

How many kingdoms of life? Eukaryotic phylogeny and philosophy of systematics

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Abstract

According to contemporary understanding of the universal tree of life, the traditionally recognized kingdoms of eukaryotic organisms—Protista, Fungi, Animalia and Plantae—are irregularly interspersed in a vast phylogenetic tree. There are numerous groups that in any Linnaean classification advised by phylogenetic relationships (i.e. a Hennigian system) would form sister groups to those kingdoms, therefore requiring us to admit them the same rank. In practice, this would lead to the creation of ca. 25-30 new kingdoms that would now be listed among animals and plants as “major types of life”. This poses problems of an aesthetic and educational nature. There are, broadly speaking, two ways to deal with that issue: a) ignore the aesthetic and educational arguments and propose classification systems that are fully consistent with the Hennigian principles of phylogenetic classification, i.e. are only composed of monophyletic taxa; b) ignore Hennigian principles and bunch small, relatively uncharacteristic groups into paraphyletic taxa, creating systems that are more convenient. In the paper, I present the debate and analyze the pros and cons of both options, briefly commenting on the deeper, third resolution, which would be to abandon classification systems entirely.



Recent advances in eukaryotic classification and phylogeny are commented in the light of the philosophical question of the purpose and design principles of biological classification systems.

Keywords

taxonomy, systematics, philosophy of biology, eukaryotes, Protista.

Ever since Linnaeus formalized biological classification in his *Systema Naturae* (Linnaeus, 1788), there is the unresolved problem of how exactly should new taxa be created, and, more specifically, into how many subtaxa should higher-rank taxa be split. For instance, is there a convincing reason why there should be, say, 43 orders of ray-finned fish (class Actinopterygii), but only 3 orders of leeches (class Hirudinea)? Are there any objective arguments for one arrangement over another, or is it purely a matter of taste? There is a considerable body of work in philosophy of biology that discusses such issues (see Hull, 1965; 1970; Schuh and Brower, 2011 and especially Mayr and Bock, 2002).

While ongoing changes at lower ranks (i.e. species, genus, family and order) are of high importance to specialists, the public is much more likely to encounter changes at the higher ranks (from class up). Of special importance is the traditionally highest category of kingdom (now partially superseded by domain—see below) which delineates major “types of life” and is of enormous educational and heuristic value (Copeland, 1938; Cavalier-Smith, 1981). For centuries there has been slow incremental change in the classification of life at the level of kingdom. In the recent two decades, however, the rapidly increasing knowledge of the general topology of the universal tree of life, lead to the realization that traditionally distinguished kingdoms

are interspersed in a thick “bush” of major branches (see e.g. Baldauf et al., 2000). In this paper, I wish to analyze this situation, with special attention to the structure of the eukaryotic tree of life.

1. The rank of kingdom

In biological systematics, starting from Linnaeus, the rank of kingdom has long been the highest of all taxonomic ranks. In Linnaeus’ *Systema Naturae*, there were 3 of them—the animal, plant and mineral kingdom (Linnaeus, 1788), and the division of all living things into two kingdoms was retained in biology for a long time. Only recently the even higher rank of domain was introduced by Carl Woese (Woese, Kandler and Wheelis, 1990), who intended to accentuate the special character of Archaea, famously identified by him and George Fox (Woese and Fox, 1977) to be fundamentally different from both bacteria and eukaryotes; although it has been recently suggested that eukaryotes actually evolved from archaea (Williams, Foster et al., 2013). Even in Woese’s 1990 revision, however, three “primary kingdoms” were named with the idea that the rank of kingdom remains the basic level at which major “types of life” are to be identified.

The number of the kingdoms of life discerned by biologists changes through time rather slowly. A contemporary student of both introductory and advanced biological texts is almost certain to encounter the following:

- either a single kingdom of bacteria, variously called Prokaryotae, Bacteria or Monera, or, in a more modern variation, two kingdoms: the so-called true bacteria (Eubacteria, sometimes Bacteria) and the archaeans (Archaea, sometimes Archaeobacteria);

- the single kingdom of protists (usually Protista or Protoctista), which encompasses all eukaryotes not belonging to the three multicellular kingdoms (see below); in some modern sources (Ruggiero et al., 2015) there is a separate kingdom Chromista encompassing a large monophyletic subgroup of protists, including brown algae which are large, multicellular and quite complex;
- the three multicellular eukaryotic kingdoms: plants (Plantae, sometimes Viridiplantae), animals (Animalia, sometimes Metazoa) and fungi (Fungi, sometimes Mycota).

Note that the list is quite conservative, but the number of kingdoms slowly increases. Plants and animals are the two original Linnaean kingdoms of life. Protists were argued to be a separate kingdom by Ernst Haeckel in (1866). Bacteria were given a separate kingdom in 1938 (Copeland, 1938) and, interestingly, the fungi have been proposed as a kingdom separate from plants only in 1969 (Whittaker, 1969). The distinct kingdom for Archaea, as mentioned, was proposed in 1977 and Thomas Cavalier-Smith first proposed elevating Chromista to the rank of kingdom in (1981).

