered a fourth group – Nanoarchaeota. Nevertheless, the initial sectioning into two kingdoms, Crenarchaeota and Euryarchaeota, was corroborated by recent molecular analysis (Elkins et al., 2008), which is acknowledged here.

Regnum Euryarchaeida. This kingdom entails relatively few species which cells come in largely differing forms. It has been determined that the shape is a relatively stable feature and it could be of great importance for correct determination. Within this group, eight clearly defined morphological forms of cells are found: rod-like, coccoid, irregularly coccoid, lanceted, spiral, discoid, triangle-shaped and cubical. Certain representatives are Gram-positive, and others are Gram-negative (Garrity and Holt, 2001). Physiologically, the group is highly heterogeneous. Methanogenic forms occur as well as extreme halophile and hyperthermophile species. Some of these organisms inhabit niches with temperatures as high as 100°C (Pommerville, 2010).

Regnum Crenarchaeida. This kingdom consists

of hyperthermophilic prokaryotic organisms, which inhabit warm areas, rich in sulphur. For these reasons, they are mostly found in the ocean depths in vicinity of geothermal releases. Most representatives are optimally adapted to 80°C water temperature (Pommerville, 2010).

Dominium Eukaryobiota

Eukaryotes are divided into several clades: Amoebozoa, Opisthokonta, Rhizaria, Archaeplastida, Chromalveolata and Excavata (Adl et al., 2005). The clade Opisthokonta encompasses animals and fungi, as well as a number of smaller clades: Choanoflagellata, Mesomycetozoa, Filasterea, Corallochytraea, Microsporidia and Nucleariida (Adl et al., 2005). Small group of protozoans named Choanoflagellata has been classified into the Zooflagellata group by numerous authors in the second half of the 20th century (Margulis and Schwartz, 1988, 1998; Buck, 1990). However, some authors have noted that this is an unusual group of protozoans that are associated with different groups of eukaryotic microorganisms. Because of that, this group is paid more attention here than the other groups of eukaryotes.

Sleigh with co-authors (1984) proposed allocation of Choanoflagellata into a separate group. Taylor (1976), Lee (1980) and Sze (1986) postulated a hypothesis that these organisms were related to the chrysophytes. Modern genetic research showed that Choanoflagellata are a specific group, phylogenetically close to the representatives of Filasterea and Corallochytraea. Cladification system proposed by Adl with co-authors (2005) groups Choanoflagellata together with Metazoa, Fungi and Mesomycetozoa. According to these authors, representatives of Filasterea and Corallochytraea are ranked into Mesomycetozoa.

Already in late 19th century, Metschnikoff (1886) postulated that sponges originated from Choanoflagellata. This hypothesis based on the great structural resemblance of Choanoflagellata and choanocytes, which form the lining of the sponge paragastral cavity. Such point of view was corroborated by the fact that the cells with a flagellum and a collar were found only in sponges and Choanoflagellata. Second argument which supported this hypothesis was the existence of the species *Proterospongia haeckeli*, discovered by Saville-Kent (1880). Colonies of this species are 100 µm-wide spheres, build of jelly-like mass with collar cells protruding outwards. Upon a phase of intensive feeding, some of these cells move into the inner part of the jelly-like mass and attain an

amoeboid shape (Saville-Kent, 1880). The jelly-like colony mass resembles mesoglea of the sponges and the transformation of the collar cells into amoeboid cells may explain the origin of amoeboid cells in the sponge mesoglea (Hadži, 1970). At first, the critics have taken the fact that *Proterospongia haeckeli* was a freshwater organism as a main argument against this theory, since the sponges are marine animals and therefore could not stem from the freshwater life forms. This argument was dismissed when the marine representatives of these organisms were found (Nielsen, 2001). Shortly after this discovery, Brusca and Brusca (2003) formulated a hypothesis that perceived Choanoflagellata as the drastically reduced sponges.

