

# **Proposal for practical multi-kingdom classification of eukaryotes based on monophyly and comparable divergence time criteria**

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## **Summary**

Much of the ecological, taxonomic and biodiversity research relies on understanding of phylogenetic relationships among organisms. There are multiple available classification systems that all suffer from differences in naming, incompleteness, presence of multiple non-monophyletic entities and poor correspondence of divergence times. These issues render taxonomic comparisons across the main groups of eukaryotes and all life in general difficult at best. By using the monophyly criterion, roughly comparable time of divergence and information from multiple phylogenetic reconstructions, I propose an alternative classification system for the domain Eukarya to improve hierarchical taxonomical comparability for animals, plants, fungi and multiple protist groups. Following this rationale, I propose 32 kingdoms of eukaryotes that are treated in 10 subdomains. These kingdoms are further separated into 43, 115, 140 and 353 taxa at the level of subkingdom, phylum, subphylum and class, respectively (<http://dx.doi.org/10.15156/BIO/587483>). Most of the names have been used previously or these were deduced from those of the type taxa to be able to unambiguously link genera to higher taxonomic levels. In the era of phylogenomics, understanding about the phylogenetic relationships among organisms is rapidly increasing. Classifications systems must keep pace with this race to serve the research community by consistent improvements in precision in terms of taxonomic resolution and maintaining monophyly of the ingredient taxa.

## Introduction

Naming and classification of organisms represents a corner stone for communicating biota and their phylogenetic relationships. Marker gene-based analyses and, more recently, genomics methods have greatly improved our understanding of phylogenetic relationships among biological organisms and enabled phylogenetic classification of many taxonomic groups, for example bacteria and archaea (<http://taxonomicoutline.org/>), flowering plants (APG 2016), fungi (Spatafora et al. 2016) and multiple groups of protists (Berney et al. 2017). These higher-level classifications and taxonomic treatments of genera, families and orders have been incorporated into general classification systems of NCBI (<https://www.ncbi.nlm.nih.gov/taxonomy/>), SILVA (Quast et al. 2013) and many others. Several authors have attempted to formalize the classification of life (Adl et al. 2012; Cavalier-Smith 2013; Ruggiero et al. 2015; Drozdov 2017), but all these systems share several common weaknesses (Figure 1). First, these classifications include higher taxa that are intentionally kept paraphyletic due to the paucity of separating morphological characters or very small size of these groups (Figure 1b). Second, many obvious kingdom- and phylum-level groups are only described at the genus or family level, which hampers understanding their actual level of taxonomic distinctness and relative phylogenetic deepness (Figure 1c). Third, taxa at different taxonomic levels may exhibit identical names, which may cause misunderstanding especially when new higher taxa are erected and when scripts are used to assign OTUs to taxonomy (Figure 1d). Fourth, names of higher level taxa do not give a clue to non-systematicists about the ingredient taxa (e.g. supergroup ‘Opisthokonta’, phylum ‘Paramyria’ and class ‘Cristidiscoidea’ containing genera *Nuclearia* and *Fonticula*; Ruggiero et al. 2015)(Figure 1e). The same issue appears to the informal non-Linnaean names such as ‘SAR’ (Burki et al. 2007), ‘LKM11’ (Quast et al. 2013), ‘clade GS01’ (Tedersoo et al. 2017), etc., but in the two latter examples these names were introduced to communicate undescribed taxa. Fifth, some authors generate large amounts of names for most of the nodes in phylogenies, in spite of anticipating that the groups are poorly supported, sometimes paraphyletic, and subject to change in the next analysis with improved taxon sampling and more genetic information (Figure 1f). Sixth, the available classification systems, especially NCBI and SILVA include higher taxa, some of which are separated into >20 taxonomic levels (e.g. Diptera), whereas for many others, only 1-2 levels exist (Figure 1g). For example, a genus may belong directly to a class, which in turn belongs to a kingdom with no intermediate levels. The latter issue is particularly problematic when assigning taxonomy to sequencing-derived ecological data sets. In high-throughput sequencing, tens of thousands of Operational Taxonomic Units (OTUs) commonly require taxonomic assignment, which is usually performed against reference sequence databases based on BLASTn searches, Bayesian classifiers or evolutionary placement algorithms (Bik et al. 2012). Such highly skewed classifications associated with these databases hamper building hierarchical classifications within ecological data sets and may require substantial taxonomic expertise to arrange suitable-level taxonomic groups for comparison (e.g. Bates et al. 2013; Geisen et al. 2015; Bahram et al. 2016). Genera, phyla, orders and classes are the most commonly used taxonomic levels for grouping.

Out of these multiple shortcomings in classification systems, I find the issue of polyphyly and paraphyly the most problematic, because non-monophyletic entities generate taxonomic uncertainty and confusion. Use of e.g. kingdom 'Protista' and kingdom 'Choanozoa' (sensu Ruggiero et al. 2015) does reflect gross morphology, but provides very limited information about the phylogenetic placement of these groups. Already >50 years ago, Hennig (1966) argued that all taxa should be monophyletic to provide unambiguous understanding of their constituents. Similarly, Avise & John (1999) advocated for the monophyly criterion in classifications based on DNA sequence data and further argued that taxonomic ranks should reflect divergence times to enable comparisons across kingdoms. Decades later we find ourselves still swamped in classification systems comprised of non-monophyletic taxa and finding our way out among multiple synonyms caused by blurring of the boundaries between classical 'botanical' and 'zoological' systems and attempts to provide short-standing names to nearly each node in the ephemeral phylogenetic reconstructions.

Here I revise the subphylum to subdomain level classification of the Eukarya domain (Woese et al. 1990) focusing on formally described groups and neglecting informal names of 'environmental' sequence groups. Based on published molecular phylogenies, NCBI taxonomy backbone, monophyly criterion and comparable level of divergence, I propose a 10-rank alternative classification focusing on subphylum, phylum, subkingdom, kingdom and subdomain levels, with a particular attention to the main ranks above class level. This preprint seeks constructive criticism from the research community to prepare a practical consensus classification of all life that would be efficient for taxon communication among taxonomists and ecologists.

## Methods

Because multiple regularly updated and versioned classifications exist, I first sought to screen the existing systems – UniEuk ([www.unieuk.org](http://www.unieuk.org)), NCBI, GBIF ([www.gbif.org](http://www.gbif.org)), SILVA and aforementioned articles - for the best suitable taxonomic backbone. Monophyly of higher-level taxa and use of officially described names were the main criteria for selection. I compared the classifications against >200 phylogenetic studies from class to kingdom levels, giving priority to studies with larger ingroup, greater number of genes and most recent treatments (for minor deep diverging groups). In brief, the following studies were used to extract much of the class to domain level classification information: Yoon et al. (2006), Ruhfel et al. (2014), Magallon et al. (2015), Leliaert et al. (2017) (Archaeplastida); Fiore-Donno et al. (2010), Lahr et al. (2013), Cavalier-Smith et al. (2015b, 2016), Tekle et al. (2016), Kang et al. (2017), Tekle & Wood 2017 (Amoebozoa); Kolisko 2011, Kamikawa et al. (2014), Radek et al. (2014), Cavalier-Smith (2016), Yubuki et al. (2017) (Excavata); Grant et al. (2009), Riisberg et al. (2009), Brown & Sorhannus (2010), Yang et al. (2012), Cavalier-Smith & Scoble (2013), Shiratori et al. (2015, 2017), Yubuki et al. (2015), Aleoshin et al. (2016), Derelle et al. (2016), Dumack (2016), Gao et al. (2016), Krabberød et al. 2017, Reñe et al. (2017) (Harosa); Brown et al. (2009, 2013), Cavalier-Smith & Chao (2010), Zhang (2011), Glücksman et al. (2013), Nosenko et al. 2013, Paps et al. (2013), Yabuki et al.