Arguably, the most common variant found in introductory texts is the one with five kingdoms: Bacteria, Protoctista, Plantae, Animalia, Fungi, and this very division has been employed in the highly influential popular book by Lynn Margulis and Michael Chapman, *Kingdoms and Domains* (2009), which has become an authoritative source on biological megasystematics. In a recent proposal of a comprehensive classification of life, down to the level of order (Ruggiero et al., 2015), there are seven kingdoms: Archaea/Archaeobacteria, Bacteria/Eubacteria, Protozoa, Chromista, Fungi, Plantae and Animalia. This proposal is a consensus view of over 3000 taxonomists (!) and

is likely to become the standard point of reference for professional biologists for years to come, even though it has been criticized, especially with regard to specific taxonomic decisions (e.g. Tedersoo et al., 2018).

All in all, based on that quick review, it may seem that a general view of the diversity of life, and its representation in biological taxonomy, is now more or less understood, and major changes to the number of kingdom occur rarely. In reality, it is not that simple. In the past decades there has been considerable controversy surrounding the number and identity of the highest ranks in systematics, and the summary presented above might be termed the “conservative view” by some. In fact, there are sources claiming that 11-12 prokaryotic kingdoms (Petitjean et al., 2014) and 20-27 eukaryotic kingdoms (Pawlowski, 2013; Tedersoo, 2017) should be distinguished.

The purpose of the present paper is to identify the cause of that confusion and its possible resolutions, using mostly examples related to the eukaryotic tree of life.

2. Paraphyletic taxa and classification systems

Starting from Darwin himself, it has become increasingly clear that biological systematics must somehow portray evolutionary patterns. This was formalized in Willi Hennig’s *Phylogenetic Systematics* (1966) where the now-ubiquitous concepts of symplesiomorphy, synapomorphy and convergence, and the corresponding types of taxa—paraphyletic, monophyletic and polyphyletic—were formalized. Hennig forcefully argued that valid taxa should only be monophyletic groups, i.e. (true) clades, that is groups of species composed

of *all* descendants of a given species, possessing a common derivative character (synapomorphy). In the science of cladistics this has since become gospel.

While admirable, this prescription leads to “taxonomical inflation” as more and more taxa are identified. Before we illustrate it with an example relevant for the present study, let’s consider a case with more familiar taxa.

Vertebrates (subphylum Vertebrata of phylum Chordata) are divided into a number of classes. A popular list of vertebrate classes that you may hear even from a child (the specific reason for mentioning children in this context will be given below) is as follows: fish, amphibians, reptiles, birds and mammals. A better-educated person might cite the current scientific consensus that “fish” should be actually split into a number of separate classes: hagfish (Myxini), lampreys (Hyperoartia), cartilaginous fish (Chondrichthyes), ray-finned fish (Actinopterygii) and lobe-finned fish (Sarcopterygii), the reason being that “fish” is actually a paraphyletic grouping. This prescription to discuss five types of fish, which a layperson may identify as unnecessary and confusing (why five classes of fish and just one class of birds?), is a first sign of what happens when one attempts to divide a given taxon into monophyletic subtaxa.

If one were to portray the abovementioned vertebrate classes on a phylogenetic tree, something like Fig. 1 might be a reasonable representation of actual relationships.

This is, however, yet another simplification. A more careful analysis of *any* segment of the vertebrate phylogenetic tree will reveal that in between the well-known groups there are numerous groups, usually extinct, that would all require classes of their own, if the bordering taxa are given the rank of class—consult Fig. 2.

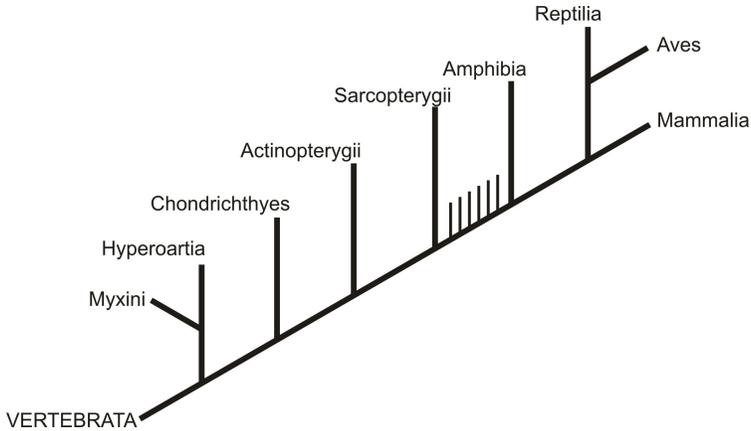


Figure 1: A highly simplified, and ultimately wrong, phylogenetic tree of extant vertebrates that attempts to include only the extant classes of subphylum Vertebrata. The ‘comb’ represents the area magnified in Fig. 2. It is clear that one cannot map a ranked classification of extant vertebrate classes onto a valid phylogenetic tree, especially because of the existence of extinct groups. Specifically, it is impossible to validly represent the actual relationships between (paraphyletic and now obsolete) Reptilia and Aves (which nest within reptiles).