Adjacent to Opisthokonta, within the Unikonta supergroup, another group was distinguished, which was composed of amoeboid protists and slime molds – Amoebozoa. Traditionally all protists with pseudopods were treated together as the Rhizopoda or Sarcodina (e.g. Goldfuss, 1817; Honigberg et al., 1964; Levine et al., 1980). Cavalier-Smith (1993) proposed seven parvkingdoms within the infrakingdom Neozoa. The representatives of three of these seven parvkingdoms are protists with pseudopodia: Actinopoda, Neosarcodina and Entamoebia. Cavalier-Smith (1998) proposed four phyla within the infrakingdom Sarcomastigota. The three representative groups of these phyla are amoeboid protists: Cercozoa, Foraminifera and Amoebozoa. The monophyly of Amoebozoa has been proposed by many authors (e.g. Baldauf et al., 2000; Bolivar et al., 2001; Milyutina et al., 2001; Arisue et al., 2002; Baptiste et al., 2002; Forget et al., 2002; Baldauf, 2003; Fahrni et al., 2003; Keeling, 2004; Nikolaev et al., 2004; Adl et al., 2005, 2012).

Cavalier-Smith (2003) stated that Apusozoa were phylogenetically closer to Bikonta rather than to Unikonta. This view was supported in several subsequent papers (Berney et al., 2004; Nikolaev et al., 2004). Cavalier-Smith and Chao (2003) postulated that Unikonta was a paraphyletic group, branching near the base of the evolutionary tree of all eukaryotes. The first phase in the evolution of eukaryotes had been the formation of a single flagellum, which contained microtubules inside its membrane sheath. It was only later that the mitochondria had been formed endosymbiotically. Two groups have stemmed from these early eukaryotic organisms – one with the flat mitochondrial cristae (Opisthokonta) and the other with the tubular cristae (Anterokonta). The Anterokonta group gave rise to biflagellated eukaryotes (Bikonta). Of all Anterokonta, only organisms from the clade

Amoebozoa have persisted to the present days. Organisms similar to the present Apusozoa are thought to be the intermediate forms between Anterokonta and Bikonta. Heliozoa is a polyphyletic assemblage of diverse unrelated groups, all of which are concentrated in the bikont part of the global eukaryotic tree. According to Kim and co-authors (2006), Apusozoa is phylogenetically close to Opisthokonta.

Within the Rhizaria clade, the morphologically heterogeneous representatives have been grouped together basing on their molecular features. The Rhizaria group was proposed by Cavalier-Smith (2002b). In addition, numerous more recent surveys (Baldauf, 2003; Keeling, 2004; Nikolaev et al., 2004) confirmed that it was a monophyletic group. Burki with co-authors (2007) and Hackett with co-authors (2007) stated that Rhizaria has close phylogenetic relationships with Chromalveolata. Baldauf (2008) named this group the “RAS-group” (Rhizaria-Alveolatae-Stramenopilae group). This group united all photoautotrophic eukaryotic organisms. Cavalier-Smith (2002b) distinguished two clades within this group: Retaria (Foraminifera and Radiolaria) and Cercozoa (Cercomonada, Haplosporidia and Plasmodiophora). Cavalier-Smith and Chao (2003) supported this opinion, whereas Nikolaev with co-authors (2004) did not endorse such ranking.

Patterson (1999b) was among the first researchers who observed close phylogenetic relationships between the Kinetoplastida, Euglenophyta, and Heterolobosea. He pointed out the swollen or discoid form of the mitochondrial cristae as well as major resemblance in the structure of their flagellar apparatus. The following molecular biology analyses showed a monophyletic nature of this group (Simpson et al., 2002, 2006; Simpson, 2003; Breglia et al., 2007; Leander et al., 2007; Rodriguez-Ezpeleta et al., 2007; Burki et al., 2008). Later on, some other related groups were added to the one discussed earlier, and all together they were united within the taxon Excavata (Cavalier-Smith, 2002b).

Pascher with co-authors (1925) grouped a large number of photosynthetic and non-photosynthetic organisms into an informal taxon, named Chromophyta, basing on the characteristics of their flagellar apparatus. It was Cristensen (1962) who ranked this group as a division Chromophyta. Cavalier-Smith (1989b) ranked this group as a kingdom and included all the current representatives of Heterokontae and Hacrobia in it. Cavalier-Smith (1981) was the first to observe phylogenetic relations

between Chromophyta and Alveolata; later on, the close relationships of these two groups were confirmed by other researchers (Patterson, 1999b; Taylor, 1999; Baldauf, 2003; Keeling, 2004; Harper et al., 2005).