(2013), Telford et al. 2015; Torruella et al. (2015), Whelan et al. (2015), Corsaro et al. (2016), Carr et al. (2017), Dohrmann & Wöhrheide (2017), Hehenberger et al. (2017), Schiffer et al. (2017), Simion et al. (2017), Tedersoo et al. (2018), (Opisthokonta); Yoon et al. (2008, 2011), Wegener Parfrey et al. (2010, 2011), Burki et al. (2012, 2016), Cavalier-Smith & Chao (2012), Yabuki et al. (2012, 2014) Cavalier-Smith et al. (2014, 2015a), Burki (2014), Katz & Grant (2014), Sharpe et al. (2015), Brown et al. (2017) (minor groups and all eukaryotes). Following the divergence time estimates of Wegener Parfrey et al. (2011), kingdoms and phyla were assigned to higher taxa that diverged roughly at >1000 and 542 Mya (as described for fungi in Tedersoo et al. 2018). These criteria were used to make the latest diverging kingdoms Metazoa and Viridiplantae comparable to other eukaryote groups. Kingdoms that formed well-supported monophyletic groups were further assigned to subdomains. For kingdoms and phyla, I proposed to use currently accepted names, prioritizing widely used names and those referring to particular taxa, which is in line with the zoological and botanical nomenclature. The few newly proposed names are derived from the names of type taxa. Comparisons between classifications are mostly performed against that of Ruggiero et al. (2015), which is the most widely followed and cited (in both positive and negative sense) recent treatment.

## Results and Discussion

### General patterns

Out of multiple classifications, the NCBI and SILVA classifications were the most updated in terms of state-of-the-art phylogenetic information. Compared with the SILVA classification, the NCBI system comprised much less putative names and codes of undescribed taxa, or these were more comprehensively classified into the Linnaean taxonomic framework. Therefore, the NCBI system (as of 12 October 2017) was selected as a baseline for further work.

Based on multiple molecular phylogenies, the monophyly criterion and roughly comparable divergence time, 32 kingdom-level groups were recovered (Figure 2). Most of these were treated at the level of class (in Ruggiero et al. 2015; see Figure 3) or at the level of phylum or no rank (in NCBI). Monophyletic kingdoms were further grouped into 10 subdomains or subdomain-level taxa, of which four (Archaeplastida, Excavata, Harosa and Opisthokonta) are comprised of >1 kingdom (Figure 3). The 32 kingdoms were further divided into 43 subkingdoms (including 14 named), 115 phyla (102), 140 subphyla (51) and 353 classes (305). The classification down to class level and genus level is given in Appendix 1 and supplementary document (<http://dx.doi.org/10.15156/BIO/587483>), respectively. The lower proportion of named taxa at the level of subranks indicates that subranks were not effectively used in most groups and were left as ‘unspecified’ if monotypic. In relatively well-studied and morphologically diverse kingdoms such as Metazoa, Viridiplantae and Fungi, subkingdoms and subphyla were commonly used to provide more natural grouping and improve resolution.

Compared with Ruggiero et al. (2015) and Adl et al. (2012), the proposed classification contains no taxa that are intentionally erected as paraphyletic. Nonetheless, it is likely that some of the taxa will turn out to be paraphyletic in more refined phylogenomic analyses. In Ruggiero et al. (2015), several taxa in each taxonomic level seem to have been treated as trash bins to accumulate orphan taxa. For example, the phylum ‘Choanozoa’ within kingdom ‘Protozoa’ includes multiple Opisthokontan protists of very different origin including ‘Aphelidea’ that belong to Fungi. Similarly, an ‘unnamed’ hacrobian phylum within the kingdom ‘Chromista’ includes several classes that are so deeply diverging that these warrant a subdomain and kingdom of their own. Furthermore, ‘Zygomycota’ within Fungi comprises multiple phyla of early diverging mycelial lineages.

## Major subdomains and kingdoms

The subdomain Opisthokonta has been interpreted differently in recent phylogenetic and classification studies by comprising only groups intimately related to Metazoa and Fungi or additionally including all minor deeply diverging taxa that diverged after the Amoebozoa (i.e., ‘Obazoa’). For practical reasons, I recommend to use the broader interpretation for Opisthokonta, because the branching order of smaller groups is not fully settled, to minimize the number of subdomain-level taxa, and use a widely known name. Because the formerly proposed ‘Apusozoa’, ‘Choanozoa’ and ‘Sulcozoa’ are strongly para- or polyphyletic, several minor deeply diverging groups were separated from these to represent distinct kingdoms (i.e., Apusozoa *s. stricto*, Breviatae, Choanoflagellozoa, Corallochytrida, Filasteriae, Ichthyosporida, Mantazoa, Planozoa, Rigifilidae). Certain earlier studies indicated that Opisthokonta in the wide sense may be paraphyletic with respect to Amoebozoa, but this is not supported in more recent and more inclusive studies (but see Brown et al. 2017). In Metazoa, it would be feasible to provide a subkingdom-level separation to Bilateria, Ctenophora (as Ctenozoa), Porifera (Porozoa) and Placozoa (Placomorpha). On the fungal side of Opisthokonta, I propose to consider Fungi and Nucleariidae (‘Cristidiscoidea’) as distinct kingdoms and recommend acceptance of nine subkingdoms within Fungi. These include Rozellomyceta (including Microsporidea) and Aphelidiomyceta that are closely related to other fungal groups (James et al. 2013; Corsaro et al. 2014; Tedersoo et al. 2018) rather than forming a cluster of their own (‘Opisthosporidia’ hypothesis; Karpov et al. 2014, 2017; Torruella et al. 2017).

The subdomain Unikontamoebae *nom. provis.* (named as such to secure no overlap with kingdom name) is comprised of the kingdom Amoebozoa and forms a coherent, well-supported sister group to Opisthokonta. Amoebozoa is comprised of three phyla (Discosida, Evosida and Tubulinida) following a recent phylogenomic analysis (Tekle & Wood 2017), which challenges the traditional split of Amoebozoa into Lobosa and Conosa. Based on the NCBI classification and published phylogenetic analyses, there is much uncertainty at the level of classes and orders (Cavalier-Smith et al. 2016; Tekle et al. 2016). The seemingly natural group Mycetozoa may be paraphyletic with respect to Archamoebidea and it is



separated into two classes - Eumycetozoa and Varioseae - within Evosida (Tekle & Wood 2017).

Harosa comprises kingdoms Stramenopila, Alveolata and Rhizaria, collectively known as 'SAR' in informal classification (Burki et al. 2007). Both Harosa and the kingdoms therein are phylogenetically well supported. Given their deep divergence, it is recommended to consider the main taxonomic groups in these kingdoms at the phylum level rather than class level. In this treatment, Stramenopila, Alveolata and Rhizaria are comprised of seven, eight and three phyla, respectively, most of which exhibit distinct ecophysiology (Cavalier-Smith 2018). The relatively recently diverged groups Foraminifera, Polycystinea and Acantharea are considered at the class level within the phylum Retaria of Rhizaria. There are several genera that may warrant recognition at the class or phylum level in Alveolata (*Palustrimonas*, *Voromonas*) and Stramenopila (*Cantina*, *Pirsonia*, *Leukarachnion*, *Platysulcus*, *Pseudophyllomitris* and multiple 'MAST' clades).

The subdomain Excavata has received much less phylogenetic hypothesis testing compared with other major groups. Based on multiple phylogenetic reconstructions, I propose eight kingdoms within Excavata, viz. Heterolobosa, Fornicata, Jakobida, Tsukubamonada, Oxymonada, Parabasalia, Euglenozoa and Malawimonada. Members of the Malawimonada are highly divergent and commonly cluster within or in a sister position to other subkingdoms, but Kolisko (2011) indicated its firm placement within Excavata when removing rapidly evolving regions causing long branches. Although Cavalier-Smith et al. (2014) consider Euglenozoa outside Excavata, other authors have demonstrated its nested position within excavates. Apart from Euglenozoa and Heterolobosa, separation of other excavate kingdoms to phyla was not attempted due to paucity of molecular phylogenetic research. Given the long branches and rapid evolution, the 'metamonad' kingdoms Parabasalia, Oxymonada and Fornicata may turn out to be paraphyletic when more detailed information accumulates.

