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Renewing Linnaean taxonomy: a proposal to restructure the highest levels of the Natural System

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ABSTRACT

During the last century enormous progress has been made in the understanding of biological diversity, involving a dramatic shift from macroscopic to microscopic organisms. The question now arises as to whether the Natural System introduced by Carl Linnaeus, which has served as the central system for organizing biological diversity, can accommodate the great expansion of diversity that has been discovered. Important discoveries regarding biological diversity have not been fully integrated into a formal, coherent taxonomic system. In addition, because of taxonomic challenges and conflicts, various proposals have been made to abandon key aspects of the Linnaean system. We review the current status of taxonomy of the living world, focussing on groups at the taxonomic level of phylum and above. We summarize the main arguments against and in favour of abandoning aspects of the Linnaean system. Based on these considerations, we conclude that retaining the Linnaean Natural System provides important advantages. We propose a relatively small number of amendments for extending this system, particularly to include the named rank of world (Latin alternative *mundis*) formally to include non-cellular entities (viruses), and the named rank of empire (Latin alternative *imperium*) to accommodate the depth of diversity in (unicellular) eukaryotes that has been uncovered. We argue that in the case of both the eukaryotic domain and the viruses the cladistic approach intrinsically fails. However, the resulting semi-cladistic system provides a productive way forward that can help resolve taxonomic challenges. The amendments proposed allow us to: (*i*) retain named taxonomic levels and the three-domain system, (*ii*) improve understanding of the main eukaryotic lineages, and (*iii*) incorporate viruses into the Natural System. Of note, the proposal described herein is intended to serve as the *starting point* for a broad scientific discussion regarding the modernization of the Linnaean system.

Key words: cladistics, eukaryogenesis, Linnaean taxonomy, Natural System, phylogenomics, viral taxonomy, tree of life.

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I. INTRODUCTION

The publication of *Systema Naturae* by Carl Linnaeus in 1735, which provided an indispensable system for studying the remarkable variety of organisms on Earth, had an enormous impact on the development of biology as a scientific discipline, reminiscent of the impact on the physical sciences of the advent of *Philosophiæ Naturalis Principia Mathematica* by Isaac Newton in 1687. The Linnaean system, with its ranks of species, genus, family, order, class, phylum and kingdom has been the framework used to classify living things that has structured the science of biology for nearly three centuries. This system provided biology students and researchers with a recognizable map of living things, not unlike how the map of the world, with continents such as North or South America, provided a system to order the countries of the world. The subsequent publication of *On the Origin of Species* (Darwin, 1859) only enhanced the value of the *Systema Naturae* because the system of taxonomic groups introduced by Linnaeus now could be refined to reflect faithfully the evolutionary steps resulting in the huge biological diversity observed. Thus, all biological research on the physiology, taxonomy, and evolution of every organism could, it seemed, be performed in the context of this unifying framework.

These early research efforts were almost entirely focused on plants and animals (in modern terms, embryophyta and metazoa). More recent breakthroughs discussed herein have enormously expanded the scope of biological research, revealing a largely unsuspected diversity of microbial lifeforms that greatly increased the metabolic scope of life. These microbes were also found to embody most of the evolutionary history of life on Earth. As discussed below, these seminal discoveries resulted in key progress in expanding and understanding the descriptions of living entities as initiated by Carl Linnaeus, but also uncovered important challenges to his system. Here we aim to provide a review of how this avalanche of novel information can be integrated into an updated Natural System to organize biological knowledge, hoping it will constitute a solid and fertile foundation for further research. Before embarking upon this review, we want to address a sensitive point regarding some negative connotations of certain rank names such as 'kingdom' or 'empire'. We are, of course, aware of unfortunate associations (such as imperialism), but decided to retain these descriptors because of their longstanding history in taxonomical usage.

II. A BRIEF LOOK AT SOME REVISIONS DURING THE HISTORY OF THE LINNAEAN SYSTEM

While an extensive overview of how the taxonomy of the Natural System came into being and changed is beyond the scope of this review, some of the salient aspects of the interaction of historical accident (for instance the fact that Linnaeus was especially focused on flowering plants, while his friend Artedi was fascinated by fishes, giving rise to a rather lopsided description of nature in the beginning) and progressive understanding of evolution during its development are relevant to the issues discussed herein. This not only provides a deeper understanding of how the system of taxonomic ranks evolved, but also illustrates the adaptability of the system.