Representatives of the clade Archaeplastida had predecessors that displayed symbiotic relationship with a prokaryotic organism capable of photosynthesis (Cavalier-Smith, 1982, 2003). Contemporary organisms of this clade have photosynthetically active plastids bordered by two membranes – the inner one has originated from the photosynthetic prokaryote and the outer membrane has stemmed from a phagocytotic vesicle that once had trapped the prokaryote during the phagocytotic process (Cavalier-Smith, 2003). All photosynthetic organisms with plastids outlined with three membranes have come into the cell by symbiotically engaging with representatives of Archaeplastida (Cavalier-Smith, 2002b; Keeling, 2004; Adl et al., 2005).

According to Cavalier-Smith (2002a), the first eukaryotic organisms were phagotrophs by nutrition and amoebflagellates by morphology. They either scaled or slid along solid substrates and have developed into two major evolutionary lines – Unikonta and Bikonta. These two groups differ primarily by their cytoskeleton structure and the development of the flagellar apparatus. Roger and Simpson (2009) acknowledged the division of eukaryotes into Unikonta and Bikonta. However, Cavalier-Smith (2010b) later on set out an opinion about Bikonta being a paraphyletic group. In the present paper, these two groups are considered as two subdominions.

Subdominium Unikonta

Subdominium Unikonta was proposed by Cavalier-Smith (2002a). Adl with co-authors (2012) proposed name Amorphea for this group. Representatives of this group are characterized by mono-flagellar cells. In certain groups, flagellum has become reduced in the course of evolution. Most representatives of Unikonta have a single centriole in their protoplast. Some species have two centrioles, but their origin is different from the one supposed for bikonts. Presumably, this was a result of convergent evolution (Cavalier-Smith, 2002a). I demarcate four kingdoms within the subdominium Unikonta: Amoebozoidea, Apusozoida, Fungida and Animalioidea. In the course of evolution of this subdominium, Amoebozoidea have branched earlier than Apusozoida (Kim et al., 2006). After branching

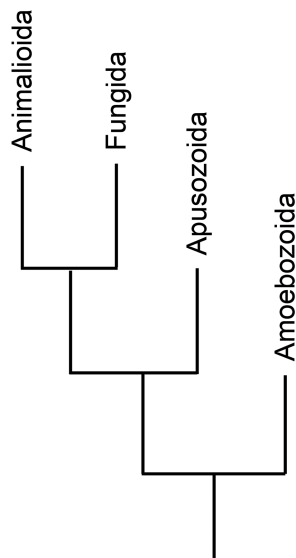


Fig. 1. Phylogenetic relationships between kingdoms of the subdominion Unikonta. Phylogenetic tree was constructed based on the conclusions drawn in the present paper.

of the above-mentioned taxa, a bifurcation took place which gave rise to two kingdoms: Fungida and Animalioidea (Fig. 1).

Regnum Amoebozoidea. This kingdom contains heterotrophic amoeboid protists. Most of them are unicellular inhabitants of the soil and aquatic ecosystems. There are also multicellular (as certain stages of life cycle) and multinuclear macroscopic representatives. Walker with co-authors (2006) described an amoeboflagellate *Breviata anathema*, previously thought to be an amoebozoan (“*Mastigamoeba invertens*”). Minge with co-authors (2009) observed phylogenetic relationships between *Breviata* and Amoebozoa. Shipunov (2009) divided the superphylum Sarcobionta into two phyla: Amoebozoa and Breviatozoa (included only genus *Breviata*). Katz with co-authors (2011) described a new species *Subulatomonas tetraspora* and determined its close phylogenetic relationship to *Breviata anathema*. Although the exact place of the genera *Subulatomonas* and *Breviata* within the dominion Eukaryota is not known (Katz et al., 2011), I propose grouping them together with Amoebozoa because the morphology of representatives of these two groups is similar. I propose two subkingdoms within the kingdom Amoebozoidea: Amoebozoides (all representatives of the group Amoebozoa) and Breviatides (*Breviata anathema* and *Subulatomonas tetraspora*).