Archaeplastida contains kingdoms Glaucocystophyta, Rhodophyta (phyla Rhodophyta and Cyanidiophyta) and Viridiplantae, which is separated into Chlorophyta and Streptophyta at the phylum level. Streptophyta is further divided into multiple subphyla, including groups representing green algae, early land plants and vascular plants – Tracheophytina. The latter is comprised of major fern and gymnosperm groups and Angiospermae at the class level. This class-level treatment represents re-organisation of major plant taxa by the level of rank or subrank due to relatively recent divergence of these plant groups relative to other kingdoms (e.g. Wegener Parfrey et al. 2011).

## Minor kingdoms and unplaced taxa

Many studies place Haptista and particularly Cryptista in a sister position to Archaeplastida, but in most studies these groups branch off separately. Haptista contains two classes (Coccolithophyceae and Pavlovophyceae), which may warrant phylum-level separation. Cryptista is comprised of three deeply diverging phyla (Figure 3). Telonemae is a small

groups comprised of two sequenced species (*Telonema antarctica* and *T. subtile*) but represented by a single species in most analyses. Telonemae is most commonly placed in a sister position to the subdomain Harosa (e.g. Cavalier-Smith & Chao 2010; Burki et al. 2012). Picozoa ('picobiliphytes') is represented by a single described species (*Picomonas judraskeda*), although the cryptic diversity of closely related marine taxa is much higher. Picozoa usually branches off separately from any major kingdom or occur in a sister position to Cryptista or Centrohelioczoa (Yoon et al. 2011; Moreira & Lopez-Garcia 2014). Centrohelioczoa is also known as 'Helioczoa', but the latter name has multiple meanings. This kingdom is comprised of 11 sequenced genera that form a coherent group with a long stem (Cavalier-Smith & von der Heyden 2007; Cavalier-Smith & Chao 2012), which warrants treatment of all taxa in a single class Centrohelea, in agreement with Ruggiero et al. (2015). This group has remarkable cryptic diversity in both saltwater and freshwater and soil habitats (Cavalier-Smith & Chao 2012).

There are a few deeply diverging taxa that cannot be reliably related to any proposed subdomain and kingdom (Appendix 1; <http://dx.doi.org/10.15156/BIO/587483>). This is at least partly ascribed to their inclusion in only a few analyses and/or based on 1-2 genes. *Collodictyon triciliatum* and *Diphylleia rotans* (phylum Collodictyonida) are placed within the class 'Endohelea' of hacrobian 'Chromista' together with 'Heliomonadida' (sensu Ruggiero et al. 2015). The latter order is located in 'Granofilosea' of harosean 'Chromista' in Bass et al. (2009) and AlgaeBASE ([www.algaebase.org](http://www.algaebase.org)). While reliable sequences of Heliomonadida are still unavailable, Collodictyonida is phylogenetically placed in a sister position to Opisthokonta, Excavata or Amoebozoa or other minor groups with long branches (Zhao et al. 2012; Cavalier-Smith et al. 2014). The most recent analyses place it in a sister position to the phylum Rigifilidia within Opisthokonta (Brown et al. 2017). *Microheliella maris* (phylum Microheliellida) is phylogenetically distinct from other taxa, but may have some affinities to Centrohelioczoa, Telonemae or Cryptista (Cavalier-Smith & Chao 2012; Yabuki et al. 2012).

## Conclusions and perspectives

Single-cell genomics and transcriptomics methods and phylogenomics analyses have become available in the last 8 years and enabled to resolve the order to phylum level internal structure in many kingdoms. However, these methods still lack sufficient power to provide reliable placement of the minor kingdoms and highly divergent obligately parasitic or anaerobic taxa that are represented by 1-2 isolates. At this stage, certainly more diversity in these groups must be captured, which is of great importance to be able to understand the entire eukaryote evolution (Pawlowski 2013). In unculturable organisms, single cells for genomics analyses can be obtained by using fluorescent probes specifically targeting their DNA (e.g. Jones et al. 2011). It can be speculated that multiple novel kingdoms and phyla are yet to be recovered, which has been demonstrated for many groups. However, as pointed out by Berney et al. (2004), many of these supposedly novel groups represent chimeric marker sequences or rapidly evolving taxa that find their position in more inclusive analyses. Out of >40 novel soil

fungal groups, three have been described or matched to sequenced specimens 24 months after analysis (Tedersoo et al. 2017).

The proposed classification of eukaryotes represents a consensus of multiple phylogenetic studies, which is based on the monophyly criterion and rough divergence time estimates (Avice & John 1999). The other four typical problems in modern classification systems (Figure 1) were accounted for as much as possible, but their handling required almost always compromises between selecting appropriate, non-overlapping, well-known names and erection of optimal number of ranks, which was partly influenced by previous use of these names and availability of phylogenetic information. The proposed names are usually directly linkable to the type genus or forms of these have been widely accepted by the research community. My team also proposed a ‘taxon hypothesis’ concept to be able to cross-link different classification systems in space and time (Tedersoo et al. 2018).

The proposal of multiple kingdoms is not new in science. For example, in pre-molecular era, Leedale (1977) presented a classification system with 18 eukaryote kingdoms, most of which represented various protist groups and early diverging Metazoa. Compared with the classification presented here, Leedale’s kingdoms included taxa from the level of class to subdomain. His treatment certainly represented state-of-the-art of the contemporary knowledge, but the system was not accepted by the scientific community. Most recently, Drozdov (2017) proposed a classification including 15 eukaryote kingdoms. However, this treatment is hardly comparable to other modern classifications, because it is a mixture of morphological and phylogenetic classifications that forces several class-level groups such as Foraminifera and Microsporidea at the kingdom level, and keeps most kingdoms paraphyletic.

In the proposed classification, the erection of 32 eukaryote kingdoms certainly catches and, perhaps, scratches the eye. I found adoption of multiple kingdoms necessary to follow the monophyly principle and to render the relatively late diverging kingdoms Metazoa and Viridiplantae better comparable to multiple protist groups in terms of divergence time. To be strict, it might still require lumping the Choanoflagellozoa to its sister group Metazoa and splitting Unikontamoebae and Excavata to additional kingdoms. Such activities may require revising the age estimates of major eukaryote groups based on additional calibration points and genomic comparisons.

Looking ahead, such multiple-kingdom classification approach would tremendously improve taxonomic resolution of Bacteria and Archaea, for which the kingdom rank is essentially unused (Woese et al. 1990). In contrast to other classifications, Drozdov (2017) erected four and seven kingdoms to accommodate phyla of Archaea and Bacteria, respectively, but most of the proposed groups are para- or polyphyletic. Since prokaryotes evolved and diverged >3 billion years ago (Sheridan et al. 2003), their classification might require another rank between kingdom and domain (for example, rejuvenating the *empire* rank) to accommodate the earliest branching clades. If monophyletic, all prokaryote groups hitherto recognized at the phylum level could be instantly ascribed to separate kingdoms given their time of divergence and improved comparability to eukaryotes



Taken together, I advocate that modernizing the classification of life is necessary for ease of communication between taxonomists, ecologists and molecular biologists. The criteria of monophyly, roughly comparable divergence times and names deduced from genus names are likely to render the names of higher-level taxa much more long-lived and acceptable to the scientific community. I hope that this preprint raises a heavy discussion among taxonomists and leads the way to a modern, global classification system of all life.

