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The eukaryotic system in the third update of the interface "Eukaryotic supergroups: Taxonomy/Biotechnology interface": Formal procedures for rank changes

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ABSTRACT. The problem of coordinating the ranks of higher eukaryotic taxa was specifically considered by us in the monograph and a recent article. However, we omitted most of the formal descriptions of the proposed taxa in the new rank. The purpose of this article is a formal description of a number of taxa established by us in the monograph "Nomenclature and rank correlation of higher taxa of eukaryotes and subsequent interface updates". Here we formally described such taxa as *Eocorticata* regn. nov., *Tsaralia* regn. nov., *Apusomonadea* intraregn. nov., *Breviatea* intraregn. nov., *Eochromista* superphyl. nov., *Zoosporia* superphyl. nov., *Eurhodophyta* div. nov., *Proteorhodophyta* div. nov., *Anaeramoebea* phyl. et cl. nov., *Calkinsea* phyl. nov., *Meteora* phyl. nov., *Syssomonadea* phyl. nov., *Chlorodendrophytina* subdiv. nov., *Chloropicophytina* subdiv. nov., *Dikaryomycotina* subdiv. nov., *Pedinophytina* subdiv. nov., *Picocystophytina* subdiv. nov., *Sanchytriomycotina* subdiv. nov., *Agaricomycia* supercl. nov., *Calcarisporiellomycia* supercl. nov., *Ceratiomyxomycia* supercl. nov., *Chytridiomycia* supercl. nov., *Entomophthoromycia* supercl. nov., *Entorrhizomycia* supercl. nov., *Kickxellomycia* supercl. nov., *Mortierellomycia* supercl. nov., *Mucoromycia* supercl. nov., *Myxogasteromycia* supercl. nov., *Monoblepharomycia* supercl. nov., *Neocallimastigomycia* supercl. nov., *Saccharomycia* supercl. nov., *Acytosteliomycetes* cl. nov., *Liceomycetes* cl. nov., *Microheliellida* cl. nov., *Paratrimastigidea* cl. nov., *Protosporangiomycetes* cl. nov., *Pycnococcophyceae* cl. nov. The main trends of further improvement of the rank structure of the eukaryote tree we see in 1) some multiplication of the supregroups described for the few taxa now located among the amoebozoans and TSAR, as well as many environmental sequences; 2) further rationalization of the *Fungi* and *Metazoa* system using intercalary taxonomic categories (including additional and not prescribed in both nomenclatural codes ones), and 3) further automatization of the ranking procedure and solving the problem of rank estimating for distant "orphan" taxa.

KEYWORDS: biotechnology/taxonomy interface; eukaryote tree; kingdoms; phyla; taxonomical ranks

СОКРАЩЕНИЯ:

APG – angiosperm phylogeny group; Art. – Article; cl. nov. (classis nova) – new class; CRuMs – collodictyonids, rigifilids, mantamonadids group; div. nov. (divisio nova) – new division (= phylum in "botanical taxa"); DNA – deoxyribonucleic acid; intraregn. nov. (intraregnum novum) – new infrakingdom; MRO – mitochondrion-related organelle; MTOC – microtubule-organizing center; regn. nov. (regnum novum) – new kingdom; RNA – ribonucleic acid; subdiv. nov. (subdivisio nova) – new subdivision; supercl. nov. (superclassis nova) – new superclass; superphyl. nov. (superphylum novum) – new superphylum; TSAR – *Telonemia*, *Stramenopila*, *Alveolata*, *Rhizaria* group; SSU – small subunit ribosomal ribonucleic acid.

INTRODUCTION

Eukaryotes are the most diverse group of living organisms, dominating in most ecosystems, except anaerobic zones. Representatives of this group are characterized by: 1) the presence of a nucleus separated from the cytoplasm by nuclear envelope; 2) DNA-based linear (rarely circular) genome organized with the participation of histones in the form of chromosomes; 3) cytoplasmic ribosomes with a sedimentation coefficient ≈80S; 4) presence of cytoplasmic endomembrane complexes: endoplasmic reticulum, Golgi apparatus, vacuoles, lysosomes, peroxisomes, glyoxisomes, sphaerosomes. Most eukaryotes have mitochondria and their absence is always secondary. Autotrophic eukaryotes are characterized by plastids of various structure, acquired, like mitochondria, in the course of symbiogenesis.

The total number of species of eukaryotic organisms could be estimated at 8.7 million, and their real diversity may be 1.5–2 times greater [1]. Eukaryotes are the dominant and edificators of most of the Earth's biomes, the creators of reef germs in the ocean and multilayered vegetation on land, marine and freshwater sediment strata, and finally, the anthropogenic formations as technosphere and urbanized environment. The technological potential of these organisms cannot be overestimated. Various eukaryote species represent a central object for agricultural technology, food technology, and biotechnology (including all industries related to biosynthesis and bioremediation). An increasing number of eukaryotes are becoming in demand in such areas as biopharmacology and bioengineering. Relevant in a practical respect is the creation of classification with the greatest predictive capabilities for optimization screening research.

Classification decisions adequately reflecting genealogical relationships between taxa, traditionally treated as natural and declared by taxonomists as the main goal of their work, is an issue of fundamental importance because it leads to knowledge progression. Besides, in practice, the heuristic power of classification approaching a natural one is invaluable too, due to increasing its prognostic power, i.e., the possibility of predicting certain properties in unexplored groups related in one or another aspect to the studied ones [2]. The predictive capabilities of the phylogenetic system are associated with the idea that the degree of divergence of groups is inversely related to the preservation of their phenotypic features including those that are in practical demand [3, 4]. At the large group level, a set of "prohibitions" for the morphophysiological convergence of organisms is developed during evolution. An exact identification of such groups opens some possibilities for predictive assessments of varying degrees of certainty, concerning both the evolutionary tendencies of organisms and some of their significant properties in terms of applied research.

In the authors' view, the time has come to create a taxonomic/biotechnological interface that allows the user-biotechnologist to quickly select the classification solution that is most adequate to modern data in order to optimize the search for new nests of technologically significant organisms presumably bearing certain properties of organisms that have already been studied in a respect needed. The creation of such a system implies a global coverage of the users' network on the one hand, and the possibility of both periodically updating the classification part of the catalogue with inclusion of all newly studied species on the other. When creating a classification part, one should be guided by consensus estimates of current phylogenomic reconstructions, keeping in mind that periodic updating of the classifier guarantees a gradual "alignment" of the current imperfections, which undoubtedly do not pass by the attention of the taxonomic community [4].

In July 2022, the authors created such a platform called "Eukaryotic supergroups: Taxonomy/Biotechnology interface" [5]. For each of the 10 supergroups (*Loukozoa*, *Amoebozoa*, *Opisthokonta*, *Discoba*, *Cryptista*, *Archaeplastida*, *Haptista*, *Rhizaria*, *Alveolata*, and *Stramenopila*), a current system was presented with a bibliography covering taxonomic primary sources and recent advances in molecular phylogenetics as well as applied significance of the group with reference to modern biotechnology research and sequenced genomes of key species. The latter is outlined both as a list of classical biotechnology fields (food technologies, biosynthesis and biomass production, bioremediation, biopharmacology, agricultural technologies) as well as animal husbandry with crop production, phytopathology, and clinical mycology and protozoology. Separately, lists of works on the latest (current year) systematic studies and, separately, works in the field of biopharmacology are presented. The information on this platform is expected to be updated annually [6, 7].

During our studies we encountered a problem of rank coordination. It can be assumed that in one form or another it will be solved within the framework of large textbooks or global phylogenies, but it is unlikely to become the subject of special consideration. We pin some hope on the development of auxiliary services at the largest aggregators of genomic information (such as GenBank), which would allow, at the user's request, to generate high-resolved trees that reflect the structure of the eukaryotic domain. Ideally, such services could completely replace the "author's" phylogenies and classifications competing in scientific media. But at the current stage of development of molecular, genomic and information technologies, this is a seemingly impossible issue.

It cannot be said that during the progress in phylogenomics, the problem of rank balancing of established groups was ignored. Particularly consistent seem to be the algologists working with *Heterokontophyta*, who merging such groups as *Xanthophyta*, *Bacillariophyta*, *Chrysophyta* and *Phaeophyta* in sole division, as well as the specialists in vascular plants, who, starting with Bremer, widely used intercalary taxonomic categories in order to avoid of divisions multiplication [8]. The latest APG recommendations proposed to consider angiosperms at the rank of subclass *Magnoliidae* with main clades of superorder rank [9] can't not a recognized as a pleasant sign. Such groups as *Fungi* and *Metazoa* are less fortunate in this regard. These two largest groups of the living world were considered for many years as separate kingdoms, and as more and more species were described, the divisions here only multiplicated. Therefore, the so-called human factor is the main obstacle to bringing the rank structure of the system to the new "phylogenetic realities".

The problem of coordinating the ranks of higher eukaryotic taxa was specifically considered by us in the monograph and a recent article [10, 11]. However, we omitted most of the formal descriptions of the proposed taxa in the new rank. The purpose of this article is a formal description of a number of taxa established by us in the monograph and subsequent interface updates. Such a description can stimulate a discussion about the rank structure of the eukaryotic megasystem and would be reflected in the creation of online-classifiers well relaed to the current knowledge.

METHOD OF PRESENTATION

Despite the ongoing talk about the transition to the phylocode [12], in practice, the classification of eukaryotes is based on the Zoological and Botanical codes of nomenclature, although only in part, since these codes apply to the names of lower- and middle-rank taxa (zoological code – up to family level, botanical – up to division level). At the phylum (division) level, these rules turn out to be useful (especially when lowering the rank of phyla to subphyla, superclasses, classes), but for names above the phylum rank, taxonomists try to adhere to the "zoological" principles names creation, using well-known descriptive ones, not "spoiled with" invented unified termination.

The International Code of Zoological Nomenclature [13] provides, in essence, very little information of interest to us. First of all, this Code says that it regulates the names of taxa in the family group, genus group and species group, and only in some, the most general form, can give extensions to the naming of higher taxa (Art 1.2). In particular, such names had to be published after 1757 (Art. 11.1), be printed in the obligatory use of the Latin alphabet (Art. 11.1), and hyphens, diacritics as well as letters such as j, k, w, and y were allowed in the original description (Art 11.2), however, the word itself may not be purely Latin, but Greek, combined, and even an anagram, the main thing is that it should be given a latinized form by the Latin termination (Art. 11.3). This name must initially be accompanied by a description or differential diagnosis from which the described taxon can be distinguished from others (Art. 13.1.1), followed by a bibliographic reference to the original source (Art. 13.1.2), or proposed as a replacement name (Art. 13.1.3). Concerning the language of the original description, the Code only recommends that this language be widely known to zoologists (Rec. 13B). The valid name of a taxon is the oldest available name applied to it, unless that name has been invalidated (Art. 23.1). Modern names (published after 1950) must not contain diacritics and ligatures (Art. 27), and the supraspecies name must always be uninomial and must always begin with a capital letter (Art. 28). The authorship of the name of a nominal taxon within a family group, genus group, or species group is not affected by the rank in which it is used (Art. 50.3.1). Strictly speaking, this rule applies to the family group, but in practice, zoologists use the same principle for higher taxa, which retain the authorship of the original describer of the corresponding name, despite its changed rank.

It should be noted that the requirement for the language of diagnosis in the Zoological Code is more flexible and moved out of the article into a [non-binding] recommendation (13B), but even in this form does not indicate any one language ("Authors should publish diagnoses of new taxa in languages widely used internationally in zoology"). This allows, for example, taxa that have appeared in the Russian-language literature not to be rejected for nomenclatural reasons.

More useful information for our purposes is provided by the Botanical Code, or, in modern sound, the International Code of Nomenclature for algae, fungi, and plants [14].