Subregnum Amoebozoides. Representatives of this subkingdom move by means of pseudopodia, usually of the lobopodia type. Some flagellated representatives of this group are also known (Smirnov et al., 2011). Mitochondrial cristae are tubular, often branched. Certain species are characterized by a locomotory stage propelled by a single flagellum, stemming from a single basal body (Adl et al., 2005).

Subregnum Breviatides. *Breviata anathema* (Minge et al., 2009) and *Subulatomonas tetraspora* (Katz et al., 2011) are two unicellular, free-living anaerobic species which form this group. They possess amoeboid cell body and a single flagellum. One basal body presents a base for the flagellum; therefore it has been named flagellatic. Next to it, at least one other basal body exists, named non flagellate. This second basal body was observed only in *B. anathema* (Roger and Simpson, 2009). *B. anathema* is considered to be amitochondriate (lacking typical aerobic mitochondria), but it harbors a kind of degenerate mitochondria-like organelles bounded by double membranes.

Regnum Apusozoida. Doflein (1916) established a new family Spironemidae. Foissner with co-authors (1988) proposed allocation of this family into a new protistan phylum, the Hemimastigophora. The order Apusomonadida was established by Karpov and Mylnikov (1989) and originally included two genera – *Apusomonas* and *Amastigomonas*. Cavalier-Smith (2002b) created the phylum Apusozoa including these two genera plus the representatives of phylum Hemimastigophora. Subsequently, many new taxa have been described (e.g. Cavalier-Smith et al., 2008; Cavalier-Smith and Chao, 2010; Glücksman et al., 2011; Yabuki et al., 2012). This kingdom comprises few free-living, heterotrophic species. They move by means of the two or more flagella. Apusozoida are cosmopolitan and can be found both in marine and fresh water ecosystems, as well as in terrestrial habitats. Nevertheless, as they occur at low population densities, they are often overlooked in the samples (Karpov, 2007/8).

Regnum Fungida. I have ranked three subkingdoms within the kingdom Fungida on the basis of their close phylogenetic relations. Fungida consists of unicellular, filamentous and even very large multicellular organisms of a relatively complex structure. The most numerous subkingdom is Fungides, comprised of fungi, whereas the other two subkingdoms have so far remained scarce in species. They do not share many common features

and the group was formed foremost based on the close phylogenetic relationships, that have been confirmed by contemporary studies. Two other groups, which I have ranked as subkingdoms, are closely related to Fungi – Nucleariides (Steenkamp et al., 2006; Baldauf, 2008) and Microsporides (Fischer and Palmer, 2005; Vossbrinck and Debrunner-Vossbrinck, 2005; Gill and Fast, 2006; Liu et al., 2006; Lee et al., 2008).

Subregnum Nucleariides. This subkingdom encompasses a limited number of species characterized by their amoeboid appearance. Body of these organisms is spherical or plate-shaped and filopodia protrude from their surface (Minelli, 2009). Nucleariides have flat mitochondrial cristae (Adl et al., 2005, 2012; Minelli, 2009).

Subregnum Microsporides. Approximately 1200 unicellular, spore-forming species constitute this subkingdom (Lee et al., 2008). They are intracellular animal parasites. Most of the known species are parasites of insects and fish, but it is assumed that they can infect members of virtually all animal taxa as well. Many species have their specific host, which makes Microsporides the good candidates for biological control of pest insects and ticks. Shape of the body is mostly irregular in certain life cycle stages. The spores contain a mononuclear or bi-nuclear (diplokaria) sporoplasm, extrusion apparatus, and a polar tube. The spores are formed from a single cell (Lee et al., 2008).

Subregnum Fungides. Fungi are a highly specific group of spore-forming eukaryotic organisms. Fungal cells are equipped with a cell wall during most, if not all phases of the life cycle (Ranković, 1994). Fungi are heterotrophs and they absorb their food. They are the most widely spread organisms on Earth. To the present day, roughly 100,000 species have been defined and existence of about 1.5 million of species was assumed (Ranković, 1994). Vegetative body of the fungi is called somatic body, occurring as cellular, non-micellar and micellar entities. Too tiny or well hidden (due to their mode of life) somatic body of the fungi is difficult to observe in nature. Fungi can also metamorphose into specific large macroscopic formations.