When Linnaeus introduced his taxonomical framework many of the rankings were not well defined or consistently used. Also, many groups were classified using superficial criteria. Linnaeus was fully aware of these concerns and kept on improving his system. A majority of (zoological) taxonomists take the 10th edition (Linnaeus, 1758) as an important starting point. In light of recent insights and more than 250 years of research, errors in this document are easy to identify, but importantly the Linnaean system contained key features that allowed it to flourish. Two crucial aspects of particular importance here are the willingness of Linnaeus to constantly update his system in light of empirical evidence, and the search for suitable criteria to distinguish groups according to their level of relatedness (i.e. reflecting their evolutionary history) in pre-genomic times.

An illustrative example of the importance of using suitable criteria for identifying taxonomic groups is that Linnaeus grouped bats with 'Quadrupedia' (Mammalia) and not with birds, intuiting that flight was not a basic characteristic useful for taxonomy. In modern parlance, it is the result of convergent evolution. Initially he did not distinguish clearly between fishes and whales or dolphins, but later on we find the latter two in one of the eight groups (orders) of the quadrupedia: the 'Cete' with four genera: *Monodon* (narwhals), *Balaena* (baleen whales), *Physeter* (sperm whales) and *Delphinus* (dolphins). When we compare this to modern insights, we find all of them still grouped together in the infraorder Cetacea (Cetaceamorpha). They are subsumed under the order Artiodactyla (even-toed ungulates) and, when compared to other living organisms, found to be related to the Hippopotamidae, illustrating how a range of adaptations allowed subgroups of these ungulates to return to water, and eventually to populate the oceans. These taxonomic modifications thus provided a better reflection of the evolutionary history of ungulates. As an evolutionarily interesting side note, the taxon Cetacea is also important for its abundance of palaeontological findings which illustrate predicted evolutionary trajectories, by uncovering the 'missing links' along the way. A valuable overview of this palaeontological evidence can be found in *Written in stone* (Switek, 2010).

The discovery of fossils of extinct ancestors of living clades led to the need to name these organisms and to place them in the Natural System, which often necessitated the introduction of higher-level groupings. It can be challenging to choose the specific level for such a new grouping, and this is important, as the rules for naming groups are dictated by their respective levels. However, the taxonomic system allows renaming upon moving a group to a different level, for instance because of changes in perceived phylogenetic relationships. That this is still an ongoing process can, again, be illustrated by the Cetaceans, where diverse molecular and fossil data are integrated to provide the best reconstruction of their evolution. Positioning key fossils can then be critical in understanding what sequence of events allowed these organisms to transition from land to life in water. The discovery of *Indohyus*, an Eocene south Asian raoellid artiodactyl (Thewissen *et al.*, 2007), more closely related to whales than any other artiodactyl fossil, opens up the possibility that the cetaceans actually evolved from an herbivore that took to water to avoid predators. How this finding will affect the phylogenetic tree of these organisms and their taxonomy is still debated [see for instance, Spaulding, O'Leary & Gatesy (2009) and Geisler & Theodor (2009)].

In dealing with organisms that are commonly referred to as reptiles and amphibians, Linnaean groupings were based on the presence/absence of legs, which is a poor taxonomic criterion, as legs can be lost secondarily. A more useful criterion, whether the organism deposits its eggs in water or, alternatively, out of water (being surrounded by protective shells) was not always readily observable at the time of Linnaeus. Novel insights regarding egg structures were then used to revise the taxonomy of these organisms.

Important aspects of these early instalments of the Natural System are: (*i*) some of the names of the groups and even of the taxonomic levels themselves were not always used consistently and (*ii*) they came about in a rather haphazard fashion. For instance, Linnaeus distinguished ranks such as class, order (although not consistently with this name), genus and species for mammals, plants, insects and other groups [in fact, the title page of the 10th edition of Linnaeus (1758), volume I, dealing with animals, uses classes, ordines, genera and species]. Although multiple groupings were at the modern family level, distinction from the order level was not always clear. Many of these groupings were used more artificially in the case of plants, which were described in volume II, appearing a year later. Despite these aspects, two of his works, the first edition of the *Species Plantarum* (Linnaeus, 1753) for plants and the 10th edition of the *Systema Naturae* (Linnaeus, 1758), are accepted as part of the starting points of nomenclature. Here we want to stress how both these early and recent developments demonstrate the flexibility of the powerful Linnaean Natural System: it has successfully incorporated many rounds of evidence-driven modifications. In this article we aim to draw inspiration from this long history of successfully modernizing the Linnaean system.