The provisions of the Botanical Code apply to all organisms traditionally considered to be algae, fungi or plants, whether fossil or non-fossil, including blue-green algae (cyanobacteria), chytrids, oomycetes, slime molds (but excluding microsporidia), and photosynthetic protozoans (Preamble). The main ranks of "botanical" taxa in descending order are: kingdom (*regnum* in Latin), division (*divisio*, *phylum*), class (*classis*), order (*ordo*), family (*familia*), genus (*genus*), and species (*species*) (Art. 3.1). If more taxa ranks are desired, terms for them are created by adding the prefix "sub-" to terms denoting primary or secondary ranks. Thus, an organism can be assigned to taxa in the following ranks (in descending order): kingdom (*regnum*), subkingdom (*subregnum*), division or phylum (*divisio* or *phylum*), supdivision or subphylum (*subdivisio* or *subphylum*), class (*classis*), subclass (*subclassis*), order (*ordo*), suborder (*subordo*), family (*familia*), subfamily (*subfamilia*), tribe (*tribus*), subtribe (*subtribus*), genus (*genus*), subgenus (*subgenus*), section (*sectio*), subsection (*subsection*), series (*series*), subseries (*subseries*), species (*species*), subspecies (*subspecies*), variety (*varietas*), subvariety (*subvarietas*), form (*forma*) and subform (*subforma*) (Art. 4.2). Additional ranks may be added to aforementioned, provided this does not lead to confusion or error (Art. 4.3).

The application of taxa names higher or lower to the family rank is determined by nomenclatural types. The use of taxa names of higher ranks is also determined by nomenclatural type, when the names are derived from the generic name. The principle of typification does not apply to names of taxa above the rank of family, with the exception of names that are automatically typified, being derived from generic names whose type is the same as that of the generic name (Art. 7.1).

The valid name publication in various groups of plants and fungi is treated as beginning at various "starting points". The names of non-fossil fungi have a starting point from Linnaeus [15] (Art. F.1.1), although the hymenomycetes names sanctioned by Fries [16] and the gasteromycetes names sanctioned by Persoon [17] are conserved against earlier post-Linnaean names.

The original spelling of the name or epithet must be preserved, except for the correction of typographical or spelling errors and standardization (letters and ligatures alien to classical Latin, transposition between *u*/*v*, *i*/*j* or *eu*/*ev*, diacritics, terminations, intentional latinization, compound forms, hyphens, apostrophes and dots) (Art. 60).

The name of a taxon above family rank is represented as a plural noun and is capitalized (Art. 16.1). Such names may either be automatically typified names (Art. 10.10) formed from a generic name in the same way as a surname, by adding an appropriate rank termination preceded by the connecting vowel o- if the termination begins with a consonant. Or they are descriptive names, not formed in such a way, which can be used without change at different ranks (here we can see a certain echo in the Zoological Code). For automatically typified names, the division or subdivision name that includes the type name, the subclass name that includes the type of adopted class name, as well as the suborder name that includes the type name must be derived from the same generic name as its corresponding higher name. The division (phylum) name has a termination *-phyta*, unless it refers to fungi, in which case the termination is *-mycota*; the subdivision (subphylum) name has a termination *-phytina*, unless it refers to fungi, in which case the termination is -mycotina. The name of the class of algae has a termination *-phyceae*, whereas in the subclass the termination is *-phycidae*. The name of the class of fungi has a termination *-mycetes*, whereas in the subclass the termination is *-mycetidae*. The name of the class in embryophytes has a termination *-opsida*, whereas in the subclass the termination is *-idae* (but not *-viridae*) (Art. 16). Automatically typified names that do not follow this rule are subject to correction without changing the author or date of publication. However, if such names are published with a non-latinized termination, they will considered as not validly published. At the same time, the terms "division" and "phylum" and their equivalents in modern languages are interpreted as referring to the same rank (Art. 3.1, note to Art. 17).

In higher-order taxa names, the word elements *-clad-*, *-cocc-*, *-cyst-*, *-monad-*, *-mycet-*, *-nemat-*, or *-phyt-*, which are the genitive singular of the stems of the second part of the name of the included genus, may be omitted before the suffix indicating rank. Such names are automatically typified when their origin is obvious or specified in the protologue. The principle of precedence does not apply above a family rank (Art. 16).

In order to be officially published, the name of a new taxon (excluding algae and fossils) published between January 1, 1935 and December 31, 2011 inclusive, must be accompanied by a description or diagnosis in Latin, or a reference to a previously and effectively published A Latin description or diagnosis, while to be officially published, the name of a new taxon published on or after January 1, 2012, must be accompanied by a Latin or English description or diagnosis, or a reference to a previously and effectively published Latin or English description or diagnosis (Art. 39).

Applications for recognition as nomenclatural repositories of organisms other than fungi must be addressed to the General Committee, which will forward the application to the Registration Committee and take action on his recommendation. Until such a recommendation is made, the mechanisms and conditions for registration, as well as the definition of scope, will be developed in consultation between the applicant, the Registration Committee and the Permanent Nomenclature Committee for the relevant group, and will be widely publicized in the taxonomic community. Registration can be proactive and/or synchronous and/or retrospective; that is, it may occur before and/or simultaneously with and/or after the actual publication of a nomenclature novelty or the actual publication of any nomenclature act (Art. 42). To be validly published, nomenclatural innovations applying to organisms treated as fungi (including fossil fungi and lichen-forming fungi) published on or after January 1, 2013 must include a re-ference in the protologue to an identifier issued for the name by a recognized repository (Art. F.5.1).

Finally, if any taxon originally assigned to a group not covered by the Botanical Code is considered to be an algae or a fungus, any of its names need only satisfy the requirements of the other relevant Code that the author has used to obtain the status equivalent to a valid publication under other than this Code. The Code used by the author is determined by internal evidence, regardless of any claim by the author about the group of organisms to which the taxon belongs. However, a name created in zoological nomenclature in accordance with the Coordination Principle cannot be officially published under this Code until it actually appears in publication as an accepted name of a taxon (Art. 45.1). The name of a taxon treated as a fungus published on or after January 1, 2019 is invalid if it is a later homonym of a prokaryotic or protozoan name (Art. F.6.1). For the last article some minor revisions to the wording were proposed with the addition of some examples [18].

Thus, the Botanical Code gives us the opportunity to operate with taxa at a level below the phylum and above the class. Below the class lies an area of little interest for megasystematics, whereas between the class and the phylum of multicellular plants and fungi, a great deal of work remains to be done for higher-rank taxonomists, given that nowadays's ranks of *Chloroplastida* subdivisions are unreasonably raised. First of all, the Botanical Code clearly prescribes taxonomic categories (phylum, class…), recommends the formation of intercalary categories associated with rank reduction, but also does not exclude other (non-regulated) interstitial categories. In this regard, it seems to us that the intercalary category of the superclass is very promising at current state of our knowledge; the unification of the terminations marking them for different groups of botanical objects was proposed by Moore [19]:

fungi: *-mycia*;
algae: *-phycia*;
cormophytes: *-itia.*

Secondly, the Botanical Code allows the use of untypified names above the family level, which, however, are also subject to terminations unification. This is an important circumstance that makes it possible not to typify such widely known names as *Myxomycota*, *Oomycota*, *Rhodophyta*, *Embryophyta*. That does not prevent giving them standardized terminations when raising or lowering their rank. Changing the name to a typified one is thus optional and makes sense only when the taxon strongly associated with a certain descriptive name has split into several taxa of the same rank, as happened, for example, with the *Zygomycota*.

Thirdly, the Botanical Code gives clear references to needed name features (in its basic provisions resembling the Zoological Code). There are some specifics associated with names of organisms treated as *Fungi*. So, *Microsporidia*, despite the fact that they are often classified as part of *Fungi*, are fundamentally declared to be not subject of the Botanical Code. In addition, from January 1, 2013, all newly described fungal taxa (including taxa of higher rank) must be accompanied by a registration number, which is not required for other taxa whose naming is regulated by the Botanical Code.

Since the naming of taxa above the phylum level is not covered by the Botanical Code, although the latter leads to accuracy in rearrangements between phylum and class levels, the naming of taxa having kingdom and suprakingdom rank seems to be closer in spirit to the decisions of the Zoological Code – first of all, an independent from the rank association of taxon authorship with corresponding name and an absence of requirement to terminations unification. It is these principles that we propose to be guided by in anyone revision of the eukaryotic megasystem.

In the following outline of the eukaryotic system, we denote the rank of a taxon by a fixed number of indentations filled with black circles (•).

RESULTS

Condensed *Eukarya* system

We adopt a nine-kingdom system of eukaryotes with three subdomains:

Domain *Eukarya*
• subdomain *Excavata*
• • kingdom *Archezoa*
• • kingdom *Discoba*
• subdomain *Obimoda*
• • kingdom *Crumalia*
• • kingdom *Amoebozoa*
• • kingdom *Obazoa*
• subdomain *Corticata*
• • kingdom *Eocorticata*
• • kingdom *Haptista*
• • kingdom *Tsaralia* (TSAR)
• • kingdom *Plantae*
• • • superphylum *Cryptista*
• • • superphylum *Glaucophyta*
• • • superphylum *Rhodophyta*
• • • superphylum *Chloroplastida*.

New taxa in *Excavata* subdomain

Two large groups of clinical and bioremediation importance, *Archezoa* and *Discoba*, we united in this subdomain, although such a uniting is still one of the few controversial points even in the molecular systematics era.

The *Archezoa* supergroup comprises anaerobic or microaerophilic eukaryotes, some representatives with modified non-respiratory mitochondria (e.g. hydrogenosomes or mitosomes), or without mitochondria. Cells are flagellated, ancestrally with four kinetosomes per kinetid, though a great variation exists; some free-living, many endobiotic, some parasitic.

The cell body plan of the *Discoba* representatives is reduced to a dikinetid state (2–3 flagella or many pairs), while usually three microtubule roots depart from a pair of kinetosomes. Many taxa are characterized by trans-splicing, i.e. the formation of a giant unsplitted transcript during RNA processing. Cells are usually large and, in different groups, are characterized by various particular adaptations, such as paraxial road, kinetoplast, or undulating membrane. Mitochondria, if present, are with discoid, rarely tubular cristae, but in some taxa they are reduced to peroxisomes or mitosomes. Most species are phago-heterotrophs, feeding on cytostomes or lobopodia, but there are also osmotrophs and even autotrophic forms with chloroplasts that have a 3-membrane envelope and chlorophylls *a* and *b* (euglenoids). In many euglenoids, plastids are secondarily absent, but the ability to phagotrophy has also been lost – such forms feed osmotrophically (*Rhabdomonadineae*). However, some euglenoids (*Peranematida*) are phagotrophs and are primarily devoid of plastids. The sexual process is absent. *Jakobea* is a sister/basal lineage.

The following subdomain classification is accepted by us.