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## References

- Adl SM, Simpson AGB, Lane CE, Lukes J, Bass D, Bowser SS et al. 2012. The revised classification of eukaryotes. *J. Euk. Microbiol.* 59: 429–493.
- Aleoshin VV, Mylnikov AP, Mirzaeva GS, Mikhailov KV, Karpov SA. 2016. Heterokont Predator *Develorapax marinus* gen. et sp. nov.—a model of the ochrophyte ancestor. *Front. Microbiol.* 7:1194.
- APG IV. 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Bot. J. Linn. Soc.* 181: 1-20.
- Avisé JC, John GC. 1999. Proposal for a standardized temporal scheme of biological classification for extant species. *Proc. Natl. Acad. Sci. USA* 96: 7358–7363.
- Bahram M, Kohout P, Anslan S, Harend H, Abarenkov K, Tedersoo L. 2016. Stochastic distribution of small soil eukaryotes resulting from high dispersal and drift in a local environment. *ISME J.* 10: 885–896.
- Bass D, Chao EE, Nikolaev S, Yabuki A, Ishida KI, Berney C, Pakzad U, Wylezich C, Cavalier-Smith T. 2009. Phylogeny of novel naked filose and reticulose Cercozoa: Granofilosea cl. n. and Proteomyxidea revised. *Protist* 160: 75-109.
- Bates ST, Clemente JC, Flores GE, Walters WA, Wegener Parfrey L, Knight R, Fierer N. 2013. Global biogeography of highly diverse protistan communities in soil. *ISME J.* 7: 652–659.
- Berney C, Ciuprina A, Bender S, Brodie J, Edgcomb V, Kim E, Rajan J, Parfrey LW, Adl S, Audic S, Bass D. 2017. UniEuk: Time to speak a common language in Protistology!. *J. Euk. Microbiol.* 64: 407-411.
- Berney C, Fahrni J, Pawlowski J. 2004. How many novel eukaryotic 'kingdoms'? Pitfalls and limitations of environmental DNA surveys. *BMC Biol.* 2:13.
- Bik HM, Porazinska D, Creer S, Caporaso JG, Knight R, Thomas WK. 2012. Sequencing our way towards understanding global eukaryotic biodiversity. *Trends Ecol. Evol.* 27: 233-243.
- Brown JW, Sorhannus U. 2010. A molecular genetic timescale for the diversification of autotrophic stramenopiles (Ochrophyta): substantive underestimation of putative fossil ages. *PLoS One.* 5:e12759.
- Brown MW, Heiss A, Kamikawa R, Inagaki Y, Yabuki A, Tice AK, Shiratori T, Ishida K, Hashimoto T, Simpson AG, Roger AJ. 2017. Phylogenomics places orphan protistan lineages in a novel eukaryotic super-group. *bioRxiv* 2017:227884.
- Brown MW, Sharpe SC, Silberman JD, Heiss AA, Lang BF, Simpson AG, Roger AJ. 2013. Phylogenomics demonstrates that breviate flagellates are related to opisthokonts and apusomonads. *Proc. R. Soc. Lond. B* 280:20131755.
- Brown MW, Spiegel FW, Silberman JD. 2009. Phylogeny of the “forgotten” cellular slime mold, *Fonticula alba*, reveals a key evolutionary branch within Opisthokonta. *Mol. Biol. Evol.* 126: 2699-2709.
- Burki F, Kaplan M, Tikhonenkov DV, Zlatogursky V, Minh BQ, Radaykina LV, Smirnov A, Mylnikov AP, Keeling PJ. 2016. Untangling the early diversification of eukaryotes: a phylogenomic study of the evolutionary origins of Centrohelida, Haptophyta and Cryptista. *Proc. R. Soc. B* 283: 20152802.
- Burki F, Okamoto N, Pombert JF, Keeling PJ. 2012. The evolutionary history of haptophytes and cryptophytes: phylogenomic evidence for separate origins. *Proc. R. Soc. B* 279: 2246–2254.
- Burki F, Shalchian-Tabrizi K, Minge M, Skjæveland Å, Nikolaev SI, Jakobsen KS, Pawlowski J. 2007. Phylogenomics reshuffles the eukaryotic supergroups. *PloS One* 2:e790.

- Burki F. 2014. The eukaryotic tree of life from a global phylogenomic perspective. Cold Spring Harbor Persp. Biol. 6:a016147.
- Carr M, Richter DJ, Fozouni P, Smith TJ, Jeuck A, Leadbeater BS, Nitsche F. 2017. A six-gene phylogeny provides new insights into choanoflagellate evolution. Mol. Phyl. Evol. 107: 166-178.
- Cavalier-Smith T, Chao EE, Lewis R. 2015a. Multiple origins of Heliozoa from flagellate ancestors: new cryptist subphylum Corbihelia, superclass Corbistoma, and monophyly of Haptista, Cryptista, Hacrobia and Chromista. Mol. Phyl. Evol. 93: 331–362.
- Cavalier-Smith T, Chao EE, Lewis R. 2016. 187-gene phylogeny of protozoan phylum Amoebozoa reveals a new class (Cutosea) of deep-branching, ultrastructurally unique, enveloped marine Lobosa and clarifies amoeba evolution. Mol. Phyl. Evol. 99: 275-296.
- Cavalier-Smith T, Chao EE, Snell EA, Berney C, Fiore-Donno AM, Lewis R. 2014. Multigene eukaryote phylogeny reveals the likely protozoan ancestors of opisthokonts (animals, fungi, choanozoans) and Amoebozoa. Mol. Phyl. Evol. 81: 71-85.
- Cavalier-Smith T, Chao EE. 2010. Phylogeny and evolution of apusomonadida (protozoa: apusozoa): new genera and species. Protist 161: 549-576.
- Cavalier-Smith T, Chao EE. 2012. *Oxnerella micra* sp. n. (Oxnerellidae fam. n.), a tiny naked centrohelid, and the diversity and evolution of heliozoa. Protist 163: 574-601.
- Cavalier-Smith T, Fiore-Donno AM, Chao E, Kudryavtsev A, Berney C, Snell EA, Lewis R. 2015b. Multigene phylogeny resolves deep branching of Amoebozoa. Mol. Phyl. Evol. 83: 293-304.
- Cavalier-Smith T, Scoble JM. 2013. Phylogeny of Heterokonta: *Incisomonas marina*, a uniciliate gliding opalozoan related to *Solenicola* (Nanomonadea), and evidence that Actinophryida evolved from raphidophytes. Eur. J. Protistol. 49: 328-353.
- Cavalier-Smith T, von der Heyden S. 2007. Molecular phylogeny, scale evolution and taxonomy of centrohelid heliozoa. Mol. Phyl. Evol. 44: 1186–1203
- Cavalier-Smith T. 2013. Early evolution of eukaryote feeding modes, cell structural diversity, and classification of the protozoan phyla Loukozoa, Sulcozoa, and Choanozoa. Eur. J. Protistol. 49: 115-178.
- Cavalier-Smith T. 2016. Higher classification and phylogeny of Euglenozoa. Eur. J. Protistol. 56: 250-276.
- Cavalier-Smith T. 2018. Kingdom Chromista and its eight phyla: a new synthesis emphasising periplastid protein targeting, cytoskeletal and periplastid evolution, and ancient divergences. Protoplasma. In press.
- Corsaro D, Michel R, Walochnik J, Venditti D, Müller KD, Hauröder B, Wylezich C. 2016. Molecular identification of *Nucleophaga terricolae* sp. nov. (Rozellomycota), and new insights on the origin of the Microsporidia. Parasitol. Res. 115: 3003-3011.
- Corsaro D, Walochnik J, Venditti D, Steinmann J, Müller K-D, Michel R. 2014. Microsporidia-like parasites of amoebae belong to the early fungal lineage Rozellomycota. Parasitol. Res. 113: 1909–1918.
- Derelle R, López-García P, Timpano H, Moreira D. 2016. A phylogenomic framework to study the diversity and evolution of stramenopiles (= heterokonts). Mol. Biol. Evol. 33: 2890-2898.
- Dohrmann M, Wörheide G. 2017. Dating early animal evolution using phylogenomic data. Sci. Rep. 7:3599.
- Drozdo AL. 2017. Principle of conservatism of cellular structures as the basis for construction of the multikingdom system of the organic world. In: Abdurakhmanov IY (ed). Phylogenetics. InTech Open, pp. 3-26.
- Dumack K. 2016. Novel Lineages in Cercozoa and Their Feeding Strategies. Thesis. Universität zu Köln, Köln.