It is clear that in order to divide the taxa listed in Fig. 2 into classes, one would have to give each genus presented in that figure its own high-level taxon (here: most likely class). The alternative is accepting paraphyletic taxa, for instance by grouping all stem tetrapods (Tiktaalik... Crassigyrinus) in a single class. It clearly goes against phylogenetic systematics, which is usually defended by biologists working with specific groups of organisms as the only method of creating taxonomies that is commensurate with the theory of evolution (see e.g. Williams and Kocielek, 2007).

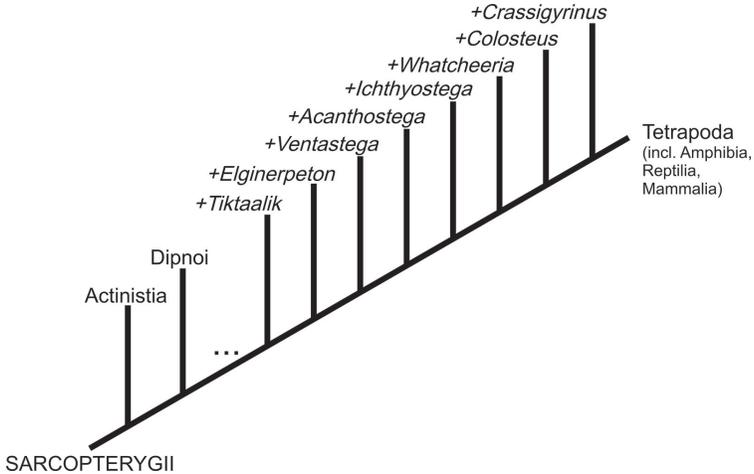


Figure 2: A slightly more realistic representation of a segment of the vertebrate phylogenetic tree, based on (Swartz, 2012) (with many taxa removed, most notably a large group of early sarcopterygians, denoted by an ellipsis). The improvement over Fig. 1 is mostly in that: a) the term Sarcopterygii is now correctly represented to also include all tetrapods, while in common usage, represented in Fig. 1, it refers only to coelacanth (which belong to Actinistia) and lungfish (which belong to Dipnoi); b) a number of extinct (marked by a cross) genera are presented.

There are ways to avoid that, one of which is the so-called sequencing convention proposed by Nelson (1972) and developed by Wiley (1981) and others, which partly automates the ranking process in various branches of the phylogenetic tree. But for now, let's assume that we want to hold on to strict Hennigian principles; what would be the consequences? Quite simple: the necessity to create a complete system of monophyletic taxa, in case of vertebrates, would lead to the erection of tens, if not hundreds, classes of vertebrates which defeats the simplifying purpose of classification. Another so-

lution would be to erect a large number of taxa of intermediate rank—this has been done, for example, by McKenna & Bell in their influential classification of mammals (1997):

- class Mammalia
 - subclass Prototheria
 - subclass Theriiformes
 - * infraclass +Allotheria
 - * infraclass +Eutriconodonta
 - * infraclass Holotheria
 - superlegion +Kuehneotheria
 - superlegion Trechnotheria
 - legion +Symmetrodonata
 - legion Cladotheria
 - * sublegion +Dryolestoidea
 - * sublegion Zatheria
 - infralegion +Peramura
 - infralegion Tribosphenida
 - ...

It is worth noting that the authors of that classification are paleontologists and their system is clearly intended as an answer to the problem of finding a proper taxonomic space for extinct groups. As a result, a staggering number of ranks were created. In “core Linnaean” taxonomy classes are composed of orders, i.e. class and order are neighboring ranks. In McKenna & Bell’s system one will find between them: subclasses, infraclasses, superlegions, legions, sublegions, infralegions, supercohorts, cohorts, magnorders, superorders, grandorders and mirorders. The term “taxonomic inflation” may thus

have two meanings: the creation of an impractically large number of equally-ranked taxa and the creation of an impractically large number of ranks.

Let's now discuss these two alternatives in more detail.

3. The solutions

Solution I: classifications with only monophyletic taxa

As mentioned above, strictly adhering to Hennig's prescription to accept only monophyletic taxa leads to "taxonomic inflation"—which seems to go against the aesthetic intuition of those biologists who dread the idea of splitting a given, let's say, phylum, into 50 classes (Cavalier-Smith, 1998).

Surprisingly, the solution that has been commonly employed is to do something perhaps even more drastic: to drop altogether the Linnaean "logic" of classification which is based on the simple idea that taxa of a given rank are divided into a number of subordinate taxa of the same lower rank—i.e. kingdoms are divided *only* into phyla; phyla are divided *only* into classes; classes *only* into orders etc. In other words, every order belonging to a given phylum must *also* belong to a certain class (or, in some cases, be included as *incertae sedis*, i.e. temporarily awaiting class attribution). In many modern classifications, however, there are *missing ranks*. As an example, consider the classification of vertebrates presented by the eminent paleontologist Michael Benton in his *Vertebrate Palaeontology* (Benton, 2014, p.433nn):

- superclass Tetrapoda:
 - family Elginerpetontidae
 - *Ventastega*
 - *Acanthostega*
 - *Ichthyostega*
 - *Tulerpeton*
 - family Colosteidae
 - family Crassigyrinidae
 - family Whatcheeriidae
 - family Baphetidae
 - class Neotetrapoda [where amphibians, reptiles, birds and mammals can be found—L.L.]