• • Kingdom *Archezoa* Caval.-Sm.
• • • • • • Phylum *Parabasalia* Honigberg
• • • • • • • • • Class *Hypotrichomonadea* Cepicka, Hampl et Kulda
• • • • • • • • • Class *Pimpavickea* Boscaro et Keeling
• • • • • • • • • Class *Trichomonadea* Kirby
• • • • • • • • • Class *Lophomonadea* Boscaro et Keeling
• • • • • • • • • Class *Trichonymphea* Poche
• • • • • • • • • Class *Cristamonadea* Cepicka, Hampl et Kulda
• • • • • • • • • Class *Dienamoebea* Boscaro et Keeling
• • • • • • • • • Class *Monocercomonadea* Boscaro et Keeling
• • • • • • • • • Class *Tritrichomonadea* Cepicka, Hampl et Kulda
• • • • • • • • • Class *Spirotrichonymphea* Grasse
• • • • • • Phylum *Anaeramoebea*[I] (sole class and order)
• • • • • • Phylum *Preaxostyla* Simpson
• • • • • • • • • Class *Anaeromonadea* Caval.-Sm.
• • • • • • • • • Class *Paratrimastigidea*[II]
• • • • • • Phylum *Oxymonada* Karpov
• • • • • • • • • Class *Oxymonadidae* ined.
• • • • • • • • • Class *Polymastigidea* ined.
• • • • • • • • • Class *Streblomastigidea* ined.
• • • • • • • • • Class *Pyrsonymphidea* ined.
• • • • • • • • • Class *Saccinobaculidea* ined.
• • • • • • Phylum *Fornicata* Simpson
• • • • • • • • • Class *Carpediemonadea* Caval.-Sm.
• • • • • • • • • Class *Eopharingea* Caval.-Sm.
• • • • • • Phylum *Planomonada* Tedersoo (sole class and order)
• • Kingdom *Discoba* Simpson in Hampl et al.
• • • • • Superphylum *Jakobea* Caval.-Sm.
• • • • • • Phylum *Jakobida* Leontyev (sole class and order)
• • • • • • Phylum *Tsukubea* Caval.-Sm. (sole class and order)
• • • • • Superphylum *Percolozoa* Caval.-Sm.
• • • • • • Phylum *Pharyngomonada* Caval.-Sm. et Nikolaev (sole class and order)
• • • • • • Phylum *Tetramitia* Caval.-Sm.
• • • • • • • • • Class *Lyromonadea* Caval.-Sm.
• • • • • • • • • Class *Heterolobosea* Page et Blanton
• • • • • Superphylum *Euglenozoa* Caval.-Sm.
• • • • • • Phylum *Kinetoplastida* Margulis
• • • • • • • • • Class *Kinetoplastea* Honigberg
• • • • • • Phylum *Diplonemia* Caval.-Sm.
• • • • • • • • • Class *Diplonemea* Caval.-Sm.
• • • • • • Phylum/Division *Euglenophyta* Pascher
• • • • • • • • • Class *Entosiphonea* Caval.-Sm.
• • • • • • • • • Class *Euglenophyceae* Schoenichen in Eyfurth et Schoenichen
• • • • • • • • • Class *Peranemea* Caval.-Sm.
• • • • • • • • • Class *Ploeotarea* Caval.-Sm.
• • • • • • • • • Class *Stavomonadea* Caval.-Sm.
• • • • • • Phylum *Calkinsea* ined.[III] (sole class and order).

The following new taxa we formally describe here.

I. *Anaeramoebea* Zmitr., Perelygin et Zharikov phyl. et cl. nov.

Marine anaerobic amoebae or amoeboflagellates with acristate mitochondrion-related organelles and a large centriolar centrosome with a trilaminar core. Actively moving amoebae uninucleate, fan-shaped, with a flattened antero-lateral hyaline zone and globular granuloplasm. Posterior hyaline projections present at least in some cells; multinucleate plasmodia present in some species. Flagellated stage may be present in some species, with two or four subapically inserted thickened flagella. Genus example: *Anaeromoeba*. Táborský et al. (Protist, 168: 495–526, 2017).

II. *Paratrimastigidea* Zmitr., Perelygin et Zharikov cl. nov.

Four-flagellated, one flagellum directed anteriorly, one posteriorly, and others laterally, the posterior flagellum has two vanes with thickened vane margins; both vanes have a paracrystalline substructure; ventral side of the cell is shaped in the form of a broad groove. Dense network of rough endoplasmic reticulum extends from the nucleus towards the posterior end of the cell. A single stacked Golgi apparatus is located posterior and to the left of the basal bodies; the kinetid consists of four basal bodies, four microtubular roots, and various microtubules and fibers associated with the basal bodies and roots; the arrangement of the basal bodies is asymmetrical. Rod-shaped mitochondrion-related organelles resembling hydrogenosomes dispersed throughout the cell. Genus example: *Paratrimastix* Zhang et al. (Protist, 166: 468–491, 2015).

III. *Calkinsea* Zmitr., Perelygin et Zharikov phyl. nov.

Heterotrophic biflagellate with a large nucleus on the anterior ventral side and a battery of tubular extrusomes linked to an extrusomal pocket located adjacent to the nucleus. Feeding apparatus supported by both fibrous structures and microtubules that are derived from ventral root; rod-shaped epibiotic bacteria above superficial layer of mitochondrion-derived organelles with reduced or absent cristae. Genus example: *Calkinsia* Lackey. See Yubuki et al. [20].

New taxa in *Obimoda* subdomain

Such important groups as amoebozoans and opisthokonts, are united in this subdomain. We named this group *Obimoda* [11] as an anaphony playing on fragments such as *OBazoa*, *AMOebozoa*, and *MantaMOnadida*, and substitute for *Opimoda* (*Opisthokonta* plus *Amoebozoa*).

The *Amoebozoa* supergroup unites protozoans capable of amoeboid locomotion with steady flow of the cytoplasm or occasional eruptions in some groups or amoeboid locomotion involving the extension and retraction of pseudopodia or subpseudopodia with little coordinated movement of the cytoplasm. Cells more or less naked, often with well differentiated glycocalyx. In several groups, cells are covered with a tectum or a cuticle. Some groups are testate, i.e. enclosed in a flexible or hard extracellular envelope with one to several pores. Mitochondrial cristae tubular (ramicristate), with few exceptions; mitochondria are secondarily reduced to mitochondrion-related organelles (MRO) in archamoebians. Most are only reported to be asexual, but sex and life cycles consistent with sex have been reported in *Tubulinea*, *Evosea*, and *Discosea*. Many taxa exhibit either sporocarpic or sorocarpic sporulation. Biflagellated, uniflagellated or multiflagellated stages in the life cycle of some taxa; some taxa exhibit reduction of the bikont kinetid to a unikont one.

The *Opisthokonta* supergroup is characterized by a single posterior cilium without mastigonemes, present in at least one life cycle stage or secondarily lost; a pair of kinetosomes or centrioles, sometimes modified; the flat (rarely tubular) mitochondrial cristae in unicellular stage. Two inclusive clades, *Holozoa* and *Holomycota*, comprise the lion's share of euks' species diversity. *Breviatea* and *Apusomonadida* are sister/basal lineages (*Obazoa* clade = *Opisthokonta* + *Breviatea* and *Apusomonadida*, see [21]).

The following subdomain classification is accepted by us.

• • Kingdom *Crumalia* Zmitr., Perelygin et Zharikov [see 10]
• • • • • • Phylum *Malawimonadea* Caval.-Sm. (sole class and order)
• • • • • • Phylum *Mantamonada* Zmitr., Perelygin et Zharikov (sole class and order)
• • • • • • Phylum *Rigifilida* Zmitr., Perelygin et Zharikov (sole class and order)
• • • • • • Phylum *Collodictyonida* Zmitr., Perelygin et Zharikov (sole class and order)
• • Kingdom *Amoebozoa* Caval.-Sm.
• • • • • • Phylum *Lobosa* Schultze
• • • • • • • • • Class *Tubulinea* Smirnov et al.
• • • • • • • • • • Order *Euamoebida* Lepsi
• • • • • • • • • • Order *Arcellinida* Kent
• • • • • • • • • • Order *Leptomyxida* Pussard et Pons
• • • • • • • • • • Order *Nolandida* Smirnov et al.
• • • • • • • • • • Order *Echinamoebida* Caval.-Sm. et al.
• • • • • • • • • Class *Discosea* Caval.-Sm. et al.
• • • • • • • • • • Order *Flabellinia* Smirnov et al.
• • • • • • • • • • Order *Longamoebia* Smirnov et al.
• • • • • • Phylum *Conosa* Caval.-Sm.
• • • • • • • Subphylum *Variosea* Caval.-Sm.
• • • • • • • • • Class *Varipodida* Caval.-Sm.
• • • • • • • • • Class *Phalansteriida* Hibberd
• • • • • • • • • Class *Holomastigida* Lauterborn
• • • • • • • Subphylum *Archamoebae* Caval.-Sm.
• • • • • • • • • Class *Mastigamoebida* Caval.-Sm.
• • • • • • • • • Class *Pelobiontida* Caval.-Sm.
• • • • • • • Subphylum *Mycetozoa* de By ex Rostaf.
• • • • • • Superclass *Dictyosteliomycia* Caval.-Sm.
• • • • • • • • • Class *Acytosteliomycetes*[IV] (sole order)
• • • • • • • • • Class *Dictyosteliomycetes* Doweld (sole order)
• • • • • • Superlass *Ceratiomyxomycia*[V]
• • • • • • • • • Class *Protosporangiomycetes*[VI] (sole order)
• • • • • • • • • Class *Ceratiomyxomycetes* D. Hawksw., B. Sutton et Ainsw. in Leontyev et al. (sole order)
• • • • • • Superclass *Myxogasteromycia*[VII]
• • • • • • • • • Class *Liceomycetes*[VIII]
• • • • • • • • • • Order *Cribrariales* T. Macbr.
• • • • • • • • • • Order *Liceales* E. Jahn
• • • • • • • • • • Order *Reticulariales* Leontyev, Schnittler, S. L. Stephenson, Novozh. et Shchepin
• • • • • • • • • • Order *Trichiales* T. Macbr.
• • • • • • • • • Class *Physaromycetes* Doweld
• • • • • • • • • • Order *Clastodermatales* Leontyev, Schnittler, S. L. Stephenson, Novozh. et Shchepin
• • • • • • • • • • Order *Echinosteliales* G. W. Martin
• • • • • • • • • • Order *Echinosteliopsidales* L. S. Olive
• • • • • • • • • • Order *Meridermatales* Leontyev, Schnittler, S. L. Stephenson, Novozh. et Shchepin
• • • • • • • • • • Order *Physarales* T. Macbr.
• • • • • • • • • • Order *Stemonitidales* T. Macbr.
• • Kingdom *Obazoa* Brown et al.
• • • Infrakingdom *Breviatea*[IX] (sole phylum, class, order)
• • • Infrakingdom *Apusomonadea*[X] (sole phylum, class, order)
• • • Infrakingdom *Opisthokonta* Copeland
• • • • Subkingdom *Holomycota* Liu et al.
• • • • • Superphylum *Cristidiscoidea* Caval.-Sm.
• • • • • • Phylum *Fonticulida* Tedersoo et al.
• • • • • • Phylum *Nuclearida* Tedersoo et al.