- Fiore-Donno AM, Nikolaev SI, Nelson M, Pawlowski J, Cavalier-Smith T, Baldauf SL. 2010. Deep phylogeny and evolution of slime molds (Mycetozoa). *Protist* 161: 55-70.
- Gao F, Warren A, Zhang Q, Gong J, Miao M, Sun P, Xu D, Huang J, Yi Z, Song W. 2016. The all-data-based evolutionary hypothesis of ciliated protists with a revised classification of the phylum Ciliophora (Eukaryota, Alveolata). *Sci. Rep.* 6:24874.
- Geisen S, Tveit AT, Clark IM, Richter A, Svenning MM, Bonkowski M, Urich T. 2015. Metatranscriptomic census of active protists in soils. *ISME J.* 9: 2178-2190.
- Glücksman E, Snell EA, Cavalier-Smith T. 2013. Phylogeny and evolution of Planomonadida (Sulcozoa): eight new species and new genera *Fabomonas* and *Nutomonas*. *Eur. J. Protistol.* 49: 179-200.
- Grant J, Tekle YI, Anderson OR, Patterson DJ, Katz LA. 2009 Multigene evidence for the placement of a heterotrophic amoeboid lineage *Leukarachnion* sp. among photosynthetic stramenopiles. *Protist* 160: 376-385.
- Hehenberger E, Tikhonenkov DV, Kolisko M, del Campo J, Esaulov AS, Mylnikov AP, Keeling PJ. 2017. Novel predators reshape holozoan phylogeny and reveal the presence of a two-component signaling system in the ancestor of animals. *Curr. Biol.* 27: 2043-2050.
- Hennig W. 1966. Phylogenetic systematics. *Annu. Rev. Entomol.* 10: 97-116.
- James TY, Pelin A, Bonen L, Ahrendt S, Sain D, Corradi N, Stajich JE. 2013. Shared signatures of parasitism and phylogenomics unite Cryptomycota and Microsporidia. *Curr. Biol.* 23: 1548–1553.
- Jones MDM, Forn I, Gadelha C, Egan MJ, Bass D, Massana R, Richards TA. 2011. Discovery of novel intermediate forms redefines the fungal tree of life. *Nature* 474: 200-203.
- Kamikawa R, Kolisko M, Nishimura Y, Yabuki A, Brown MW, Ishikawa SA, Ishida KI, Roger AJ, Hashimoto T, Inagaki Y. 2014. Gene content evolution in Discobid mitochondria deduced from the phylogenetic position and complete mitochondrial genome of *Tsukubamonas globosa*. *Genome Biol. Evol.* 6: 306-315.
- Kang S, Tice AK, Spiegel FW, Silberman JD, Pánek T, Čepička I, Kostka M, Kosakyan A, Alcântara D, Roger AJ, Shadwick LL. 2017. Between a pod and a hard test: the deep evolution of amoebae. *Mol. Biol. Evol.* 34: 2258-2270.
- Karpov SA, Mamkaeva MA, Aleoshin VV, Nassonova E, Lilje O, Gleason FH. 2014. Morphology, phylogeny, and ecology of the aphelids (Aphelidea, Opisthokonta) and proposal for the new superphylum Opisthosporidia. *Front. Microbiol.* 5:112
- Karpov SA, Torruella G, Moreira D, Mamkaeva MA, López-García P. 2017. Molecular phylogeny of *Paraphelidiumletcheri* sp. nov. (Aphelida, Opisthosporidia). *J. Euk. Microbiol.* 5: 573–578.
- Katz LA, Grant JR. 2014. Taxon-rich phylogenomic analyses resolve the eukaryotic tree of life and reveal the power of subsampling by sites. *Syst. Biol.* 64: 406-415.
- Kolisko M. 2011. Molecular Phylogeny of Amitochondriate Excavates. Thesis. Dalhousie University, Halifax.
- Krabberød AK, Orr RJ, Bråte J, Kristensen T, Bjørklund KR, Shalchian-Tabrizi K. 2017. Single cell transcriptomics, mega-phylogeny, and the genetic basis of morphological innovations in Rhizaria. *Mol. Biol. Evol.* 34: 1557-1573.
- Lahr DJ, Grant JR, Katz LA. 2013. Multigene phylogenetic reconstruction of the Tubulinea (Amoebozoa) corroborates four of the six major lineages, while additionally revealing that shell composition does not predict phylogeny in the Arcellinida. *Protist* 164: 323-339.
- Leliaert F, Tronholm A, Lemieux C, Turmel M, DePriest MS, Bhattacharya D, Karol KG, Fredericq S, Zechman FW, Lopez-Bautista JM. 2016. Chloroplast phylogenomic analyses reveal the deepest-branching lineage of the Chlorophyta, Palmophyllophyceae class. nov. *Sci. Rep.* 6:25367.

- Magallon S, Gómez-Acevedo S, Sánchez-Reyes LL, Hernández-Hernández T. 2015. A metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. *New Phytol.* 207: 437-453.
- Moreira D, López-García P. 2014. The rise and fall of Picobiliphytes: how assumed autotrophs turned out to be heterotrophs. *Bioessays* 36: 468-474.
- Nosenko T, Schreiber F, Adamska M, Adamski M, Eitel M, Hammel J, Maldonado M, Müller WE, Nickel M, Schierwater B, Vacelet J. 2013. Deep metazoan phylogeny: when different genes tell different stories. *Mol. Phyl. Evol.* 67: 223-233.
- Paps J, Medina-Chacón LA, Marshall W, Suga H, Ruiz-Trillo I. 2013. Molecular phylogeny of unikonts: new insights into the position of apusomonads and ancyromonads and the internal relationships of opisthokonts. *Protist* 164: 2–12.
- Pawlowski J. 2013. The new micro-kingdoms of eukaryotes. *BMC Biol.* 11:40.
- Quast C, Pruesse E, Yilmaz P, Gerken J, Schweer T, Yarza P, Peplies J, Glöckner FO. 2013. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. *Nucl. Ac. Res.* 41: 590–596.
- Radek R, Strasser JF, Krüger J, Meuser K, Scheffrahn RH, Brune A. 2017. Phylogeny and Ultrastructure of *Oxymonas jouteli*, a Rostellum-free Species, and *Opisthomitus longiflagellatus* sp. nov., Oxymonadid Flagellates from the Gut of *Neotermes jouteli*. *Protist* 165: 384-399.
- Reñé A, Alacid E, Ferrera I, Garcés E. 2017. Evolutionary trends of Perkinsozoa (Alveolata) characters based on observations of two new genera of parasitoids of dinoflagellates, *Dinovorax* gen. nov. and *Snorkelia* gen. nov. *Front. Microbiol.* 8:1594.
- Riisberg I, Orr RJ, Kluge R, Shalchian-Tabrizi K, Bowers HA, Patil V, Edvardsen B, Jakobsen KS. 2009. Seven gene phylogeny of heterokonts. *Protist* 160: 191-204.
- Ruggiero MA, Gordon DP, Orrell TM, Bailly N, Bourgoin T, Brusca RC, Cavalier-Smith T, Guiry MD, Kirk PM. 2015. A higher level classification of all living organisms. *PLoS One* 10: e0119248.
- Ruhfel BR, Gitzendanner MA, Soltis PS, Soltis DE, Burleigh JG. 2014. From algae to angiosperms—inferring the phylogeny of green plants (Viridiplantae) from 360 plastid genomes. *BMC Evol. Biol.* 14:23.
- Schiffer P, Robertson H, Telford MJ. 2017. Molecular data from Orthonectid worms show they are highly degenerate members of phylum Annelida not phylum Mesozoa. *bioRxiv* 2017:235549.
- Sharpe SC, Eme L, Brown MW, Roger AJ. 2015. Timing the origins of multicellular eukaryotes through phylogenomics and relaxed molecular clock analyses. *Adv. Mar. Genomics* 2: 3-29.
- Sheridan PP, Freeman KH, Brenchley JE. 2003. Estimated minimal divergence times of the major bacterial and archaeal phyla. *Geomicrobiol. J.* 20: 1-14.
- Shiratori T, Nakayama T, Ishida KI. 2015. A new deep-branching stramenopile, *Platysulcus tardus* gen. nov., sp. nov. *Protist* 166: 337-348.
- Shiratori T, Thakur R, Ishida KI. 2017. *Pseudophyllomitus vesiculosus* (Larsen and Patterson 1990) Lee, 2002, a poorly studied phagotrophic biflagellate is the first characterized member of stramenopile environmental clade MAST-6. *Protist* 168: 439-451.
- Simion P, Philippe H, Baurain D, Jager M, Richter DJ, Di Franco A, Roure B, Satoh N, Quéinnec É, Ereskovsky A, Lapébie P. 2017. A large and consistent phylogenomic dataset supports sponges as the sister group to all other animals. *Curr. Biol.* 27: 958-967.
- Spatafora JW, Chang Y, Benny GL, Lazarus K, Smith ME, Berbee ML, Bonito G, Corradi N, Grigoriev I, Gryganskyi A, James TY. 2016. A phylum-level phylogenetic classification of zygomycete fungi based on genome-scale data. *Mycologia* 108: 1028-1046.