This is a remarkable solution. Note that it clearly opposes the centuries-old tradition, formalized by Linnaeus, to create consistent, complete hierarchies. Here we have a superclass that is composed of a single class, 5 families and 4 genera.

The missing ranks may look unsettling at first, but this convention is quickly gaining popularity, as it seems to offer a welcome rescue from the otherwise inescapable alternatives discussed in the previous paragraph. A recent classification of eukaryotes, published first in 2005 (Adl, Simpson, Farmer et al., 2005), then in a revised form in 2012 (Adl, Simpson, Lane et al., 2012), employs precisely that methodology. Note that this is an extremely well-respected classification, created by a consortium that includes world-class experts in eukaryotic diversity (such as Alastair Simpson or Sergei Karpov). The pair of papers is now amongst the most oft-quoted articles in the field, which means in practice that it is now a point of departure in any discussion of eukaryote classification.

In both papers the ranks are altogether dropped. Curiously, the taxa are presented in a semi-ordered hierarchical form where sub-

ordinate taxa are given more black dots. For instance, in the earlier paper (Adl, Simpson, Farmer et al., 2005) the group Opisthokonta is presented as follows (numerous taxa have been omitted):

OPISTHOKONTA

- Fungi
- Basidiomycota
- Urediniomycetes
- Ustilaginomycetes
- Ascomycota
- *Neoelecta*
- Taphrinomycotina
- ...
- Mesomycetozoa
- Aphelidea
- *Corallochytrium*
- *Capsaspora*
- Ichthyosporea
- *Ministeria*
- Nucleariida
- Choanomonada
- Metazoa
- Porifera
- Silicispongia
- Hexactinellida
- Demospongiae (...)

Let's note a few properties of this classification method. First of all, the four main groups of Opisthokonta (the ones with a single dot, i.e. fungi, mesomycetozoans, choanomonads and animals) are, to the best of current phylogenetic knowledge, monophyletic. This makes them perfect for the role of taxa in an openly Linnaean sys-

tem, that is at the same time in line with Hennig's rules of phylogenetic classification. The taxa with the same number of dots, however, represent radically different ranks in previously published classifications. The group Mesomycetozoa, as presented here, is composed of three genera (*Corallochytrium*, *Capsaspora* and *Ministeria*), two classes (Aphelidea and Ichthyosporea) and one order (Nucleariida). One might of course erect classes for all of them, which however, often leads to taxonomic inflation, as mentioned in the previous section.

Let's now specifically discuss the problem of kingdoms. If we hold on to the idea that equal "ranks" in the classification by Adl *et al.* should be given equal Linnaean ranks, we would be forced to create two additional kingdoms Choanomonada and Mesomycetozoa, that would be placed alongside Fungi and Metazoa/Animalia in the, most likely, superkingdom Opisthokonta (plus other kingdoms in other superkingdoms). That is, in fact, a fairly popular point of view, expressed for instance by Tedersoo (2017), who includes kingdoms Choanoflagellozoa (essentially synonymous with Adl *et al.*'s Choanomonada) and Ichthyosporia (Ichthyosporea is a synonym of Mesomycetozoa in many classification systems). It is worth noting that Tedersoo's system might be thought of as a good demonstration of what happens if one attempts to create a Linnaean system adhering to Hennigian constraints, based on modern understanding of eukaryotic phylogeny (the classification by Adl *et al.* is listed by Tedersoo as one of his main sources of information). The result? His system has 32 eukaryotic kingdoms. Let's cite his own opinion on that fact: "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 [...]" (Tedersoo, 2017, p.8).

Note that Adl *et al.* themselves stand *against* such practices, calling such artificially created higher-level taxa “superfluous” (Adl, Simpson, Lane *et al.*, 2012, p.430), therefore openly arguing for classification with missing taxa.

Solution II: classifications with paraphyletic taxa

The most vocal contemporary proponent of that solution is probably Thomas Cavalier-Smith, a controversial figure among microbiologists, who, however, is at the same time undoubtedly one of the most influential personas in the field of eukaryotic systematics. His contributions include the early recognition, and naming, of Excavata, Opisthokonta, Rhizaria and Chromista—all of them being now largely accepted, and the latter three: most likely monophyletic, mega-grouping of eukaryotes. In his proposed classification of life (with six kingdoms) (Cavalier-Smith, 1998) there is a long section on “philosophical preliminaries”, where the necessity for admitting paraphyletic taxa is forcefully defended. His two main arguments against the Hennigian requirement to limit taxa to clades are as follows:

1) It leads to instability. Each new discovery in biology—be it a paleontological or molecular novelty, or simply the discovery of a new species or a reinterpretation of anatomical data—may lead to the reassessment of a monophyletic taxon as paraphyletic, which would force the biologists to update classification systems. In practice it would mean hundreds, if not thousands, of revisions every year.