III. EXCITING BUT UNFINISHED WORK

The following review of the current status of the taxonomy of the main groups of the tree of life indicates that important progress in understanding the diversity of life remains to be fully integrated into a universally accepted Natural System. In these considerations it is important to distinguish between the Natural System and the tree of life, which tend to be used interchangeably: the Natural System refers to the Linnaean taxonomic edifice constructed to try to describe, as completely as possible, the actual historic evolution of life on earth (i.e. the tree of life). An important aim of this review is to evaluate how to integrate the following foundational discoveries into the Linnaean Natural System.

(i) The number of highest-level taxa in the Natural System, the organisms belonging to these highest-level taxa, and the name of their rank remains to be formalized. The development of electron microscopy helped consolidate the prokaryote–eukaryote dichotomy (Stanier & van Niel, 1962), which is considered a core tenet of cell biology, although criticized by some (see e.g. Pace, 2009). For a historical review see Sapp (2005). However, these two groups have existed outside of accepted taxonomy and the name of the taxonomic rank of these two groups has remained unestablished. Taxonomy of prokaryotic organisms was greatly complicated by their lack of body plans as found in animals, or flowers and seeds found in plants. The use of small subunit ribosomal RNA (SSU-rRNA) in molecular phylogeny revolutionized taxonomy (particularly that of prokaryotes), and revealed a fundamental prokaryote dichotomy (Woese & Fox, 1977). In 1990, the cornerstone of the Bacteria–Archaea–Eukaryote tripartite division of cellular life (see also Fig. 1) was established with the name 'domain' for the taxonomic rank of these groups introduced by Woese, Kandler & Wheelis (1990). However, this proposal was never canonized by international taxonomic committees. In a high-profile discussion between Ernst Mayr and Carl Woese (Mayr, 1998; Woese, 1998), 'empire' was proposed as an alternative name for this taxonomic level, but this proposal did not gain traction. In addition, the question how to resolve the apparent inconsistency of including the prokaryote–eukaryote dichotomy as well as the three-domain division of the Natural System, both in university textbooks and in scientific literature, was left unaddressed [see e.g. Pace (2006, 2009), van der Gulik, Hoff & Speijer (2017) and Whitman (2009)]. We have previously discussed our arguments in favour of both the

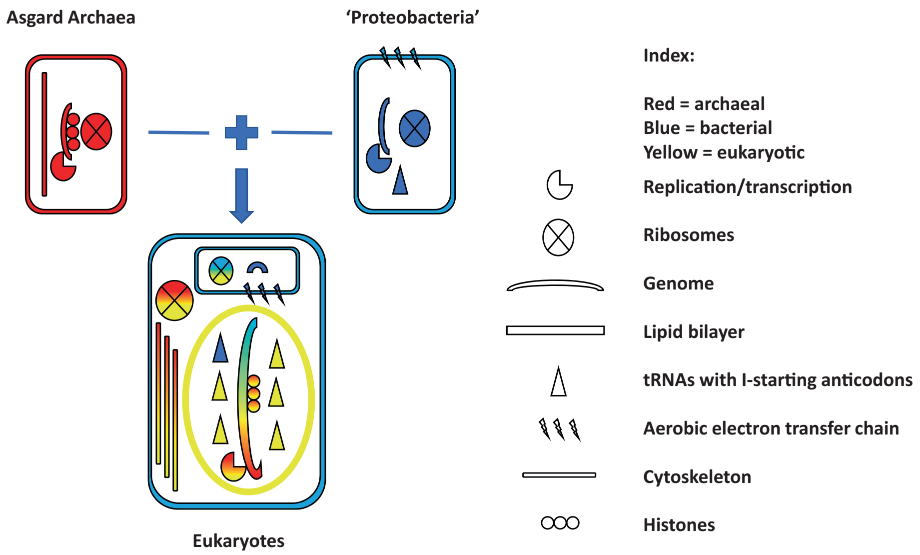

Fig. 1. A schematic overview of some of the defining characteristics (listed on the right) of the three domains of life, stressing the hybrid character of eukaryotes resulting from the merging of prokaryotes (indicated by blue lines and arrow between the cells). Red represents archaeal, blue represents bacterial, and yellow represents eukaryotic characteristics. For further details, see Section V.2. The two compartments indicated in the eukaryotic cell are the nucleus (yellow circle) and the mitochondrion (blue rectangle). The proteobacterial ancestor of the mitochondrion also had an outer membrane (not shown). tRNA refers to transfer RNA anticodon modifications.

three-domains-of-life paradigm, as well as the continued use of the term 'prokaryote' (van der Gulik *et al.*, 2017). Here we wish to stress further that the widely used terms 'prokaryotes' (Archaea and Bacteria) and 'protists' (unicellular eukaryotic groups) remain useful because they capture important *stages* in the evolution of life: until eukaryogenesis, there were only prokaryotic cells (indicated in Fig. 2 as the prokaryotic period), and until the emergence of eukaryotic multi-cellularity, there were only protists living alongside prokaryotes (indicated in Fig. 2 as the mixed microbial period).