Regnum Animalioida. I have ranked three subkingdoms within this kingdom on the base of close phylogenetic relations. This highly divergent group consists of unicellular, colonial and even very large multicellular organisms of a complex structure. The most numerous group is Metazoa, which I have grouped into a subkingdom Animalidae, with related representatives of Ichthyosporea, Corallochytra, Filasterea and Choanoflagellata (Shalchian-

Tabrizi et al., 2008). The group Mesomycetozoa was introduced into the literature as a DRIP-clade by Ragan with co-authors (1996). Ichthyosporea, Corallochytra and Filasterea, together with the group Nucleariida were ranked into Mesomycetozoa (Adl et al., 2005). In this paper, the Nucleariida group is ranked into the kingdom Fungida, in accordance with the previously cited studies. Due to many common features of sponges and Choanoflagellata and the major differences between sponges and the rest of the animal kingdom species, I propose grouping of the clades Porifera and Choanoflagellata into a common subkingdom named Choanozoides. Based on the presented perception and in agreement with the earlier defined nomenclature, I propose a separation of the following three subkingdoms within the kingdom Animalioida – Mesomycetozoides, Choanozoides and Animalioides.

Subregnum Mesomycetozoides. The representatives of this group do not share many common distinctive characteristics. They live as parasites in the body of fish, birds, mammals, and crustaceans. Some species of this subkingdom are free-living forms. Their mitochondrial cristae are usually plate-like (Adl et al., 2005).

Subregnum Choanozoides. This subkingdom consists of more than 5000 species. They are mostly unicellular or colonial organisms, which move by means of a single flagellum. Sessile forms have also been distinguished within this group. Mitochondrial cristae are plate-like. Most Choanozoides feed as phagotrophs and a few species have green chromoplasts that enable them to photosynthesize. The protoplast contains a single nucleus. All representatives are free-living forms; they inhabit freshwater and marine ecosystems.

Subregnum Animalioides. These organisms are multicellular and heterotrophic; they usually swallow their food and digest it inside the body. Most representatives of this kingdom are mobile organisms. They occur in all biogeographic areas, occupying various ecological niches and displaying highly variable morphological and metabolic features. They do not have a cell wall; molecules of collagen, proteoglycan and adhesive glycoproteins are found in their extracellular matrix. Their cells can move during certain ontogenic developmental stages. Common characteristics have been observed in the course of development of a zygote. Namely, in the course of cleavage, a blastula is formed, to become gastrula by germ layer formation in the most. Animals have a gastric cavity with one or two openings. In case of two openings, one is frontal – the mouth, and the other opening is situated posteriorly and it is called anal opening.

Subdominium Bikonta

This taxonomic group was proposed by Cavalier-Smith (2002b). The main feature of the group is the presence of bi-flagellated cells. Even though certain representatives do not have a flagellum at all, the concept suggests that the predecessors of this group had two flagella. Bikonta are divided into two groups: Excavata and the group that consists of Archaeplastida, Cryptomonads and Haptophytes, Stramenopiles, Alveolata and Rhizaria (Roger and Simpson, 2009). The second group was named Corticataes (Cavalier-Smith, 2010b). The clade that consists of Cryptomonads and Haptophytes, together with a few minor groups, was named Hacrobia (Okamoto et al., 2009). However, the most recent phylogenomic analysis doubts the common origin of haptophytes and cryptophytes (Burki et al., 2012). In this paper, I have given the Excavata and Corticataes a status of kingdom, and I have corrected their names in agreement with the above defined nomenclature – Excavatida and Corticatida.