2) It is not practical. Let’s quote Cavalier-Smith himself: “Whether a taxon is paraphyletic or not is irrelevant to its validity as a taxon. It is also irrelevant to many of the uses to which classifications are put, such as arranging specimens in a museum, organising

the chapters in a biology textbook, or providing a convenient label, e.g. bacteria or fungi, for a group of similar organisms” (Cavalier-Smith, 1998, p.212).

As a result, Cavalier-Smith for about two decades has become an active opponent of Hennigian classification, especially in the field of microbiology. Every year or two he proposes a new system of classification, sometimes general, most often specific to a group of eukaryotes (Cavalier-Smith, 2002; 2013; 2016), usually being a carefully crafted compromise between contemporary phylogenetic knowledge and practicality. His 1998 system (Cavalier-Smith, 1998) has six kingdoms:

- empire/superkingdom Prokaryota*
 - kingdom Bacteria* [note: Archaeobacteria are to be found here, as an infrakingdom]
- empire/superkingdom Eukaryota
 - kingdom Protozoa*
 - * subkingdom Archezoa*
 - * subkingdom Neozoa*
 - kingdom Animalia
 - kingdom Fungi
 - kingdom Plantae
 - kingdom Chromista

All openly paraphyletic (“almost certainly paraphyletic” in his own words) taxa are marked with an asterisk. It is interesting to note that, while Cavalier-Smith openly opposes Hennigian phylogenetic systematics, his “illegal” taxonomies are highly popular. A quick look into any contemporary paper on eukaryotic systematics will reveal a number of high-level taxa formally defined by Cavalier-Smith, many

of them known or suspected to be paraphyletic. The reason is simple: his classifications are extremely convenient, because they are invariably composed in such a way as to include only a minimal number of taxa *and* ranks which are *usually* monophyletic, but sometimes are paraphyletic if that makes for a convenient system. The reader is referred to the above-cited paper (Cavalier-Smith, 1998) where his philosophy of biological classification is explained in detail.

On a side, and probably more personal, note: the zoologists reading this paper may find it interesting to go through his proposed classification of the animal kingdom (Cavalier-Smith, 1998, pp.235–237) which offers, in the opinion of the author of this paper, a refreshing look at the list of animal phyla. As currently recognized, there is somewhere around 30-35 phyla—consult any modern textbook on zoology—that only recently began to be grouped into a few large monophyletic groups, such as Spiralia, Ecdysozoa or Deuterostomia. Other than that, there is a confusing diversity of tiny phyla, most of them unknown to the general public: how many non-zoologists know of Kinorhyncha, Loricifera, Gnathostomulida (jaw worms) or Acanthocephala (spiny-headed worms)? Cavalier-Smith groups all animals into 22 phyla—still a long list, but, especially with the aid of his clear, succinct diagnoses, is much more manageable. The classification includes some, but rather few, paraphyletic taxa.

Solution III: abandon classification systems

The third solution would be to run away from the problem, so to speak, and refrain from explicitly writing down classifications, and discuss biological diversity through phylogenetic trees only. This has been proposed from time to time by certain scientists and philoso-

phers (the proposal has been reviewed and critiqued by Michael Benton (2000)). While reading biological literature, one finds this sentiment expressed from time to time, especially by specialists working with rapidly changing classification systems. There is a fascinating, heated dialogue that ensued during the 1970 First International Conference on Ephemeroptera, recorded in this conference's proceedings (Peters and Peters, 1973, pp.151–154), where a group of entomologists become increasingly frustrated by their inability to create a classification system based on the otherwise clear phylogenetic evidence presented by one of the participants (Edmunds Jr, 1973). In fact, all the problems discussed in this paper with regard to higher ranks are mentioned during that discussion, which is about families, subfamilies and genera of Ephemeroptera, which makes for a great read.

There are at least two large groups in biology that have abandoned updating the classification of the organisms they are working with: botanists working with flowering plants and malacologists.

In the first case, one would be hard-pressed to find a recent authoritative classification of flowering plants, because the focus of the communal effort has long been the creation of better and better phylogenies, not taxonomies. The Angiosperm Phylogeny Group regularly publishes the new view on plant phylogeny, employing formal taxa only to the level of order (see e.g. Chase et al., 2016). All the higher-rank taxa are abandoned, and no higher-rank taxonomies are officially accepted by APG.

The exactly same process had happened in the field of malacology, where for years there were no formal definitions of gastropod taxa above the level of superfamily (see Bouchet and Rocroi, 2005). Interestingly, the situation visibly upset some of the workers in the field who started spontaneously grouping the newly defined families and superfamilies into orders, those into superorders, subclasses

etc. Last year in a revision of the 2005 classification (Bouchet, Rocroi et al., 2017), the authors surrendered and included higher-ranked taxa, although the system is now very “messy”: it includes numerous intermediate-level ranks that correspond to the unranked clades in the previous classification—there are classes, subclasses, infraclasses, cohorts, subcohorts, superorders, orders, suborders and infraorders in the system, plus a handful of openly paraphyletic “grades”. The struggle of malacologists to bring back Linnaean classification into the world of Hennigian unranked lists à la Adl *et al.* leads to exactly the same problems that were discussed in the previous sections.