• • • • •Superphylum *Zoosporia*[XI]
• • • • • •Phylum *Opisthosporidia* Karpov et al.
• • • • • • • • •Class *Aphelidiomycetes* Tedersoo et al. (sole order)
• • • • • • • • •Class *Microsporidia* Corliss et Levine (six orders)
• • • • • • • • •Class *Rozellida* E. Lara (sole order)
• • • • • • • • •Class *Rudimicrosporia* Sprague (sole order)
• • • • • •Phylum/Division *Eumycota* Arx
• • • • • • •Subdivision *Chytridiomycotina* Caval.-Sm.
• • • • • • • •Superclass *Chytridiomycia*[XII]
• • • • • • • • •Class *Chytridiomycetes* Caval.-Sm. (two orders)
• • • • • • • • •Class *Cladochytriomycetes* Tedersoo et al. (sole order)
• • • • • • • • •Class *Mesochytriomycetes* Tedersoo et al. (sole order)
• • • • • • • • •Class *Lobulomycetes* Tedersoo et al. (sole order)
• • • • • • • • •Class *Polychytriomycetes* Tedersoo et al. (sole order)
• • • • • • • • •Class *Rhizophlyctidomycetes* Tedersoo et al. (sole order)
• • • • • • • • •Class *Rhizophydiomycetes* Tedersoo et al. (sole order)
• • • • • • • • •Class *Spizellomycetes* Tedersoo et al. (sole order)
• • • • • • • • •Class *Synchytriomycetes* Tedersoo et al. (sole order)
• • • • • • • •Superclass *Monoblepharomycia*[XIII]
• • • • • • • • •Class *Monoblepharidomycetes* J. H. Schaffn. (sole order)
• • • • • • • • •Class *Hyaloraphidiomycetes* Doweld (sole order)
• • • • • • • •Superclass *Neocallimastigomycia*[XIV]
• • • • • • • • •Class *Neocallimastigomycetes* M. J. Powell (sole order)
• • • • • • •Subdivision *Olpidiomycotina* Doweld
• • • • • • • • •Class *Olpidiomycetes* Doweld (sole order)
• • • • • • •Subdivision *Sanchytriomycotina*[XV]
• • • • • • • • •Class *Sanchytriomycetes* Tedersoo et al. (sole order)
• • • • • • •Subdivision *Blastocladiomycotina* Tedersoo et al.
• • • • • • • • •Class *Blastocladiomycetes* T. James (sole order)
• • • • • • • • •Class *Physodermatomycetes* Tedersoo et al. (sole order)
• • • • • • •Subdivision *Basidiobolomycotina* Teredsoo et al.
• • • • • • • • •Class *Basidiobolomycetes* Doweld (sole order)
• • • • • • •Subdivision *Enthomophthoromycotina* Humber
• • • • • • • •Superclass *Entomophthoromycia*[XVI]
• • • • • • • • •Class *Entomophthoromycetes* Humber (sole order)
• • • • • • • • •Class *Neozygitomycetes* Humber (sole order)
• • • • • • • •Superclass *Kickxellomycia*[XVII]
• • • • • • • • •Class *Kickxellomycetes* Tedersoo et al. (sole order)
• • • • • • • • •Class *Asellariomycetes* Tedersoo et al. (sole order)
• • • • • • • • •Class *Barbatosporomycetes* Tedersoo et al. (sole order)
• • • • • • • • •Class *Dimargaritomycetes* Tedersoo et al. (sole order)
• • • • • • • • •Class *Harpellomycetes* Tedersoo et al. (sole order)
• • • • • • • • •Class *Ramicandelaberomycetes* Tedersoo et al. (sole order)
• • • • • • •Subdivision *Zoopagomycotina* Benny
• • • • • • • • •Class *Zoopagomycetes* Doweld (sole order)
• • • • • • •Subdivision *Glomeromycotina* Spatafora et Stajich
• • • • • • • • •Class *Archaeosporomycetes* Sieverd., G. A. Silva, B. T. Goto et Oehl (sole order)
• • • • • • • • •Class *Glomeromycetes* Caval.-Sm. (two orders)
• • • • • • • • •Class *Paraglomeromycetes* Oehl, G. A. Silva, B. T. Goto et Sieverd. (sole order)
• • • • • • •Subdivision *Mucoromycotina* Benny
• • • • • • • •Superclass *Mucoromycia*[XVIII]
• • • • • • • • •Class *Endogonomycetes* Doweld (sole order)
• • • • • • • • •Class *Mucoromycetes* Doweld (sole order)
• • • • • • • • •Class *Umbelopsidomycetes* Tedersoo et al. (sole order)
• • • • • • • •Superclass *Mortierellomycia*[XIX]
• • • • • • • • •Class *Mortierellomycetes* Doweld (sole order)
• • • • • • • •Superclass *Calcarisporiellomycia*[XX]
• • • • • • • • •Class *Calcarisporiellomycetes* Tedersoo et al. (sole order)
• • • • • • •Subdivision *Dikaryomycotina*[XXI]
• • • • • • • •Superclass *Entorrhizomycia*[XXII]
• • • • • • • • •Class *Entorrhizomycetes* Begerow, Stoll et R. Bauer (sole order)
• • • • • • • •Superclass *Agaricomycia*[XXIII]
• • • • • • • • •Class *Agaricomycetes* Doweld (22 orders)
• • • • • • • • •Class *Agaricostilbomycetes* R. Bauer, Begerow, J. P. Samp., M. Weiss et Oberw. (sole order)
• • • • • • • • •Class *Atractiellomycetes* R. Bauer, Begerow, J. P. Samp., M. Weiss et Oberw. (sole order)
• • • • • • • • •Class *Bartheletiomycetes* Thines (sole order)
• • • • • • • • •Class *Classiculomycetes* R. Bauer, Begerow, J. P. Samp., M. Weiss et Oberw. (sole order)
• • • • • • • • •Class *Cryptomycocolacomycetes* R. Bauer, Begerow, J. P. Samp., M. Weiss et Oberw. (sole order)
• • • • • • • • •Class *Cystobasidiomycetes* R. Bauer, Begerow, J. P. Samp., M. Weiss et Oberw. (five orders)
• • • • • • • • •Class *Dacrymycetes* Doweld (sole order)
• • • • • • • • •Class *Exobasidiomycetes* Begerow, M. Stoll et R. Bauer (eight orders)
• • • • • • • • •Class *Malasseziomycetes* Denchev et T. Denchev (sole order)
• • • • • • • • •Class *Microbotryomycetes* R. Bauer, Begerow, J. P. Samp., M. Weiss et Oberw. (eigt orders)
• • • • • • • • •Class *Mixiomycetes* R. Bauer, Begerow, J. P. Samp., M. Weiss et Oberw. (sole order)
• • • • • • • • •Class *Moniliellomycetes* Q. M. Wang, F. Y. Bai et Boekhout (sole order)
• • • • • • • • •Class *Peribolosporomycetes* Witfeld, M. A. Guerreiro, H. D. T. Nguyen et Begerow (sole order)
• • • • • • • • •Class *Pucciniomycetes* R. Bauer, Begerow, J. P. Samp., M. Weiss et Oberw. (five orders)
• • • • • • • • •Class *Spiculogloeomycetes* Q. M. Wang, F. Y. Bai, M. Groenew. et Boekhout (sole order)
• • • • • • • • •Class *Tremellomycetes* Doweld (six orders)
• • • • • • • • •Class *Tritirachiomycetes* Aime et Schell (sole order)
• • • • • • • • •Class *Wallemiomycetes* Zalar, de Hoog et Schroers (sole order)
• • • • • • • • •Class *Ustilaginomycetes* R. Bauer, Oberw. et Vánky (two orders)
• • • • • • • •Superclass *Saccharomycia*[XXIV]
• • • • • • • • •Class *Alloascoideomycetes* M. Groenew., Hittinger, Opulente et A. Rokas (sole order)

•••••••••Class *Archaeorhizomycetes* Rosling et T. Y. James (sole order)
•••••••••Class *Arthoniomycetes* O. E. Erikss. et Winka (two orders)
•••••••••Class *Dipodascomycetes* M. Groenew., Hittinger, Opulente et A. Rokas (sole order)
•••••••••Class *Dothideomycetes* O. E. Erikss et Winka (42 orders)
•••••••••Class *Eurotiomycetes* O. E. Erikss. et Winka (16 orders)
•••••••••Class *Laboulbeniomycetes* Engl. (three orders)
•••••••••Class *Lecanoromycetes* O. E. Erikss. et Winka (22 orders)
•••••••••Class *Leotiomycetes* O. E. Erikss. et Winka (12 orders)
•••••••••Class *Lichinomycetes* V. Reeb, Lutzoni et Cl. Roux (sole order)
•••••••••Class *Lipomycetes* M. Groenew., Hittinger, Opulente et A. Rokas (sole order)
•••••••••Class *Neolectomycetes* O. E. Erikss. et Winka (sole order)
•••••••••Class *Novakomycetes* Dlauchy, Péter et Čadež (sole order)
•••••••••Class *Orbiliomycetes* O. E. Erikss. et Baral (sole order)
•••••••••Class *Pezizomycetes* O. E. Erikss. et Winka (sole order)
•••••••••Class *Pichiomycetes* M. Groenew., Hittinger, Opulente et A. Rokas (sole order)
•••••••••Class *Pneumocystomycetes* O. E. Erikss. et Winka (sole order)
•••••••••Class *Saccharomycetes* O. E. Erikss. et Winka (sole order)
•••••••••Class *Schizosaccharomycetes* O. E. Erikss. et Winka (sole order)
•••••••••Class *Sordariomycetes* O. E. Erikss. et Winka (43 orders)
•••••••••Class *Sporopachydermiomycetes* M. Groenew., Hittinger, Opulente et A. Roka (sole order)
•••••••••Class *Taphrinomycetes* O. E. Erikss. et Winka (sole order)
•••••••••Class *Trigonopsidomycetes* M. Groenew., Hittinger, Opulente et A. Rokas (sole order)
•••••••••Class *Xylobotryomycetes* Voglmayr et Jaklitsch (sole order)
••••Subkingdom *Holozoa* Lang
•••••Superphylum *Ichtyosporea* Caval.-Sm. (sole phylum, class, order)
•••••Superphylum *Pluriformea* Hehenberger et al.
••••••Phylum *Corallochytrea* Caval.-Sm. (sole class and order)
••••••Phylum *Syssomonadea*[XXV] (sole class and order)
••••••Phylum *Filozoa* Shalchian-Tabrizi et al.
•••••••Subphylum *Filasterea* Shalchian-Tabrizi et al. (sole class and order)
•••••••Subphylum *Choanozoa* Caval.-Sm.
••••••••Superclass *Choanoflagellatea* Caval.-Sm.
•••••••••Class *Choanoflagellata* Kent (two orders)
••••••••Superclass *Metazoa* Haeckel
•••••••••[rank lowering needed] *Porifera* Grant
•••••••••[rank lowering needed] *Eumetazoa* Bütschli

The following new taxa we formally describe here.

IV. *Acytosteliomycetes* Zmitr., Perelygin et Zharikov cl. nov. (MB 856976).

Amoeboid stage from uninucleate amoebae to multinucleate reticulate plasmodia characterized by producing long filose subspeudopodia anastomosing in some taxa; ciliated amoebae possesses one to several, reduced unikont kinetids per cell, not associated with the nucleus; species without ciliated amoebae have akinetid amoebae that germinate from spores; sporocarps in all species with single, nondeciduous spores; cysts of some species displaying sculpturing as well. Genus example: *Acytostelium* Raper (Mycologia 48: 179, 1956). New order *Acytosteliales* was described [22], comprising the two families *Acytosteliaceae* and *Cavenderiaceae*, which differs from *Dictyosteliales* and the unplaced genus *Synstelium* together by having in the SSU rRNA gene C (not T) in the nucleotide position 539 and CTC (not CTA) in the positions 1448–1450. The rank increase seems to be necessary here for the overall balancing of the amoebozoan tree based on the correlation of mycetozoans clade with a subphylum level and its differentiation into three large lineages (dictyostelids, ceratiomyxids and myxogastrids). Sole order.

V. *Ceratiomyxomycia* Zmitr., Perelygin et Zharikov supercl. nov. (MB 856977).

Ciliated amoebae with rootlets as in mycetozoans with rootlet 3 consisting of a band of only two microtubules; protostelioid sporocarps with a microscopic stalk with one to four, sometimes more, spores; life cycle with; giving rise to a uninucleate to multinucleate obligate amoebae that develops into one or more sporocarps; prespore cells site of meiotic prophase and meiosis completed in spore complement. Genus example: *Ceratiomyxa* J. Schröt. in Engler et Prantl (Nat. Pflanzenfam., Teil. I 1: 16, 1889). The rank increase seems to be necessary here for the overall balancing of the amoebozoan tree based on the correlation of mycetozoans clade with a subphylum level and its differentiation into three large lineages (dictyostelids, ceratiomyxids and myxogastrids). Two classes (see above).

VI. *Protosporangiomycetes* Zmitr., Perelygin et Zharikov cl. nov. (MB 856978).

Obligate amoebae uninucleate to plurinucleate, often resembling very early developmental stages of myxogastrid plasmodia; individually developing into a single two to four-spored sporocarp. Genus example: *Protosporangium* L. S. Olive et Stoian. (J. Protozool. 19: 563, 1972). The rank increase seems to be necessary here for the overall balancing of the amoebozoan tree based on the correlation of mycetozoans clade with a subphylum level and its differentiation into three large lineages (dictyostelids, ceratiomyxids and myxogastrids).

VII. *Myxogasteromycia* Zmitr., Perelygin et Zharikov supercl. nov. (MB 856979).

Multinucleate plasmodium differentiates into one or more multinucleate spore-forming masses where the cell cleaves into individual, uninucleate spores that undergo meiosis after spore wall development in sexual species; sporocarps can be individual sporangia (with or without stalks), clustered sporangia, aethalia or plasmodium-shaped plasmodiocarps; fruiting bodies initially covered with an extracellular peridium and may contain thread-like spore-suspending capillitium; spores germinating as bikont ciliated amoebae with rootlets as with eumycetozoans with rootlet 3 consisting of a band of several microtubules. The rank increase seems to be necessary here for the overall balancing of the amoebozoan tree based on the correlation of mycetozoans clade with a subphylum level and its differentiation into three large lineages (dictyostelids, ceratiomyxids and myxogastrids). Two classes (see above).