- 525 Tedersoo L, Bahram M, Puusepp R, Nilsson RH, James TY. 2017. Novel soil-inhabiting
- 526 clades fill gaps in the fungal tree of life. *Microbiome* 5: 42.
- 527 Tedersoo L, Kõljalg U, Bahram M, Döring M, Schigel D, May T, Sanchez-Ramirez S,
- 528 Ryberg M, Abarenkov K. 2018. Classification and communication and of higher-level
- 529 fungal taxa and a tool for evolutionary ecological analyses. *New Phytol.* Pending revision.
- 530 Tekle YI, Anderson OR, Katz LA, Maurer-Alcalá XX, Romero MA, Molestina R. 2016.
- 531 Phylogenomics of ‘Discosea’: a new molecular phylogenetic perspective on Amoebozoa
- 532 with flat body forms. *Mol. Phyl. Evol.* 99: 144-154.
- 533 Tekle YI, Wood FC. 2017. Longamoebia is not monophyletic: Phylogenomic and
- 534 cytoskeleton analyses provide novel and well-resolved relationships of amoebozoan
- 535 subclades. *Mol. Phyl. Evol.* 114: 249-260.
- 536 Telford MJ, Budd GE, Philippe H. 2015. Phylogenomic insights into animal evolution. *Curr.*
- 537 *Biol.* 25: 876-887.
- 538 Torruella G, de Mendoza A, Grau-Bove X, Anto M, Chaplin MA, del Campo J, Eme L,
- 539 Pérez-Cordón G, Whipps CM, Nichols KM, Paley R. 2015. Phylogenomics reveals
- 540 convergent evolution of lifestyles in close relatives of animals and fungi. *Curr. Biol.* 25:
- 541 2404-2410.
- 542 Torruella G, Grau-Bove X, Moreira D, Karpov SA, Burns J, Sebe-Pedros A, Volcker E,
- 543 Lopez-Garcia P. 2017. The transcriptome of *Paraphelidium tribonemae* illuminates the
- 544 ancestry of Fungi and Opisthosporidia. *bioRxiv* 2017:233882.
- 545 Wegener Parfrey L, Grant J, Tekle YI, Lasek-Nesselquist E, Morrison HG, Sogin ML,
- 546 Patterson DJ, Katz LA. 2010. Broadly sampled multigene analyses yield a well-resolved
- 547 eukaryotic tree of life. *Syst. Biol.* 59: 518–533.
- 548 Wegener Parfrey L, Lahr DJG, Knoll AH, Katz LA. 2011. Estimating the timing of early
- 549 eukaryotic diversification with multigene molecular clocks. *Proc. Natl. Acad. Sci. USA*
- 550 108: 13624–13629.
- 551 Whelan NV, Kocot KM, Moroz LL, Halanych KM. 2015. Error, signal, and the placement of
- 552 Ctenophora sister to all other animals. *Proc. Natl. Acad. Sci. USA* 112: 5773-5778.
- 553 Woese CR, Kandler O, Wheelis ML. 1990. Towards a natural system of organisms: proposal
- 554 for the domains Archaea, Bacteria, and Eucarya. *Proc. Natl. Acad. Sci. USA* 87: 4576-4579.
- 555 Yabuki A, Chao EE, Ishida KI, Cavalier-Smith T. 2012. *Microheliella maris* (Microhelida
- 556 ord. n.), an ultrastructurally highly distinctive new axopodial protist species and genus, and
- 557 the unity of phylum Heliozoa. *Protist* 163: 356-388.
- 558 Yabuki A, Ishida KI, Cavalier-Smith T. 2013. *Rigifila ramosa* n. gen., n. sp., a filose
- 559 apusozoan with a distinctive pellicle, is related to *Micronuclearia*. *Protist* 164: 75-88.
- 560 Yabuki A, Kamikawa R, Ishikawa SA, Kolisko M, Kim E, Tanabe AS, Kume K, Ishida KI,
- 561 Inagaki Y. 2014. *Palpitomonas bilix* represents a basal cryptist lineage: insight into the
- 562 character evolution in Cryptista. *Sci. Rep.* 4:4641.
- 563 Yang EC, Boo GH, Kim HJ, Cho SM, Boo SM, Andersen RA, Yoon HS. 2012. Supermatrix
- 564 data highlight the phylogenetic relationships of photosynthetic stramenopiles. *Protist* 163:
- 565 217-231.
- 566 Yoon HS, Grant J, Tekle YI, Wu M, Chaon BC, Cole JC, Logsdon JM, Patterson DJ,
- 567 Bhattacharya D, Katz LA. 2008. Broadly sampled multigene trees of eukaryotes. *BMC*
- 568 *Evol. Biol.* 8: 14.
- 569 Yoon HS, Müller KM, Sheath RG, Ott FD, Bhattacharya D. 2006. Defining the major
- 570 lineages of red algae (Rhodophyta). *J. Phycol.* 42: 482-492.
- 571 Yoon HS, Price DC, Stepanauskas R, Rajah VD, Sieracki ME, Wilson WH, Yand EC, Duffy
- 572 S, Bhattacharya D. 2011. Single-cell genomics reveals organismal interactions in
- 573 uncultivated marine protists. *Science* 332: 714-717.

- Yubuki N, Pánek T, Yabuki A, Čepička I, Takishita K, Inagaki Y, Leander BS. 2015. Morphological identities of two different marine stramenopile environmental sequence clades: *Bicosoeca kenaiensis* (Hilliard, 1971) and *Cantina marsupialis* (Larsen and Patterson, 1990) *gen. nov., comb. nov.* J. Euk. Microbiol. 62: 532-542.
- Yubuki N, Zadrobílková E, Čepička I. 2017. Ultrastructure and molecular phylogeny of *Iotanema spirale gen. nov. et sp. nov.*, a new lineage of endobiotic Fornicata with strikingly simplified ultrastructure. J. Euk. Microbiol. 64: 422-433.
- Zhang ZQ. 2011. Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness. Zootaxa 3148: 1-237.
- Zhao S, Burki F, Bråte J, Keeling PJ, Klaveness D, Shalchian-Tabrizi K. 2012. *Collodictyon*—an ancient lineage in the tree of eukaryotes. Mol. Biol. Evol. 29: 1557-1568.

## Figure legends

**Figure 1.** Conceptual scheme indicating major problems in current classification systems. (a) hierarchical classification indicating an example focal group (in red); (b) para- and polyphyletic taxa (clades in red); (c) lack of higher-level resolution and information about taxonomic deepness (clades in dashed line); (d) overlapping names across multiple ranks (names in red); (e) names linguistically unrelated to any ingredient taxon (Greek letters); (f) ephemeral names used for multiple, often poorly supported clades (letters with prim); and (g) differential resolution among taxa in different clades. Letters depict taxon names.

**Figure 2.** Unrooted taxon tree indicating the proposed kingdom-level classification of the Eukarya domain. Different colours indicate subdomains.

**Figure 3.** Comparison of higher level classification of Ruggiero et al. (2015; right pane) and the proposed classification (left pane). Red and blue fonts indicate paraphyletic and polyphyletic taxa, respectively; different branch colours depict subdomains; dashed lines indicate corresponding taxon names that differ between classifications.