The case of gastropod classification illustrates, however, that even specialists working in very narrow fields need balanced ranked classification systems. It is not only for the purposes of educating the young, writing books or organizing museum expositions that we need neat, logical classifications with no missing ranks and a small number of distinctive, easy to remember taxa. The specialists need them too. The option to abandon classification systems seems to be not viable, especially that it is both trivial and tempting to create a list of clades from a phylogenetic tree, adding ranks to some or all taxa, which would be a *de facto* classification, just like Benton did in his *Vertebrate Palaeontology*.

4. Summary

Our increasing knowledge of biodiversity, especially in the case of microbiology, both prokaryotic and eukaryotic, will inevitably lead to the escalation of the problems presented in this paper. Because it doesn't seem plausible that classification systems will be altogether abandoned (which would leave us only with phylogenetic

trees, sometimes presented as unranked lists), it seems that we must somehow solve the problem of creating classification systems in the times of abundant phylogenetic data.

Broadly speaking, there seem to be two directions that one might take: 1) to follow phylogenetic data to the letter; 2) to follow intuition and convenience. Simply put, the option 1) would mean having only proper monophyletic taxa, but a highly impractical system; and the option 2) would mean having also paraphyletic taxa *and* a system that is practical.

In the special case of eukaryotic kingdoms, the first route would lead to a revolution in biological classification of life and numerous kingdoms currently unknown to the general public would be introduced (Tedersoo, 2017), such as Oxymonada, Breviatea or Filasteriae, that would now be listed alongside plants, animals and fungi as “major types of life”. Alternatively, one might drop the traditional kingdoms altogether and define the currently recognized eukaryotic “supergroups” (e.g. Keeling et al., 2005) as kingdoms, and what we know recognize as kingdoms would have to be downranked into sub-kingdoms or “microkingdoms” (Pawlowski, 2013). This would be the resulting classification:

- kingdom Excavata
- kingdom Amoebozoa
- kingdom Opisthokonta (incl. fungi and animals)
- kingdom Archaeplastida (incl. plants)
- kingdom Rhizaria
- kingdom Alveolata
- kingdom Heterokonta

Obviously, this would *not* solve the problem, if one would stubbornly keep on sticking to Hennigian rules. First of all, Excavata may be

paraphyletic (He et al., 2014), in which case we would have to split it into monophyletic groups, resulting in a classification system alike to this:

- kingdom Euglenozoa (former Excavata)
- kingdom Heterolobosea (former Excavata)
- kingdom Jakobea (former Excavata)
- kingdom Metamonada (former Excavata)
- kingdom Amoebozoa
- kingdom Opisthokonta (incl. fungi and animals)
- kingdom Archaeplastida (incl. plants)
- kingdom Rhizaria
- kingdom Alveolata
- kingdom Heterokonta

Secondly, there is at least a dozen groups of eukaryotes that don't fit neatly into any of the supergroups, including *Tsukubamonas* and *Malawimonas*, Cavalier-Smith's *Varisulca*, Apusozoa, but also much better-known groups such as Cryptophyta or Haptophyta. Consequently, in Tedersoo's system, there *are* kingdoms Malawimonada, Tsukubamonada, Apusozoa, Cryptista and Haptista which brings us to square one. Obviously, replacing traditional kingdoms with eukaryotic supergroups is *not* a solution.

The second option—to retain the general structure of the present classification of life into kingdoms—is not fully satisfactory, either, because the old kingdom Protozoa is now known to be a large, highly structured group that deserves proper recognition and can't be rightfully treated as an unstructured bunch of “amoeba and such” (see Patterson, 1999). Its representatives have very little in common with each other and include multicellular forms similar to fungi (mycetozoa slime molds, acrasids) and plants (brown algae),

single-celled large predatory heterotrophs (ciliates), intracellular parasites (kinetoplastids) and endosymbionts (syndineas); colonial filterers (choanoflagellates), multinucleate “superamoebae” (labyrinthomyces) and tens of other forms. Small steps, such as Cavalier-Smith’s proposal for the kingdom of Chromista, might be seen a sign of a more conservative process of a slow, incremental change, not dictated by blind adherence to formalized ideals, but rather by educational values.

At the moment it is uncertain which approach will dominate, but it’s clear that creating a top-level classification of life congruent with our contemporary knowledge of eukaryote phylogeny will require us to resign from at least some philosophical principles of biological systematics.