VIII. *Liceomycetes* Zmitr., Perelygin et Zharikov cl. nov. (MB 856983).

(Alternative name and rank for *Myxomycetes* subclass *Lucisporomycetidae* Leontyev, Schnittler, S. L. Stephenson, Novozh. et Shchepin, Phytotaxa 299: 315, 2019).

Spores mostly colored (brownish, olivaceous, golden-yellow, orange, reddish, violet); mostly without stalk and columella; capillitium, when present, tubular; plus molecular apotypies. Genus example: *Licea* Schrad. (Nov. Gen. Pl.: 16, 1797). Four orders (see above).

IX. *Breviatea* Zmitr., Perelygin et Zharikov intraregn. nov.

Free-living biflagellate heterotrophic anaerobic amoebae bearing mitochondrion-related organelle (sometimes irregularly cristate). Genus example: *Breviata* Walker et al. (J. Eukaryot. Microbiol. 53: 65–78, 2006). Higher rank monophyletic lineage basal to the opisthokonts. Sole phylum, class, order.

X. *Apusomonadea* Zmitr., Perelygin et Zharikov intraregn. nov.

Heterotrophic small-sized gliding flagellates bearing as a rule two flagella and proboscis, formed partly or entirely by the anterior flagellum surrounded by a membranous sleeve; pellicle under the dorsal cell membrane extends into the proboscis sleeve and into a skirt that covers the sides of the cell. Mitochondrial cristae tubular. Two smooth heterokont flagella without paraxonemal rods and with short simple transition zones. Both kinetosomes have a thin cylinder and a cartwheel structure. The kinetosome of the anterior flagellum associates with a broad right microtubular root, a dorsal left root of two microtubules and with a striated fibrillar root. The kinetosome of the posterior flagellum associates with a rhizostyle. There are two basic cell plans: 1) with a round cell body and a mastigophore, a projection of the cell containing both basal bodies at its end, and 2) with an oval or oblong cell that generally forms pseudopodia from the ventral surface, with no mastigophore, and the proboscis comprising solely the flagellum and the sleeve. Genus example: *Apusomonas* Alexeieff (Zhurn. Mikrobiol. 4: 141, 1917). Higher rank monophyletic lineage basal to the opisthokonts. Sole phylum, class, order.

XI. *Zoosporia* Zmitr., Perelygin et Zharikov superphyl. nov.

Unikont flagellates, intracellular amitochondriate sporozoans (microsporidians), monocentric, polycentric, or filamentous fungi. Mitochondria with flat, rarely tubular cristae. Monophylectic clade, comprising two ≈phyla, *Fungi* (*Eumycota*) and *Opisthosporidia*.

XII. *Chytridiomycia* Zmitr., Perelygin et Zharikov supercl. nov. (MB 856984).

Saprotrophic, biotrophic or endobiotic moulds – monocentric, polycentric or filamentous. Zoospores possesing as a rule one posterior flagellum with a kinetosome and non-functional centriole, and a microbody-lipid globule complex. Mitochondrial cristae flat. Golgi apparatus with stacked cisternae. Meiosis mostly zygotic, nuclear envelope fenestrated at poles during mitosis. Genus example: *Chytridium* A. Braun (Betrachtungen über die Erscheinung der Verjüngung in der Natur, insbesondere in der Lebens- und Bildungsgeschichte der Pflanze: 198, 1851). The alternative rank – division *Chytridiomycota* M. J. Powell, Mycol. Res. 111: 513, 2007 – we lowered during the rank balancing of the opisthokont tree. Eight classes (see above).

XIII. *Monoblepharomycia* Zmitr., Perelygin et Zharikov supercl. nov. (MB 856985).

Saprotrophic filamentous moulds with a basal holdfast or rhizoids, possesing terminal sporangia. Zoospores possesing one posterior flagellum with a kinetosome and non-functional centriole, elongate, tapered toward the anterior end, capable of swim. Mitochondrial cristae flat. Sexual reproduction oogamous with participation of non-flagellated female gametes borne in oogonia. Genus example: *Monoblepharis* Cornu (Bull. Soc. bot. Fr. 18: 59, 1871). The alternative rank – division *Monoblepharomycota* Doweld, Prosyllabus tracheophytorum: Tentamen systematis plantarum vascularium (Tracheophyta): 77. 2001 – we lowered during the rank balancing of the opisthokont tree.

XIV. *Neocallimastigomycia* Zmitr., Perelygin et Zharikov supercl. nov. (MB 856986).

Anaerobic moulds living in digestive system of herbivorous mammals – monocentric or polycentric, with extensive rhizoids or a bulbous haustorium-like structures. Zoospores posteriorly unflagellate or polyflagellate (bearing up to 20 flagella) that may adhere together, without non-flagellated centrioles, are capable of amoeboid movement. Mitochondria reduced to hydrogenosomes. Genus example: *Neocallimastix* Vavra et Joyon ex Heath, Bauchop et Skipp, Can. J. Bot. 61(1): 304, 1983. The alternative rank – division *Neocallimastigomycota* M. J. Powell, Mycol. Res. 111: 516, 2007 – we lowered during the rank balancing of the opisthokont tree. Sole class.

XV. *Sanchytriomycotina* Zmitr., Perelygin et Zharikov subdiv. nov. (MB 856987).

Epibiotic/parasitic on xanthophyceans monocentric moulds which penetrates host wall with rhizoid system. There is a rounded to elongated anatropous sporangium and amoeboid zoospores with filopodia and posterior pseudocilium (reduced immotile flagellum). Mitochondrial cristae flat. Sexual reproduction not known. Example genus: *Sanchytrium* Karpov et Aleoshin in Karpov, Mamanazarova, Popova, Aleoshin, James, Mamkaeva, Tcvetkova, Vishnyakov et Longcore (Fungal Biol. 121: 735, 2017). The alternative rank – division *Sanchytriomycota* Galindo, López-García, Torruella, Karpov et Moreira, Nature Communications 12, 4973, 2021 – we lowered during the rank balancing of the opisthokont tree. Sole class (see above).

XVI. *Entomophthoromycia* Zmitr., Perelygin et Zharikov supercl. nov. (MB856988).

Arthropod pathogenic, saprobic or phytopathogenic terrestrial moulds with vegetative stage as coenocytic hyphae, hyphal bodies, or yeast-like; cells broad, walled or protoplastic. Mitochondrial cristae flat. Conidiophores simple or digitate, each branch forming one conidiogenous cell and one conidium. Primary spores are conidia, uni- to multinucleate, usually forcibly discharged; usually forming one or more types of secondary conidia. Resting spores are homothallic zygospores or azygospores. Example genus: *Entomophthora* Fresenenius 1856 (Bot. Ztg. 14: 883, 1856). The alternative rank – division *Entomophthoromycota* Humber, Mycotaxon 120: 482, 2012 – we lowered during the rank balancing of the opisthokont tree. Two classes (see above).

XVII. *Kickxellomycia* Zmitr., Perelygin et Zharikov supercl. nov. (MB 856989).

Saprotrophic, mycoparasitic or endobiotic filamentous terrestrial moulds. Hyphae endobiotic or subaerial, branched, or unbranched, regularly septate. Septa with median, disciform cavities containing plugs. Mitochondrial cristae flat. Asexual reproduction by 1- or 2-spored merosporangia, trichospores, or arthrospores. Sexual reproduction by zygospores that are globose, biconical, or allantoid and coiled. Example genus: *Kickxella* Coem. (Bull. Soc. R. Bot. Belg. 1: 156, 1862). The alternative rank – subdivision *Kickxellomycotina* Benny, Mycol. Res. 111: 518, 2007 – we lowered during the rank balancing of the opisthokont tree. Six classes (see above).

XVIII. *Mucoromycia* Zmitr., Perelygin et Zharikov supercl. nov. (MB 856990).

Saprotrophic or endobiotic filamentous terrestrial moulds, forming broad multinuclear hyphae. Septa occurring only in separating reproductive cells. Mitochondrial cristae flat. Sexual reproduction, if present, by zygospores formed as result of gametangial conjugation. Zygospores globose, smooth or ornamented, produced on suspensor cells. Asexual reproduction by chlamydospores or sporangiospores produced in sporangia and sporangioles. Example genus: *Mucor* Fresenius (Beitr. Mykol. 1: 7, 1850). The alternative rank – division *Mucoromycota* Doweld, Prosyllabus Tracheophytorum, Tentamen systematis plantarum vascularium (Tracheophyta): 77, 2001 – we lowered during the rank balancing of the opisthokont tree. Three classes (see above).

XIX. *Mortierellomycia* Zmitr., Perelygin et Zharikov supercl. nov. (MB 856991).

Saprotrophic terrestrial moulds producing dichotomously branching, anastomosing hyphae, bearing stylospores. Mitochondrial cristae flat. Sporangiophores initially coenocytic, irregularly septate when mature. Asexual reproduction by sporangia and sporangioles. Sporangia spherical, multi-spored, without columella. Sporangioles terminal, borne on erecting hyphae. Sporangiospoes ellipsoid or globose or irregular, smooth or ornamented. Zygospores naked. Example genus: *Mortierella* Coem. (Bull. Acad. R. Sci. Belg., Cl. Sci., ser. 2 15: 536, 1863). The alternative rank – subdivision *Mortierellomycotina* Kerst. Hoffm., K. Voigt et P. M. Kirk, Mycotaxon 115: 360, 2011 – we lowered during the rank balancing of the opisthokont tree.

XX. *Calcarisporiellomycia* Zmitr., Perelygin et Zharikov supercl. nov. (MB 856992).

Saprotrophic terrestrial filamentous moulds with septate multinucleate hyphae. Vegetative hyphae hyaline, smooth, thin-walled. Mitochondrial cristae flat. Sporangiophores simple when present, hyaline, smooth, arising from undifferentiated hyphae. Sporangia one-spored, ellipsoid, with or without a small columella. Sporangiospores uninucleate, hyaline, smooth, thin-walled, ovoid to ellipsoid, with a rounded base. Chlamydospores, when present, born laterally on short hyphae, one-celled, elongate to globose, thick-walled, spiny. Sexual process unknown. Example genus: *Calcarisporiella* de Hoog (Stud. Mycol. 7: 68, 1974). The alternative rank – *Calcarisporiellomycota* Tedersoo et al. Index Fungorum ID: 554019, 2018 – we lowered during the rank balancing of the opisthokont tree.

XXI. *Dikaryomycotina* Zmitr., Perelygin et Zharikov subdiv. nov. (MB 856993).

Saprotrophic, biotrophic (including mycorrhizal and lichenized) of endophytic terrestrial or secondarily aquatic fungi possessing hyphae demonstrating dikaryotic condition at least in some stage of life cycle. Dikaryons results from cytoplasmic fusion of two haploid, monokaryotic hyphae. Clamp connections in basidiomycetous fungi and croziers in ascomycetous fungi are structures that function in the apportioning of nuclei to daughter cells following mitosis in dikaryotic hyphae, may be homologous. Hyphae are regularly septate, whereas unicellular forms were derived by reduction. In alternative rank the name *Dicaryomycota* was published by Kendrick [23], without specifying the diagnosis (nom. inval.), whereas the name *Dikarya* is invalid, too, because it is described without a standardized termination (ICNAFP, Art. 16.2).

XXII. *Entorrhizomycia* Zmitr., Perelygin et Zharikov supercl. nov. (MB 856994).

Endobiotic or phytopathogenic terrestrial fungi, forming intracellular septate coils bearing haustoria and terminal teliospores that germinate internally by becoming four-celled. Mitochondrial cristae flat. Hyphae with regular septa, with or rarely without dolipores, without Woronin bodies or membrane caps. Example genus: *Entorrhiza* C. A. Weber (Bot. Ztg. 42: 378, 1884). The alternative rank – *Entorrhizomycota* R. Bauer, Garnica, Oberw., K. Riess, M. Weiß et Begerow, PLoS One 10.e0128183:10, 2015 – we lowered during the rank balancing of the opisthokont tree.