Regnum Excavatida. The kingdom Excavatida is relatively small and consists of organisms that differ from each other in their morphology, ultrastructure and ecology. Therefore, autotrophic, heterotrophic, parasitic and symbiotic species are found among Excavata. This kingdom includes some parasites that are of a high medical importance, such as representatives of genera *Giardia*, *Leishmania*, *Trichomonas* and *Trypanosoma* (Adl et al., 2005, 2012). Since many species do not have typical mitochondria, some biologists considered Excavata as a very old eukaryotic group that had appeared before the origin of these endosymbiosis-derived organelles. Cavalier-Smith (1983) postulated a hypothesis of Excavata being a common predecessor for all other eukaryotes. Plesiomorphic characteristic of these organisms is the presence of an excavate type cytostome, that has been secondarily lost in certain representatives (Adl et al., 2005, 2012). Still, most of the species contain highly altered mitochondria (Simpson, 2003). Most of the representatives with mitochondria are characterized by tubular or discoid cristae, whereas fewer have laminar cristae. Most of the representatives have two, four or more flagella (Simpson, 2003).

Regnum Corticatida. Basing on the phylogenetic tree proposed by Burki and co-authors (2012) (Fig. 2), I propose dividing this kingdom into six subkingdoms: Archaeplastides, Cryptophytides, Haptophytides, Rhizarides, Stramenopilides and Alveolatides.

Names have been modified in agreement with the previously defined nomenclature.

Subregnum Archaeplastides. This is a rather large group of organisms with differing morphological, physiological, ultrastructural and ecological features. The most important common characteristic of these organisms and a base for their monophyletic ranking is the presence of plastids with two membranes. This fact implies that the plastids of these organisms evolved from symbiotic blue green prokaryotes (Adl et al., 2005, 2012). Plastids of all other groups are surrounded by three or four membranes.

Subregnum Cryptophytides. This subkingdom consists of autotrophic, phagotrophic and heterotrophic organisms, which inhabit both marine and freshwater environment. They are all unicellular organisms, mobile by the means of flagella or pseudopodia and have ejectisomes.

Subregnum Haptophytides. This subkingdom consists of both autotrophic and phagotrophic organisms. They are unicellular, colonial or filamentous. Motile cells often possess a haptonema. All the representatives are free-living forms; they inhabit freshwater and marine ecosystems.

Subregnum Rhizarides. This subkingdom encompasses a large number of unicellular species. These are ultrastructurally complex organisms. Morphologically, they differ from each other; still, most species have amoeboid appearance and move by the means of filopodia, reticulopodia, lobopodia and axopodia (Adl et al., 2005). Many species form shells around their protoplasm that largely vary in shape and chemical composition; they can be highly complex in structure. Due to their hard shells, many of the species are known as microfossils. Almost all representatives have mitochondria with tubular cristae.

Subregnum Stramenopilides. Many species of this group are mobile cells with two flagella (Adl et al., 2005, 2012). The flagella are usually heterokont – one flagellum carries numerous mastigonemes and the other one does not. Mitochondria are characterized by tubular cristae (Adl et al., 2005, 2012). Most representatives are autotrophic, and fewer are heterotrophic.

Subregnum Alveolatides. This group typically has cortical alveoles, although they can be secondarily absent. Cortical alveoles are flattened vesicles, lined up to form a continuous layer beneath the cell membrane. Mitochondria are characterized by tubular or ampular cristae (Adl et al., 2005, 2012). Both heterotrophs and autotrophs are found among these organisms.

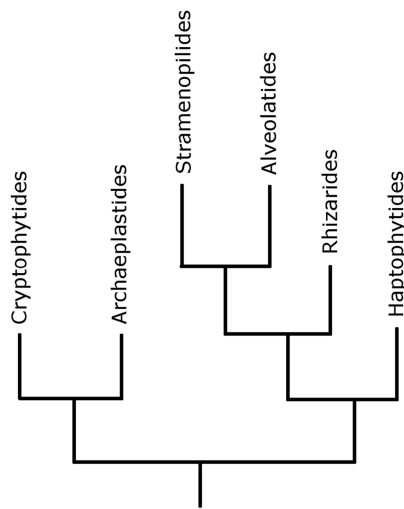


Fig. 2. Phylogenetic relationships between subkingdoms of the kingdom Corticata. Phylogenetic tree was constructed based on the conclusions drawn in the present paper.

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