Bibliography

- Adl, S.M., Simpson, A.G.B., Farmer, M.A. et al., 2005. The new higher level classification of eukaryotes with emphasis on the taxonomy of protists. *The Journal of Eukaryotic Microbiology* [Online], 52(5), pp.399–451. Available at: <https://doi.org/10.1111/j.1550-7408.2005.00053.x> [Accessed 21 May 2019].
- Adl, S.M., Simpson, A.G.B., Lane, C.E. et al., 2012. The revised classification of eukaryotes. *The Journal of Eukaryotic Microbiology* [Online], 59(5), pp.429–493. Available at: <https://doi.org/10.1111/j.1550-7408.2012.00644.x> [Accessed 21 May 2019].
- Baldauf, S.L., Roger, A.J., Wenk-Siefert, I. and Doolittle, W.F., 2000. A kingdom-level phylogeny of eukaryotes based on combined protein data. *Science*, 290(5493), pp.972–977. Available at: <https://doi.org/10.1126/science.290.5493.972>.
- Benton, M.J., 2014. *Vertebrate Palaeontology*. Fourth edition. Chichester, West Sussex; Hoboken, NJ: Wiley Blackwell.

- Benton, M.J., 2000. Stems, nodes, crown clades, and rank-free lists: is Linnaeus dead? *Biological Reviews*, 75(4), pp.633–648. Available at: <https://doi.org/10.1111/j.1469-185X.2000.tb00055.x>.
- Bouchet, P. and Rocroi, J.-P., 2005. Classification and nomenclator of gastropod families. *Malacologia: International Journal of Malacology*, 47(1-2), pp.1–397. [Accessed 28 May 2019].
- Bouchet, P., Rocroi, J.-P. et al., 2017. Revised Classification, Nomenclator and Typification of Gastropod and Monoplacophoran Families. *Malacologia*, 61(1-2), pp.1–526. Available at: <https://doi.org/10.4002/040.061.0201>.
- Cavalier-Smith, T., 1981. Eukaryote kingdoms: Seven or nine? *Biosystems*, 14(3), pp.461–481. Available at: [https://doi.org/10.1016/0303-2647\(81\)90050-2](https://doi.org/10.1016/0303-2647(81)90050-2).
- Cavalier-Smith, T., 1998. A revised six-kingdom system of life. *Biological Reviews*, 73(3), pp.203–266. Available at: <https://doi.org/10.1111/j.1469-185X.1998.tb00030.x>.
- Cavalier-Smith, T., 2002. The phagotrophic origin of eukaryotes and phylogenetic classification of Protozoa. *International Journal of Systematic and Evolutionary Microbiology* [Online], 52(2), pp.297–354. Available at: <https://doi.org/10.1099/00207713-52-2-297> [Accessed 21 May 2019].
- Cavalier-Smith, T., 2013. Early evolution of eukaryote feeding modes, cell structural diversity, and classification of the protozoan phyla Loukouzoa, Sulcozoa, and Choanozoa. *European Journal of Protistology*, 49(2), pp.115–178. Available at: <https://doi.org/10.1016/j.ejop.2012.06.001>.
- Cavalier-Smith, T., 2016. Higher classification and phylogeny of Euglenozoa. *European Journal of Protistology* [Online], 56, pp.250–276. Available at: <https://doi.org/10.1016/j.ejop.2016.09.003> [Accessed 28 May 2019].
- Chase, M.W. et al., 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* [Online], 181(1), pp.1–20. Available at: <https://doi.org/10.1111/boj.12385> [Accessed 28 May 2019].

- Copeland, H.F., 1938. The Kingdoms of Organisms. *The Quarterly Review of Biology* [Online], 13(4), pp.383–420. Available at: <<https://www.jstor.org/stable/2808554>> [Accessed 28 May 2019].
- Edmunds Jr, G., 1973. Some critical problems of family relationships in the Ephemeroptera. In: Peters, W. and Peters, J. eds. *Proceedings of the First International Conference on Ephemeroptera. Florida Agriculture and Mechanical University, August 17-20, 1970*. Leiden: Brill, pp.145–154.
- Haeckel, E., 1866. *Generelle morphologie der organismen. Allgemeine grundzüge der organischen formen-wissenschaft, mechanisch begründet durch die von Charles Darwin reformirte descendenztheorie. 2. bd. Allgemeine entwicklungsgeschichte der organismen* [Online]. Berlin: Verlag von G. Reimer. Available at: <<https://www.biodiversitylibrary.org/bibliography/3953>>.
- He, D. et al., 2014. An alternative root for the eukaryote tree of life. *Current Biology* [Online], 24(4), pp.465–470. Available at: <https://doi.org/10.1016/j.cub.2014.01.036> [Accessed 28 May 2019].
- Hennig, W., 1966. *Phylogenetic Systematics* (D. Davis and R. Zangerl. Trans.). Chicago, Ill.: University of Illinois Press.
- Hull, D.L., 1965. The effect of essentialism on taxonomy—two thousand years of stasis (I). *The British Journal for the Philosophy of Science*, 15(60), pp.314–326. Available at: <https://doi.org/10.1093/bjps/XV.60.314>.
- Hull, D.L., 1970. Contemporary systematic philosophies. *Annual Review of Ecology and Systematics*, 1(1), pp.19–54. Available at: <https://doi.org/10.1146/annurev.es.01.110170.000315>.
- Keeling, P.J. et al., 2005. The tree of eukaryotes. *Trends in Ecology & Evolution*, 20(12), pp.670–676. Available at: <https://doi.org/10.1016/j.tree.2005.09.005>.
- Linnaeus, C., 1788. *Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis (vol. 9)* [Online]. Lipsiae [Leipzig]: Impensis Georg Emanuel Beer, Available at: <<https://www.biodiversitylibrary.org/bibliography/545>>.