XXIII. *Agaricomycia* Zmitr., Perelygin et Zharikov supercl. nov. (MB 856995).

(Alternative name and rank – *Basidiomycota* R. H. Whittaker ex Moore, Bot. Mar. 23: 371, 1980). One of two largest groups of dikarya associated with a trivial *Fungi* concept. Hyphae have an electron-dense (multilayered or visually single-layered) wall, are divided by septa into mononuclear, binuclear or multinuclear segments. The septal pore may resemble a simple ascomycetous pore, may be closed by a compact plug, but in most it has a ridge-like thickening on both sides (doliolum). The basic cell wall polysaccharide is chitin immersed into matrix formed by (1→3)-β/(1→6)β-glucans. Unlike ascomycetous fungi, the content of guanine-cytosine pairs of the total DNA of basidiomycotes exceeds 50%. In addition, basidiomycetous fungi differ from ascomycetous ones in a number of biochemical features, e.g. the formation of urease, siderochromes, the type of ubiquinone system, which allows, for example, to clearly distinguish basidiomycetous yeasts from ascomycetous ones. Karyogamy and meiosis occurs in the basidium producing exogeneous basidiospores (in the genus *Mixia*, a secondary transition to enteroblastic sporogenesis is observed). Example genus: *Agaricus* L. (Sp. Pl. 2: 1171, 1753). 20 classes (see above).

XXIV. *Saccharomycia* Zmitr., Perelygin et Zharikov supercl. nov. (MB856996).

(Alternative name and rank – *Ascomycota* R. H. Whittaker, Quart. Rev. Biol. 34: 220, 1959). The largest group of dikarya. Hyphae are characterized by a two-layered wall (a thin electron-dense outer layer and a thickened electron-transparent inner layer) and are divided into multinucleate segments ("cells") by centripetally growing septa with a remaining central pore. Sometimes the pores of ascomycetous fungi are closed by a membrane formation called a pore cap. The main component of the cell wall is chitin, immersed in matrix formed by (1→3)-β/(1→6)β-glucan or galactomannoproteins. Mitochondria have flat or (in yeast) tubular cristae. Karyogamy and meiospore formation occur endogenously in asci. There are many asexual mitosporic taxa. Many ascomycetous fungi are reduced to yeast phase. Example genus: *Saccharomyces* Meyen (Arch. Naturgesch. 4: 100, 1838). 24 classes (see above).

XXV. *Syssomonadea* Zmitr., Perelygin et Zharikov phyl. nov.

Heterotrophic amoeboflagellates with pleomorphic life cycle. Swimming stage unikont, with smooth flagellum that emerges from the middle-lateral point of the cell, turns back, and directs backwards during swimming. Mitochondrial cristae flat. Floating cells move downwards to transform into amoeboflagellates by generating wide lobopodia and thin short filopodia, and slowing the flagellar beating. These cells can be transformed into the cyst (zoosporangium), or give rise shapeless aggregates. Sole genus: *Syssomonas* Tikhonenkov et al. (Current Biology. 27: 2043–2050, 2017).

New taxa in *Corticata* subdomain

Such important groups as plants, cryptists, haptists, rhizarians and chromalveolates, are united in this subdomain.

The *Cryptista* supergroup unites flagellates characterized by oval cells of constant shape, obliquely cut at the anterior end, with a pronounced ventral groove, equipped at the anterior end in the region of the pharynx with two flagella – long, bearing two rows of simple mastigonemes and short, bearing one row of mastigonemes and two apical filaments. Mitochondria having flat cristae. Plastids of autotrophic forms contain a nucleomorph, chlorophylls *a* and *c*, as well as a number of additional pigments (phycoerythrin, phycocyanins). There are primary colorless (*Goniomonas*) and secondarily colorless (*Chilomonas*) cryptomonads. Katablepharids are heterotrophic flagellates, the cell body plan of which comparable with that of cryptomonads, but differs in a more developed digestive apparatus, the nature of the flagellar membrane, and tubular mitochondrial cristae.

The *Archaeplastida* (*Plantae*) are basically biflagellate (the number of cilia varies from 0 to 16, sometimes cilia and centrioles secondarily lost), predominantly autotrophic organisms, the plastids of which are the result of the primary endosymbiosis with cyanobacteria. The root system in ciliate forms characterized by cruciform lying of microtubular roots. The cilia either smooth or scaly. The chloroplasts envelopes double membrane, photosynthetic pigments are chlorophylls *a* and *b*, or in red algae, instead of chlorophyll *b*, phycoerythrins/phycocyanins. Glaucophytes acquired cyanelles primarily or secondarily, but in the last case the primary endosymbiont has a cyanobacterial nature too. Mitochondrial cristae are predominantly flat, although some rhodophytes have vesicular cristae. Among the archaeplastids, all types of multicellular plant body organization are observed, including the "crown" one, vascular plants.

The *Haptista* supergroup is charactirezed by microtubule-based appendages (haptonema or axopodia) used for feeding and complex mineralized (siliceous or calcareous) scales in many species. Two major groups. Haptophytes: autotrophic or heterotrophic flagellates have two (rarely four) smooth or rough unequal flagella at their anterior end. Between the flagella there is a filamentous structure – the haptonema which serves to attach to the substrate, move and capture food. In contrast to the ciliar axoneme, a transverse section of the haptoneme shows a bundle of 6–8 microtubules surrounded by cisterns of endoplasmic reticulum. Plastids containing chlorophylls *a* and *c* as well as fucoxanthin, are covered with a membrane of the endoplasmic reticulum. Mitochondria with tubular cristae. Cells naked or covered with organic scales (*Prymnesium* – freshwater unicellular algae), in some marine forms with large calcareous scales of complex structure (*Coccolithus* – marine unicellular algae). The life cycle alternates between stationary and motile stages. The sexual process is not known. *Centrohelids*: heterotrophic unicellular amoeboid organisms with long radially arranged axopodia diverging from a single center, the axoplast. The pellicle bearing trichocysts and scale deposits of various shapes and compositions. Mitochondria with flat cristae. Predominantly freshwater planktonic forms. The sexual process is not known.

The *Rhizaria* supergroup unites mainly amoeboid heterotrophic (in some cases – *Chlorarachnion* – having an autotrophic eukaryotic symbiont) organisms capable of forming the rhizopodia – long, narrow and often branched pseudopodia. Amoeboid cells can fuse to form plasmodia. All rhizarians are aerobes with mitochondria having tubular cristae. In some groups, at certain stages of the life cycle, the flagellated cells with two unequal smooth anterior cilia may form. The cytostome is absent. The cell can form lorica or skeletal structures penetrating the cytoplasm. In parasitic forms, the cytoskeleton undergoes reduction, and the plasmodia of such forms resemble the vegetative body of some fungi. The sexual process is expressed in many groups. *Rhizaria* include many soil amoebae as well as radiolarians and foraminifera living in the Ocean. Of the mycological objects related to rhizarians the group of plasmodiophorids can be mentioned.

The *Alveolata* supergroup is characterized by a cortical alveolae, sometimes secondarily lost; with ciliary pit or micropore; mitochondrial cristae tubular or ampulliform. A characteristic feature of many alveolate groups is cell covers in the form of a pellicle with cortical alveolae and subpellicular microtubules, or with large cisterns surrounded by a membrane. Single-celled, rarely colonial, mononucleate or multinucleate organisms, bearing, at least at a certain stage of the life cycle, two or many cilia. The nucleus of representatives of dinoflagellates is poor in histones, in ciliates the nuclear dualism is observed. Mitochondria with tubular (very rarely flate or ampulliform) cristae, in anaerobic ciliates can be replaced by hydro-genosomes. Aquatic organisms that inhabit the ocean and fresh waters; a number of groups have adapted to the development of arthropods and warm-blooded animals in the internal environment. Endosymbiotic dinoflagellates take part in the creation of reef biogerms.

Many representatives of diverse *Stramenopila* supergroup have a characteristic "visiting card" – two flagella that differ sharply from each other, and the motor one is furnished with tripartite mastigonemes located in two rows, while the backward flagellum remains smooth. Sometimes the tail cilium is reduced (hyphochytrids) or the cell is provided with many cilia (opalinates). In proteromonads, both flagella are smooth, and mastigonemes are located in the back of the cell and called somatonemata. In the transition zone of the flagellum, there are structures called single or double helix, which are another unique feature of some groups. Dikinetide have four microtubular roots. The rhizoplast (a cross-striated cord connecting dikinetide with the nucleus or mitochondria) is often expressed. The group is represented by a variety of types of organization, i.e. monades, amoeboid, coccoid, mycelial, filamentous, heterotrichal, lamellar or parenchymatous; frequent colonial forms. The tissue organization of brown algae has something in common with that of green and red algae – convergence in this case is based on the patterns of transformation of the multifilamentous thallus. The organization of labyrinthulae is an ectoplasmic network with cells capable of moving inside it – has no convergent analogues in the living world. Autotrophic forms contain plastids surrounded by a 4-membrane envelope, representing a derivative of the red algal endosymbiont (the fourth membrane is an element of the endoplasmic reticulum that envelops the plastid). The additional chlorophylls are *c1* and *c2*, as well as α-, β-, ε-carotenes. Opalinates and proteromonads do not have any structures indicating a former autotrophic life and, apparently, are primarily heterotrophic. Mitochondria with tubular cristae. The sexual process is present or absent.

The following subdomain classiification is accepted by us.