**Appendix 1.** Subdomain to subphylum level classification of eukaryotes with ingredient classes indicated.

**Associated material.** Tedersoo L. 2017. Proposed practical classification of the domain Eukarya based on the NCBI system and monophyly and comparable divergence time criteria. (<http://dx.doi.org/10.15156/BIO/587483>)

**Appendix 1.** Subdomain to subphylum level classification of eukaryotes with ingredient classes indicated. Other groups not described at particular taxonomic level are included as ‘unspecified’ taxa. The full NCBI-based classification table down to genus level is given in the associated material (<http://dx.doi.org/10.15156/BIO/587483>)

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subdom. Archaeplastida	
kgd. Glaucocystophantae	
phyl. Glaucocystophyta	cl. Glaucocystophyceae
kgd. Rhodophantae	
phyl. Cyanidiophyta	cl. Cyanidiophyceae
phyl. Rhodophyta	cl. Bangiophyceae
	cl. Compsopogonophyceae
	cl. Florideophyceae
	cl. Rhodellophyceae
	cl. Stylonematophyceae
kgd. Viridiplantae	
phyl. Chlorophyta	
subphyl. Chlorophytina	cl. Chlorodendrophyceae
	cl. Chlorophyceae
	cl. Mamiellophyceae
	cl. Nephroselmidophyceae
	cl. Palmophyllaceae
	cl. Pedinophyceae
	cl. Pyramimonadaceae
	cl. Trebouxiophyceae
	cl. Ulvophyceae
	cl. unspecified
phyl. Streptophyta	
subphyl. Anthocerotophytina	cl. Leiosporocerotopsida
	cl. Anthocerotopsida
subphyl. Bryophytina	cl. Andreaebryopsida
	cl. Andreaeopsida
	cl. Bryopsida
	cl. Oedipodiopsida
	cl. Polytrichopsida
	cl. Sphagnopsida
	cl. Takakiopsida
	cl. Tetrarhiopsida
subphyl. Charophytina	cl. Charophyceae
subphyl. Chlorokybophytina	cl. Chlorokybophyceae
subphyl. Coleochaetophytina	cl. Coleochaetophyceae
subphyl. Klebsormidiophytina	cl. Klebsormidiophyceae
subphyl. Marchantiophytina	cl. Haplomitriopsida
	cl. Jungermanniopsida
	cl. Marchantiopsida
subphyl. Mesostigmatophytina	cl. Mesostigmatophyceae

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subphyl. Zygnemophytina	cl. Zygnemophyceae
subphyl. Tracheophytina	cl. Angiospermae
	cl. Cupressopsida
	cl. Cycadopsida
	cl. Ginkgopsida
	cl. Gnetopsida
	cl. Lycopodiopsida
	cl. Pinopsida
	cl. Polypodiopsida
subdom. Excavata	
kgd. Euglenozoa	
phyl. Euglenida	cl. unspecified
phyl. Glycomonada	cl. Diplonemea
	cl. Kinetoplastea
phyl. Postgaardia	cl. Postgaardea
phyl. unspecified	cl. Entosiphonidea
kgd. Fornicata	cl. unspecified
kgd. Heterolobosa	
phyl. Heterolobosida	cl. Heterolobosea
	cl. unspecified
kgd. Jakobida	cl. unspecified
kgd. Malawimonada	cl. Malawimonadea
kgd. Oxymonada	cl. unspecified
kgd. Parabasalia	cl. unspecified
kgd. Tsukubamonada	cl. Tsukubamonadea
subdom. Harosa	
kgd. Alveolata	
phyl. Acavomonada	cl. Acavomonadea
phyl. Apicomplexa	cl. Aconoidasida
	cl. Coccidia
	cl. Gregarinasina
	cl. unspecified
phyl. Chromerida	cl. Chromerea
phyl. Ciliophora	
subphyl. Intramacronucleata	cl. Armophorea
	cl. Colpodea
	cl. Litostomatea
	cl. Nassophorea
	cl. Oligohymenophorea
	cl. Phyllopharyngea
	cl. Plagiopylea
	cl. Prostomatea
	cl. Spirotrichea
subphyl. Postciliodesmatophora	cl. Heterotricha
	cl. Karyorelictea
subphyl. unspecified	cl. unspecified
phyl. Colpodellida	cl. Colpodellidea
phyl. Colponemidia	cl. Colponemea

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phyl. Dinophyta	cl. Dinophyceae
phyl. Perkinsozoa	cl. Perkinsea
phyl. unspecified	cl. Ellobiopsea
phyl. unspecified	cl. unspecified
kgd. Rhizaria	
phyl. Endomyxa	cl. Haplosporidea
	cl. unspecified
phyl. Filosa	cl. Chloerarachnea
	cl. Granofilosea
	cl. Imbricatea
	cl. Sarcomonadea
	cl. Thecofilosea
	cl. Tremulidea
	cl. unspecified
phyl. Retaria	cl. Acantharea
	cl. Foraminifera
	cl. Polycystinea
	cl. Taxopodea
phyl. unspecified	cl. Metromonadea
phyl. unspecified	cl. unspecified
kgd. Stramenopila	
phyl. Bicosoecida	cl. Bikosea
phyl. Developayellida	cl. Developea
phyl. Hyphochytria	cl. Hyphochytriomycetes
phyl. Labyrinthulida	cl. Labyrinthulomycetes
phyl. Ochrophyta	cl. Aurearenophyceae
	cl. Bacillariophyceae
	cl. Bolidophyceae
	cl. Chrysophyceae
	cl. Dictyochophyceae
	cl. Eustigmatophyceae
	cl. Pelagophyceae
	cl. Phaeophyceae
	cl. Phaeothamniophyceae
	cl. Pinguiphyceae
	cl. Raphidophyceae
	cl. Schizocladiophyceae
	cl. Synchromophyceae
	cl. Xanthophyceae
phyl. Oomycota	cl. Oomycetes
phyl. Opalinata	cl. unspecified
phyl. unspecified	cl. Nanomonadea
phyl. unspecified	cl. Placididea
phyl. unspecified	cl. unspecified
subdom. Opisthokonta	
kgd. Apusozoa	
phyl. Apusomonada	cl. Apusomonadea
kgd. Breviatae	

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phyl. Breviatida	cl. Breviatea
kgd. Choanoflagellozoa	
phyl. Choanoflagellata	cl. Choanoflagellea
kgd. Corallochytria	
phyl. Corallochytrida	cl. Corallochytreia
kgd. Filasteriae	
phyl. Filasterida	cl. Filasterea
kgd. Fungi	
subkgd. Aphelidiomyceta	
phyl. Aphelidiomycota	cl. Aphelidiomycetes
subkgd. Blastocladiomyceta	
phyl. Blastocladiomycota	cl. Blastocladiomycetes
subkgd. Chytridiomyceta	
phyl. Chytridiomycota	cl. Chytridiomycetes
	cl. Cladochytridiomycetes
	cl. Lobulomycetes
	cl. Mesochytridiomycetes
	cl. Polychytridiomycetes
	cl. Rhizophlyctidomycetes
	cl. Rhizophyidiomycetes
	cl. Spizellomycetes
	cl. Synchytridiomycetes
	cl. unspecified
phyl. Monoblepharomycota	cl. Hyaloraphidiomycetes
	cl. Monoblepharidomycetes
	cl. Sanchytridiomycetes
subkgd. Chytridiomyceta	
phyl. Neocallimastigomycota	cl. Neocallimastigomycetes
subkgd. Dikarya	
phyl. Ascomycota	
subphyl. Pezizomycotina	cl. Arthoniomycetes
	cl. Collemopsidiomycetes
	cl. Coniocybomycetes
	cl. Dothideomycetes
	cl. Eurotiomycetes
	cl. Geoglossomycetes
	cl. Laboulbeniomycetes
	cl. Lecanoromycetes
	cl. Leotiomycetes
	cl. Lichinomycetes
	cl. Orbiliomycetes
	cl. Pezizomycetes
	cl. Sordariomycetes
	cl. Xylonomycetes
	cl. unspecified
subphyl. Saccharomycotina	cl. Saccharomycetes
subphyl. Taphrinomycotina	cl. Archaeorhizomycetes
	cl. Neoelectromycetes