- Margulis, L. and Chapman, M.J., 2009. *Kingdoms and Domains: An Illustrated Guide to the Phyla of Life on Earth*. 4th ed. London: Academic Press.
- Mayr, E. and Bock, W.J., 2002. Classifications and other ordering systems. *Journal of Zoological Systematics and Evolutionary Research*, 40(4), pp.169–194. Available at: <https://doi.org/10.1046/j.1439-0469.2002.00211.x>.
- McKenna, M.C. and Bell, S.K., 1997. *Classification of Mammals: Above the Species Level*. New York: Columbia University Press.
- Nelson, G.J., 1972. Phylogenetic relationship and classification. *Systematic Biology*, 21(2), pp.227–231. Available at: <https://doi.org/10.1093/sysbio/21.2.227>.
- Patterson, D.J., 1999. The diversity of Eukaryotes. *The American Naturalist*, 154(S4), S96–S124. Available at: <https://doi.org/10.1086/303287>.
- Pawlowski, J., 2013. The new micro-kingdoms of eukaryotes. *BMC Biology* [Online], 11(1), p.40. Available at: <https://doi.org/10.1186/1741-7007-11-40> [Accessed 28 May 2019].
- Peters, W. and Peters, J., eds., 1973. *Proceedings of the First International Conference on Ephemeroptera. Florida Agriculture and Mechanical University, August 17-20, 1970*. Leiden: Brill.
- Petitjean, C., Deschamps, P., López-García, P. and Moreira, D., 2014. Rooting the domain Archaea by phylogenomic analysis supports the foundation of the new kingdom Proteoarchaeota. *Genome Biology and Evolution* [Online], 7(1), pp.191–204. Available at: <https://doi.org/10.1093/gbe/evu274> [Accessed 28 May 2019].
- Ruggiero, M.A. et al., 2015. A Higher Level Classification of All Living Organisms. *PLOS ONE* [Online], 10(4), e0119248. Available at: <https://doi.org/10.1371/journal.pone.0119248> [Accessed 28 May 2019].
- Schuh, R.T. and Brower, A.V.Z., 2011. *Biological Systematics: Principles and Applications*. Ithaca, NY: Cornell University Press. Available at: <https://doi.org/10.7591/9780801462436>.
- Swartz, B., 2012. A marine stem-tetrapod from the Devonian of western North America. *PLOS ONE* [Online], 7(3), e33683. Available at: <https://doi.org/10.1371/journal.pone.0033683> [Accessed 28 May 2019].

- Tedersoo, L., 2017. Proposal for practical multi-kingdom classification of eukaryotes based on monophyly and comparable divergence time criteria. *bioRxiv* [Online], p.240929. Available at: <https://doi.org/10.1101/240929> [Accessed 28 May 2019].
- Tedersoo, L. et al., 2018. High-level classification of the Fungi and a tool for evolutionary ecological analyses. *Fungal Diversity* [Online], 90(1), pp.135–159. Available at: <https://doi.org/10.1007/s13225-018-0401-0> [Accessed 28 May 2019].
- Whittaker, R.H., 1969. New concepts of kingdoms of organisms. *Science*, 163(3863), pp.150–160. Available at: <https://doi.org/10.1126/science.163.3863.150>.
- Wiley, E., 1981. *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. New York: John Wiley.
- Williams, D.M. and Kocielek, J.P., 2007. Pursuit of a natural classification of diatoms: History, monophyly and the rejection of paraphyletic taxa. *European Journal of Phycology* [Online], 42(3), pp.313–319. Available at: <https://doi.org/10.1080/09670260701419921> [Accessed 28 May 2019].
- Williams, T.A., Foster, P.G., Cox, C.J. and Embley, T.M., 2013. An archaeal origin of eukaryotes supports only two primary domains of life. *Nature*, 504(7479), pp.231–236. Available at: <https://doi.org/10.1038/nature12779>.
- Woese, C.R., Kandler, O. and Wheelis, M.L., 1990. Towards a natural system of organisms: proposal for the domains Archaea, Bacteria, and Eucarya. *Proceedings of the National Academy of Sciences* [Online], 87(12), pp.4576–4579. Available at: <https://doi.org/10.1073/pnas.87.12.4576> [Accessed 28 May 2019].
- Woese, C.R. and Fox, G.E., 1977. Phylogenetic structure of the prokaryotic domain: The primary kingdoms. *Proceedings of the National Academy of Sciences* [Online], 74(11), pp.5088–5090. Available at: <https://doi.org/10.1073/pnas.74.11.5088> [Accessed 28 May 2019].