• •Kingdom *Eocorticata*[XXVI]
• • • • • •Phylum *Hemimastigophora* Foissner et al. (sole class and order)
• • • • • •≈Phylum *Provora* Tikhonenkov et al. (sole class and order)
• • • • • •Phylum *Meteora*[XXII] (sole class and order)
• •Kingdom *Haptista* Caval.-Sm. et al.
• • • • • •Division *Haptophyta* Hibberd
• • • • • • • • •Class *Pavlovaphyceae* Edvardsen et al. (sole order)
• • • • • • • • •Class *Prymnesiophyceae* Hibberd (seven orders)
• • • • • •Phylum *Centroplasthelida* Febvre-Chevalier et Febvre
• • • • • • • • •Class *Pterocystida* Caval.-Sm., von der Heyden (three orders)
• • • • • • • • •Class *Panacanthocystida* Shishkin et Zlatogursky (two orders)
• •Kingdom *Tsaralia*[XXIII]
• • • • •Superphylum *Eochromista*[XXIX]
• • • • • •Phylum *Telonemia* Shalchian-Tabrizi et al. (sole class and order)
• • • • •Superphylum *Rhizaria* Caval.-Sm.
• • • • • •Phylum *Gymnosphaerida* Poche (sole class and order)
• • • • • •Phylum *Cercozoa* Caval.-Sm.
• • • • • • • • •Class *Cercomonadida* Poche (sole order)
• • • • • • • • •Class *Cryomonadida* Caval.-Sm. (sole order)
• • • • • • • • •Class *Glissomonadida* Howe et al. (sole order)
• • • • • • • • •Class *Ebriacea* Lemmermann (sole order)
• • • • • • • • •Class *Euglyphida* Copeland (sole order)
• • • • • • • • •Class *Helkesea* Caval.-Sm. (sole order)
• • • • • • • • •Class *Pansomonadidae* Vickerman et al. (sole order)
• • • • • • • • •Class *Paracercomonadida* Caval.-Sm. (sole order)
• • • • • • • • •Class *Thaumatomastigidae* Patterson, Zölfell (sole order)
• • • • • • • • •Class *Thecofilosea* Caval.-Sm. (five orders)
• • • • • • • • •Class *Tectofilosida* Caval.-Sm. (sole order)
• • • • • • • • •Class *Ventricleftida* Howe et al. (sole order)
• • • • • • • • •Class *Viridiraptoridae* Hess, Melkonian (sole order)
• • • • • •Phylum *Metromonadea* Howe et al. (sole class and order)
• • • • • •Phylum *Chlorarachnea* Hibberd, Norris (sole class and order)
• • • • • •Phylum *Granofilosea* Howe et al. (sole class and order)
• • • • • •Phylum *Endomyxa* Caval.-Sm.
• • • • • • • • •Class *Phytomyxea* Engler et Prantl
• • • • • • • • •Subclassis *Plasmodiophorida* Cook (sole class and order)
• • • • • • • • •Subclassis *Phagomyxida* Caval.-Sm.
• • • • • • • • •Class *Filoretidae* Caval.-Sm. (sole order)
• • • • • • • • •Class *Gromiida* Reuss (sole order)
• • • • • • • • •Class *Vampyrellida* Hess et al. (sole order)
• • • • • •Phylum *Ascetosporea* Caval.-Sm.
• • • • • • • • •Class *Haplosporida* Caullery et Mensil (sole order)
• • • • • • • • •Class *Paradiniidae* Schiller (sole order)
• • • • • •Phylum *Retaria* Caval.-Sm.
• • • • • • • • •Class *Acantharea* Haeckel (sole order)
• • • • • • • • •Class *Foraminifera* d'Orbigny (13 orders)
• • • • • • • • •Class *Polycystinea* Ehrenberg (two orders)
• • • • • • • • •Class *Taxopodida* Fol (sole order)
• • • • • •Phylum *Aquavolonida* Bass et Berney
• • • • • • • • •Class *Tremulida* Howe et al. (sole order)
• • • • •Superphylum *Alveolata* Caval.-Sm.
• • • • • •Phylum *Acavomonidia* Tikhonenkov et al. (sole class and order)
• • • • • •Phylum *Colponemidia* Tikhonenkov et al. (sole class and order)
• • • • • •Phylum *Apicomplexa* Levine
• • • • • • • • •Class *Aconoidasida* Mehlhorn et al. (two orders)
• • • • • • • • •Class *Blastogregarinea* Chatton et Villeneuve (sole order)
• • • • • • • • •Class *Coccidia* Leuckart (four orders)
• • • • • • • • •Class *Gregarinasina* Dufour (three orders)
• • • • • •Phylum *Perkinsozoa* Noren et Moestrup
• • • • • • • • •Class *Perkinsida* Levine (sole order)
• • • • • • • • •Class *Phagodiniida* Caval.-Sm. (sole order)
• • • • • • • • •Class *Rastromonadida* Caval.-Sm. et Chao (sole order)
• • • • • •Division *Dinophyta* Jeffrey
• • • • • • • • •Class *Blastodiniphyceae* Fensome et al. (sole order)
• • • • • • • • •Class *Dinophyceae* F. E. Fritsch (16 orders)

•••••••••Class *Noctilucophyceae* Fensome et al. (sole order)
•••••••••Class *Syndiniophyceae* Loeblich (sole order)
••••••Phylum *Colpodellida* Caval.-Sm. (sole class and order)
••••••Phylum *Ciliophora* Doflein
•••••••••Class *Colpodea* Small et Lynn (four orders)
•••••••••Class *Nassophorea* Small et Lynn (three orders)
•••••••••Class *Oligohymenophorea* de Puytorac et al. (10 orders)
•••••••••Class *Phyllopharyngea* de Puytorac et al. (nine orders)
•••••••••Class *Plagiopylea* Small et Lynn (sole order)
•••••••••Class *Prostomatea* Schewiakoff (two orders)
•••••••••Class *Spirotrichea* Bütschli (10 orders)
•••••Superphylum *Heterokonta* Caval.-Sm.
••••••Phylum *Bicosoecea* Caval.-Sm. (sole class and order)
••••••Phylum *Developea* Aleoshin et al. (sole class and order)
••••••Phylum/Division *Heterokontophyta* Moestrup, R. A. Andersen et Guiry
•••••••••Class *Actinophryida* Hartmann (sole order)
•••••••••Class *Bacillariophyceae* Hendey (38 orders)
•••••••••Class *Bolidophyceae* Guillou et al. (sole order)
•••••••••Class *Chrysophyceae* Pascher (four orders)
•••••••••Class *Chrysoparadoxophyceae* Whetherbee (sole order)
•••••••••Class *Dictyochophyceae* Silva (sole order)
•••••••••Class *Eustigmatophyceae* Hibberd et Leedale (two orders)
•••••••••Class *Mediophyceae* Jouse et Proshkina-Lavrenko in Medlin et Kaczmarska (sole order)
•••••••••Class *Olisthodiscophyceae* Graf et Yoon (sole order)
•••••••••Class *Pelagophyceae* Andersen et al. (sole order)
•••••••••Class *Phaeophyceae* Hansgirg (13 orders)
•••••••••Class *Phaeosacciophyceae* Graf et al. (sole order)
•••••••••Class *Phaeothamniophyceae* Bailey et al. (sole order)
•••••••••Class *Pinguiophyceae* Kawachi et al. (sole order)
•••••••••Class *Raphidophyceae* Chadefaud (sole order)
•••••••••Class *Schizocladiophyceae* Kawai et al. (sole order)
•••••••••Class *Synchromophyceae* Horn et al. (sole order)
•••••••••Class *Xanthophyceae* Fritsch (seven orders)
••••••Phylum/Division *Hyphochytriomycota* Whittaker (sole class and order)
••••••Phylum/Division *Peronosporomycota* Dick
•••••••••Class *Peronosporomycetes* Dick (three orders)
•••••••••Class *Saprolegniomycetes* Hawksworth (seven orders)
••••••Phylum *Pirsonionea* Caval.-Sm. (sole class and order)
••••••Phylum *Sagenista* Caval.-Sm.
•••••••••Class *Eogyrea* Caval.-Sm. et Scoble (sole order)
•••••••••Class *Labyrinthulea* L. S. Olive (two orders)
••••••Phylum *Opalinata* Wenyon
•••••••••Class *Proteromonadea* Grasse (sole order)
•••••••••Class *Opalinatea* Wenyon (two orders)
••••••Phylum *Placidozoa* Caval.-Sm. (sole class and order)
••••••Phylum *Platysulcea* Caval.-Sm. (sole class and order)
••Kingdom *Plantae* Haeckel
•••••Superphylum *Cryptista* Adl et al.
••••••Division *Cryptophyta* Silva
•••••••••Class *Palpitomonadophyceae* Su Liu et Bing Liu (sole order)
•••••••••Class *Katablepharidophyceae* N. Okamoto et I. Inouye (sole order)
•••••••••Class *Cryptomonadophyceae* Pascher ex Schoenichem (three orders)
•••••••••Class *Microheliellida*[XXX] (sole order)
•••••Superphylum *Glaucophyta* Adl et al.
••••••Division *Glaucocystophyta* L. Kies et B. P. Kremer (sole class and order)
•••••Superdivision *Rhodophyta* Karpov
••••••Division *Rhodelphidiophyta* Gavryluk et al. (sole class and order)
••••••Division *Cyanidiophyta* Bold et Wynne (sole class and order)
••••••Division *Proteorhodophyta*[XXXI]
•••••••••Class *Compsopogonophyceae* G. W. Saunders et Hommersand (three orders)
•••••••••Class *Porphyridiophyceae* M. Shameel (sole order)
•••••••••Class *Rhodellophyceae* Caval.-Sm. (sole order)
•••••••••Class *Stylonematophyceae* H. S. Yoon, K. M. Müller, R. G. Sheath, F. D. Ott et D. Bhattacharya (two orders)
••••••Division *Eurhodophyta*[XXXII]
•••••••••Class *Bangiophyceae* Wettstein (two orders)
•••••••••Class *Florideophyceae* Cronquist (21 orders)
•••••Superdivision *Chloroplastida* Adl et al.
••••••Division *Prasinodermophyta* Li et al.
•••••••••Class *Prasinodermophyceae* Li et al. (sole order)
•••••••••Class *Palmophyllophyceae* Leliaert et al. (two orders)
••••••Division *Chlorophyta* Pascher
•••••••Subdivision *Chlorodendrophytina*[XXXIII] (sole class and order)
•••••••Subdivision *Pedinophytina*[XXXIV] (sole class with three orders)
•••••••Subdivision *Chloropicophytina*[XXXV] (sole class and order)
•••••••Subdivision *Picocystophytina*[XXXVI]
•••••••••Class *Pyramimonadophyceae* Moestrup et Daugbjerg (two orders)
•••••••••Class *Mamiellophyceae* Marin, Melkonian (three orders)
•••••••••Class *Nephroselmidophyceae* T. Nakayama, S. Suda, M. Kawachi et I. Inouye (sole order)
•••••••••Class *Pycnococcophyceae*[XXXVII] (sole order)
••••••Division *Streptophyta* Bremer
•••••••Subdivision *Chlorokybophytina* Bremer (sole class and order)
•••••••Subdivision *Mesostigmatophytina* Hoppe (sole class and order)
•••••••Subdivision *Klebsormidiophytina* Tedersoo (sole class and order)
•••••••Subdivision *Zygophytina* Jeffrey (sole class with five orders)
•••••••Subdivision *Coleochaetophytina* Bremer (sole class with two orders)
•••••••Subdivision *Charophytina* Bremer et Wanntorp (sole class and order)
•••••••Subdivision *Embryophytina* Bremer et Wanntorp (≈15 classes)

The following new taxa we formally describe here.

XXVI. *Eocorticata* Zmitr., Perelygin et Zharikov regn. nov.

[Etymology: the most ancient of the corticates, the Cavalier-Smith's group name referring to the more strengthened in comparison to discobean and amorpheans cell outer layer].

Heterotrophic flagellates of diverse morphology, mostly predators, bearing extrusomes, glycocalix and other subcortical structures. The cells flattened, vary from ovoid to spindle-shaped or star-like, in hemimastigophoreans with two rows of flagella of varying length, without mastigonemes. Meteoran cells glide over substrates along a long axis of anterior and posterior projections, and have a pair of lateral arms supported by microtubules originating from a cluster of subnuclear MTOCs. The axoneme is without paraxial structures and has a normal set of microtubules. The nucleus single, vesicular, as a rule with prominent nucleolus. Mitochondria having tubular or vesicular cristae. Example genera: *Hemimastix* W. Foissner, Blatterer, I. Foissner, *Spironematella* P. C. Silva, *Meteora* Hausmann et al., *Ancoracysta* Janouskovec. Presumably monophyletic group diverged befire the haptists, chromalveolates and plants. Other predators and environmental sequences of marine sludges can probably be settled here. The studied mitochondrial genome of some representatives turned out to be gene-rich, alike another ancient group, *Jakobea*, however, the processes of mitochondrial gene elimination could occur in different groups at different rates and is not a relationships marker.

XXVII. *Meteora* Zmitr., Perelygin et Zharikov phyl. nov.

[Etymology: referring to the genus *Meteora* Hausmann et al.]

Heterotrophic bacteriovorous nanoflagellates. Cells glide over substrates along a long axis of anterior and posterior projections, and have a pair of lateral arms that swing back and forth. Anterior-posterior cell projections are supported by microtubules originating from a cluster of subnuclear MTOCs. The arms are supported by microtubules, and neither have a flagellar axoneme-like structure. Genus example: Meteora Hausmann, Weitere, Wolf et Arndt (Eur. J. Protistol. 38: 171–177, 2002).

XXVIII. *Tsaralia* Zmitr., Perelygin et Zharikov regn. nov.

[Etymology: abbreviation adapting the TSAR-clade (*Telonema*, *Stramenopila*, *Alveolata*, *Rhizaria*) to latinized record form].

Diverse group characterized by mitochondria with tubular or vesicular cristae and streghtened cortical cell layer. Heterotrophic or containing plastids of eukaryotic origin. Basically bikont (with four microtubular kinetosomal roots), secondarily unikont, multiciliate or devoid of flagellum. Stramenopiles typically with heterokont ciliation – anterior flagellum with tripartite mastigonemes in two opposite rows and a posterior usually smooth cilium; alveolates inforced by cortical alveolae (sometimes secondarily lost), with ciliary pit or micropore; rhizarians form pseudopodia varying as simple, branching, or anastomosing patterns, often supported by microtubules, kinetocyst and other types of extrusomes along axopodia. Free-swimming, loricate, multicellular (heterokont algae, pseudofungi), plasmodial, colonial forms.