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	cl. Pneumocystidomycetes
	cl. Schizosaccharomycetes
	cl. Taphrinomycetes
phyl. Basidiomycota	
subphyl. Agaricomycotina	cl. Agaricomycetes
	cl. Dacrymycetes
	cl. Tremellomycetes
	cl. unspecified
subphyl. Pucciniomycotina	cl. Agaricostilbomycetes
	cl. Atractiellomycetes
	cl. Classiculomycetes
	cl. Cryptomycocolacomycetes
	cl. Cystobasidiomycetes
	cl. Microbotryomycetes
	cl. Mixiomycetes
	cl. Pucciniomycetes
	cl. Spiculogloeomycetes
	cl. Tritirachiomycetes
subphyl. Ustilaginomycotina	cl. Exobasidiomycetes
	cl. Malasseziomycetes
	cl. Moniliellomycetes
	cl. Ustilaginomycetes
subphyl. Wallemiomycotina	cl. Geminibasidiomycetes
	cl. Wallemiomycetes
phyl. Entorrhizomycota	cl. Entorrhizomycetes
subkgd. Mucoromyceta	
phyl. Calcarisporiellomycota	cl. Calcarisporiellomycetes
phyl. Glomeromycota	cl. Archaeosporomycetes
	cl. Glomeromycetes
	cl. Paraglomeromycetes
phyl. Mortierellomycota	cl. Mortierellomycetes
phyl. Mucoromycota	cl. Endogonomycetes
	cl. Mucoromycetes
	cl. Umbelopsidomycetes
subkgd. Olpidiomyceta	
phyl. Olpidiomycota	cl. Olpidiomycetes
subkgd. Rozellida	
phyl. Rozellomycota	cl. Microsporidea
	cl. Rozellomycetes
	cl. unspecified
subkgd. Zoopagomyceta	
phyl. Entomophthoromycota	cl. Basidiobolomycetes
	cl. Entomophthoromycetes
	cl. Neozygitomycetes
phyl. Kickxellomycota	cl. Asellariomycetes
	cl. Barbatosporomycetes
	cl. Dimargaritomycetes
	cl. Harpellomycetes

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	cl. Kickxellomycetes
phyl. Zoopagomycota	cl. Zoopagomycetes
kgd. Ichthyosporia	
phyl. Ichthyosporida	cl. Eccrinidea
	cl. Ichthyosporia
kgd. Mantazoa	
phyl. Mantamonada	cl. Mantamonadea
kgd. Metazoa	
subkgd. Bilateria	
phyl. Acanthocephala	cl. Archiacanthocephala
	cl. Eoacanthocephala
	cl. Palaeacanthocephala
	cl. Polyacanthocephala
phyl. Annelida	
subphyl. Clitellata	cl. Branchiobdellae
	cl. Hirudinida
	cl. Oligochaeta
subphyl. Polychaeta	cl. Echiura
	cl. Palpata
	cl. Scolecida
	cl. Sipuncula
subphyl. unspecified	cl. unspecified
phyl. Arthropoda	
subphyl. Chelicerata	cl. Arachnida
	cl. Merostomata
	cl. Pycnogonida
subphyl. Crustacea	cl. Branchiopoda
	cl. Cephalocarida
	cl. Malacostraca
	cl. Maxillopoda
	cl. Ostracoda
	cl. Remipedia
subphyl. Hexapoda	cl. Collembola
	cl. Diplura
	cl. Insecta
	cl. Protura
subphyl. Myriapoda	cl. Chilopoda
	cl. Diplopoda
	cl. unspecified
phyl. Brachiopoda	
subphyl. Craniiformea	cl. Craniatea
subphyl. Linguliformea	cl. Lingulata
subphyl. Phoroniformea	cl. unspecified
subphyl. Rhynchonelliformea	cl. Rhynchonellata
phyl. Bryozoa	cl. Gymnolaemata
	cl. Phylactolaemata
	cl. Stenolaemata

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phyl. Cephalochordata	cl. Cephalochordatea
phyl. Chaetognatha	cl. Sagittoidea
phyl. Craniata	
subphyl. Vertebrata	cl. Actinopteri
	cl. Amphibia
	cl. Aves
	cl. Ceratodontimorpha
	cl. Chondrichthyes
	cl. Cladistia
	cl. Crocodylea
	cl. Cyclostomata
	cl. Mammalia
	cl. Sphenodonteia
	cl. Squamata
	cl. Testudinea
	cl. unspecified
phyl. Cycliophora	cl. unspecified
phyl. Echinodermata	cl. Asteroidea
	cl. Crinoidea
	cl. Echinoidea
	cl. Holothuroidea
	cl. Ophiuroidea
phyl. Entoprocta	cl. unspecified
phyl. Gastrotricha	cl. unspecified
phyl. Gnathostomulida	cl. unspecified
phyl. Hemichordata	cl. Enteropneusta
	cl. Pterobranchia
phyl. Kinorhyncha	cl. unspecified
phyl. Loricifera	cl. unspecified
phyl. Micrognathozoa	cl. Micrognatheia
phyl. Mollusca	cl. Bivalvia
	cl. Caudofoveata
	cl. Cephalopoda
	cl. Gastropoda
	cl. Monoplacophora
	cl. Polyplacophora
	cl. Scaphopoda
	cl. Solenogastres
phyl. Myzostomida	cl. unspecified
phyl. Nematoda	cl. Chromadorea
	cl. Enoplea
	cl. unspecified
phyl. Nematomorpha	cl. Gordioida
	cl. Nectonematoida
phyl. Nemertea	cl. Anopla
	cl. Enopla
	cl. Palaeonemertea
phyl. Onychophora	cl. unspecified

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phyl. Orthonectida	cl. unspecified
phyl. Platyhelminthes	cl. Catenulida
	cl. Cestoda
	cl. Monogenea
	cl. Rhabditophora
	cl. Trematoda
	cl. Turbellaria
	cl. unspecified
phyl. Priapulida	cl. unspecified
phyl. Rhombozoa	cl. unspecified
phyl. Rotifera	cl. Bdelloidea
	cl. Monogononta
	cl. Seisonidea
phyl. Tardigrada	cl. Eutardigrada
	cl. Heterotardigrada
phyl. Tunicata	cl. Appendicularia
	cl. Ascidiacea
	cl. Thaliacea
phyl. Xenacoelomorpha	
subphyl. Acoelomorpha	cl. Acoela
	cl. Nemertodermatida
subphyl. Xenoturbellida	cl. Xenoturbellidea
subkgd. Cnidozoa	
phyl. Cnidaria	cl. Anthozoa
	cl. Cubozoa
	cl. Hydrozoa
	cl. Scyphozoa
	cl. Staurozoa
	cl. unspecified
subkgd. Ctenozoa	
phyl. Ctenophora	cl. Nuda
	cl. Tentaculata
subkgd. Placomorpha	
phyl. Placozoa	cl. unspecified
subkgd. Porizoa	
phyl. Porifera	cl. Calcarea
	cl. Demospongiae
	cl. Hexactinellida
	cl. Homoscleromorpha
kgd. Nucleariae	
phyl. Fonticulida	cl. Fonticulidea
phyl. Nuclearida	cl. Nuclearidea
kgd. Planozoa	
phyl. Planomonada	cl. Planomonadea
kgd. Rigifilae	
phyl. Rigifilidia	cl. Rigifileia
subdom. Unikontamoebae	
kgd. Amoebozoa	

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phyl. Discosida	cl. Centramoebidea
	cl. Flabellinea
	cl. unspecified
phyl. Evosida	
subphyl. Mycetozoa	cl. Eumycetozoa
	cl. unspecified
	cl. Variosea
subphyl. unspecified	cl. Archamoebidea
	cl. Cutosea
	cl. unspecified
phyl. Tubulinida	cl. Tubulinea
	cl. unspecified
phyl. unspecified	cl. unspecified
subdom. unspecified	
kgd. Centroheliozoa	
phyl. Centrohelida	cl. Centrohelea
subdom. unspecified	
kgd. Cryptista	
phyl. Cryptophyta	cl. Cryptomonadea
	cl. Pyrenomonadea
	cl. unspecified
phyl. Katablepharidophyta	cl. Katablepharidea
	cl. unspecified
phyl. Palpitophyta	cl. Palpitomonadea
subdom. unspecified	
kgd. Haptista	
phyl. Haptophyta	cl. Coccolithophyceae
	cl. Pavlovophyceae
	cl. unspecified
subdom. unspecified	
kgd. Picozoa	
phyl. Picomonada	cl. Picomonadea
subdom. unspecified	
kgd. Telonemae	
phyl. Telonemia	cl. Telonemea
subdom. unspecified	
kgd. unspecified	
phyl. Collodictyonida	cl. Collodictyonea
subdom. unspecified	
kgd. unspecified	
phyl. Microheliellida	cl. unspecified

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