XXIX. *Eochromista* Zmitr., Perelygin et Zharikov superphyl. nov.

[Etymology: referring to ancient chromalveolates].

Heterotrophic flagellates. Biflagellated cells with a proboscis-like structure located at the ciliary pole and a complex cytoskeleton composed of layers of microtubules and microfilaments; tripartite tubular hairs on the long cilium. Mitochondria with tubular cristae. Peripheral vacuoles located just beneath the cell membrane. Genus example: *Telonema* Griessmann, may consist of several genera. This grouping was created mainly to accommodate the *Telonemia*, i.e. basal chromalveolates. But it is possible to replenish this grouping with other protists of marine slugs as well as some environmental sequences.

XXX. *Microheliellida* Zmitr., Perelygin et Zharikov cl. nov.

Marine microheliozoans. Heterotrophic protists having radiate axopodia with tiny granules and centrosome. Axopodia supported by microtubules. There are tiny haptosome-like extrusomes. Flagellated stages absent. The nucleus situated aside from the cell centre. Filogranular network interconnects mitochondrion, ER, and plasma membrane. The microbody is attached to the nucleus and mitochondrion, which has vermicular tubular cristae and comparable gene-rich genome. Sole genus: *Microheliella* Caval.-Sm. et Chao (Protist 163: 574–601, 2012). Phylogenetically, this taxon belongs to the so-called pancryptista clade at the level of divergence of main *Cryptista* lineages, therefore it deserves to be raised at least to the class level.

XXXI. *Proteorhodophyta* Zmitr., Perelygin et Zharikov div. nov.

Division uniting red algae with intron-rich plastid genome and gene-rich mitochondrial genome – as a rule non-thermophilic unicellular (*Porphyridiophyceae*, *Rhodellophyceae*), filamentous (*Stylonematophyceae*) and pseudoparenchymatous (*Compsogonophyceae*) forms. Basic cell structure characteristic for the whole *Rhodophyta* superdivision (cells without flagella and centrioles, chloroplasts without external endoplasmic reticulum or unstacked thylakoids, and use phycobiliproteins as accessory pigments). Some drift in the rank structure of *Rhodophyta* is associated with the discovery of flagellate predators-rhododelphids as well as with rather isolated position of the theromphilous and acidophilous genus *Cyanidium*. Comparative genomic studies have also shown that the plastid genome of the florideae turned out to be more compact and rationalized in comparison with that of the "basal red algae", i.e. *Proteorhodophyta*.

XXXII. *Eurhodophyta* Zmitr., Perelygin et Zharikov div. nov.

Division uniting red algae with small plastid and mitochondrial genome and filamentous, pseudoparenchymatous, or parenchymatous structure (*Bangiophyceae*, *Florideophyceae*). Pit-connections present in filamentous and pseudoparechymatous forms. Basic cell structure characteristic for the whole *Rhodophyta* superdivision (cells without flagella and centrioles, chloroplasts without external endoplasmic reticulum or unstacked thylakoids, and use phycobiliproteins as accessory pigments).

XXXIII. *Chlorodendrophytina* Zmitr., Perelygin et Zharikov subdiv. nov.

Marine of freshwater green-colored (chlorophylls *a* and *b*) flagellates, but some species form a dendroid colony in which the cells are connected by stalk (remainder of mother cell theca). Cell body is covered by a thin "theca", which is derived from Golgi cysterns. Such a theca consists of many small "prasinophycean" scales fused together. Cells as a rule laterally compressed, but the cell architecture is basically radially symmetrical. Four homodynamic equal flagella emerge from anterior pit of the cell. The flagella are covered with hair scales and two layers of small scales. Mitochondria with flat cristae. There is a single chloroplast adjacent large eyespot and the pyrenoid invaginated by microtubules. Cytokinesis is mediated by the phycoplast. Example genus: *Tetraselmis* F. Stein (Organism. Infusionsthiere 3: t. 16, f. 1–3, 1878). Sole class and order.

XXXIV. *Pedinophytina* Zmitr., Perelygin et Zharikov subdiv. nov.

Marine of freshwater green-colored (chlorophylls *a* and *b*) free-living of endosymbiotic flagellates. Cell uniflagellate with rest second basal body which, during cell division, grows into a new flagellum and the cell forms two new basal bodies. The flagellum inserts laterally and lacks scales. Thin hairs have been described on some taxa. The basal bodies are inserted at opposite polarity to each other, shifted in a counterclockwise direction (resembling those of *Ulvophyceae*) but not overlapping. There is a single parietal chloroplast with a pyrenoid more or less directly opposite the flagellar insertion and an eyespot on the pyrenoid-containing part of the chloroplast. Starch is stored in the chloroplast. A contractile vacuole is present in the front end of freshwater species. The cells are uninuclear. Ejectosomes absent. Mitosis is closed throughout, without polar gaps, i.e. mitotic spindle is entirely internal. Cytokinesis takes place without a phragmoplast or phycoplast. Cell division is by longitudinal fission. Sexual reproduction is unknown. Genus example: *Pedinomonas* Korshikov (Arch. Soc. Russe Prot., 2, 1923). Sole class with three orders.

XXXV. *Chloropicophytina* Zmitr., Perelygin et Zharikov subdiv. nov.

Small (1.5–4 μm diam.) coccoid marine green (chlorophylls *a* and *b*, accessory pigments are neoxanthin, violaxanthin, antheraxanthin, zeaxanthin, lutein, loroxanthin, astaxanthin, β, β-carotene, β, ε-carotene) algae. One nucleus, one mitochondrion, one chloroplast surrounded by two membranes, containing starch grain. Pyrenoid absent. Flagella absent. Coccoid cells with layered cell wall. Sexual reproduction unknown. Genus example: *Chloropicon* Lopes dos Santos and Eikrem (Sci. Rep. 7: 14019, 2017). Sole class and order.

XXXVI. *Picocystophytina* Zmitr., Perelygin et Zharikov subdiv. nov.

Small (2–3 μm diam.) coccoid halophylic green (chlorophylls *a* and *b*, accessory pigments neoxanthin, violaxanthin, alloxanthin, monadoxanthin, diatoxanthin, lutein and zeaxanthin) algae, globose towards a trilobed shape under conditions of nutrient depletion. The ultrastructure is typical for green algae. The major component of the cell wall is polyarabinose. Genus example: *Picocystis* P. A. Lewin (Phycologia, 39: 560–565, 2000). Sole class and order.

XXXVII. *Pycnococcophyceae* Zmitr., Perelygin et Zharikov cl. nov.

Small (1.5–4.0 μm diam.) marine coccoid or biflagellate green (chlorophylls *a* and *b*, accessory pigments Mg 2,4-divinylphaeoporphyrin a_5 monomethyl ester and prasinoxanthin) algae having a resistant cell wall lacking sporopollenin. The pyrenoid has a cytoplasmic channel, which is unique among related taxa. Genus example: *Pycnococcus* Guillard et al. (J. Phycol. 27: 39–47, 1991). Sole class and order.

A multiple transition to coccoid nanoplanktonic life is obvious in various chloroplastid lineages, and an additional description of chloroplastid higher taxa of seems to be quite reasonable. During expansion of environmental molecular studies realm these taxa would be replenished with both new morphospecies and environmental sequences.

CONCLUSION

Here we have formalized some decisions in the field of the rank structure of the eukaryote system, which have been overdue in recent years. Being formally described, these taxa will willy-nilly be used in compilation classifiers until new data make adjustments to the structure, including the rank structure, of the current system. We do not expect rapid acceptance of our fungal taxa, because the current trend in the systematics of fungal organisms is further splitting of higher rank taxa and description of more and more new divisions. However, with the development of formalized approaches to the taxonomic interpretation of phylogenetic and phylogenomic information and in connection with the progress towards developments in PhyloCode, the problem of coordination the rank structure of metazoan and fungal systems with that of the general protists system may be solved in the way we have outlined.

The upper limit of rank increasing of protistan taxa was set by recent changes in the prokaryote system, in particular, by uniting of *Eukarya* and *Asgardarchaeota* into one huge domain. It is obvious that new subdomains, if we keep inflating the rank of eukaryotic supergroups beyond the current one, will become more and more crowded within one domain and then, purely technically, anyone will have to restore order in those areas of the system where the taxon ranks were stubbornly not lowered due to institutional ambitions, the number of divisions was multiplied, and the nomenclatural community remained tolerant to such inflations for decades. In terms of algal and amoeboid systems, we are more optimistic and are confident that many of our innovations will become commonplace in the near future. For example, such class as *Palpitomonadophyceae*, which we did not describe in 2022, is now formally described and used by botanists in the People's Republic of China.

The main trends of further improvement of the rank structure of the eukaryote tree we see in 1) some multiplication of the supregroups described for the few taxa now located among the amoebozoans and TSAR, as well as many environmental sequences; 2) further rationalization of the *Fungi* and *Metazoa* system using intercalary taxonomic categories (including additional and not prescribed in both nomenclatural codes), and 3) further automatization of the ranking procedure and solving the problem of rank estimating for distant "orphan" taxa.

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БИОЛОГИЧЕСКИЕ НАУКИ
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Система эукариот в третьем обновлении интерфейса «Супергруппы эукариот: таксономический/биотехнологический интерфейс»: формальные процедуры изменения ранга таксонов

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АННОТАЦИЯ. Проблема согласования рангов высших таксонов эукариот была специально рассмотрена нами в монографии “Nomenclature and rank correlation of higher taxa of eukaryotes”, где, однако, было опущено большинство формальных описаний предлагаемых таксонов в новом ранге. Целью данной статьи является формальное описание ряда таксонов, установленных нами в этой монографии и последующих обновлениях интерфейса: *Eocorticata* regn. nov., *Tsaralia* regn. nov., *Apusomonadea* intraregn. nov., *Breviatea* intraregn. nov., *Eochromista* superphyl. nov., *Zoosporia* superphyl. nov., *Eurhodophyta* div. nov., *Proteorhodophyta* div. nov., *Anaeramoebea* phyl. et cl. nov, *Calkinsea* phyl. nov., *Meteora* phyl. nov., *Syssomonadea* phyl. nov., *Chlorodendrophytina* subdiv. nov., *Chloropicophytina* subdiv. nov., *Dikaryomycotina* subdiv. nov., *Pedinophytina* subdiv. nov., *Picocystophytina* subdiv. nov., *Sanchytriomycotina* subdiv. nov., *Agaricomycia* supercl. nov, *Calcarisporiellomycia* supercl. nov., *Ceratiomyxomycia* supercl. nov., *Chytridiomycia* supercl. nov., *Entomophthoromycia* supercl. nov., *Entorrhizomycia* supercl. nov., *Kickxellomycia* supercl. nov., *Mortierellomycia* supercl. nov., *Mucoromycia* supercl. nov., *Myxogasteromycia* supercl. nov, *Monoblepharomycia* supercl. nov., *Neocallimastigomycia* supercl. nov., *Saccharomycia* supercl. nov., *Acytosteliomycetes* cl. nov., *Liceomycetes* cl. nov., *Microheliellida* cl. nov., *Paratrimastigidea* cl. nov., *Protosporangiomycetes* cl. nov., *Pycnococcophyceae* cl. nov. Основные направления дальнейшего совершенствования ранговой структуры дерева эукариот мы видим в 1) незначительном увеличении числа супергрупп, описанных для редких и новых таксонов *Amoebozoa* и TSAR, а также неидентифицированных нуклеотидных последовательностей; 2) компактизации системы *Fungi* и *Metazoa* с более широким использованием вставочных таксономических категорий и 3) дальнейшей автоматизации процедуры ранжирования таксонов и новых решений проблемы оценки ранга «орфанных таксонов».

КЛЮЧЕВЫЕ СЛОВА: биотехнологический/таксономический интерфейс; древо эукариот; таксономические ранги; филы; царства

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