(ii) The full taxonomic implications of (primary) endosymbiosis have remained unresolved. Mitochondria and chloroplasts were identified as endosymbionts derived from previously free-living bacteria [see e.g. Mereschkowsky's classic 1910 paper (Kowallik & Martin, 2021) and the publications of Ivan Wallin; e.g. Wallin (1925)]. In the 1960 s, Lynn Margulis, still publishing under the name of her first husband, became instrumental in securing wide acceptance of these insights (Sagan, 1967). These events and other key historic developments in the Linnaean system of direct importance to this review are summarized in Table 1. Subsequent work identified mitochondria as descendants of organisms known as alpha-proteobacteria (Schwartz & Dayhoff, 1978; Fan *et al.*, 2020; Keeling & Doolittle, 1997; Martijn *et al.*, 2018). The free-living bacteria that would, after being taken up by early eukaryotes, evolve into chloroplasts, were found to be related to cyanobacteria (Bhattacharya & Medlin, 1995; Nelissen *et al.*, 1995; Speijer, Hammond & Lukes, 2020). However, the taxonomic ramifications of these remarkable and profound findings remain to be fully confronted (Kurland & Andersson, 2000; Martijn *et al.*, 2018).

(iii) The taxonomy of major groups in the eukaryotes has been greatly improved but remains unfinished. The taxonomy of the domain eukaryotes has undergone multiple rounds of major modifications. The two classic kingdoms of

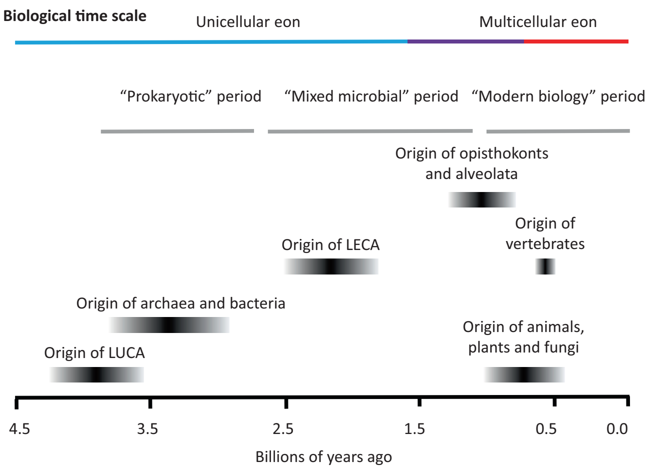

Fig. 2. A highly schematized overview of the timescale for cellular evolution. Uncertainties in the dating of origins are indicated in grey shading. The timing of several independent origins of multicellularity (i.e. the evolution of co-dependent differentiated cells in a single organism) is uncertain (purple line segment). The figure does not depict an alternative scenario in which Archaea and Bacteria did not evolve from the last universal common ancestor (LUCA), but originated independently from a non-cellular metabolic network of reactions. LECA, last eukaryote common ancestor.

Table 1. Key events during the development of the Natural System.

Year	Event
1735	Publication of *Systema Naturae* by Carl Linnaeus: kingdoms Plants and Animals are formally introduced.
1794	Proposal of the taxon Vertebrata/Invertebrata by Jean-Baptiste de Lamarck (Lamarck, 1794). The Invertebrates are split into various distinct groups.
1859	Charles Darwin publishes *On the Origin of Species by Means of Natural Selection* (Darwin, 1859).
1910	Proposal of symbiogenic origins for certain organelles by Konstantin Sergejewitch Mereschkowsky (Kowallik & Martin, 2021).
1950	Advent of cladistic methodology (see e.g. Hennig, 1980).
1962	Publication of *The Concept of a Bacterium* by Stanier & van Niel (1962). Electron microscopy consolidates the eukaryote/prokaryote dichotomy.
1967	Rediscovery of mitochondria and chloroplasts as endosymbionts by Lynn Margulis (Sagan, 1967).
1969	Proposal of a five-kingdom system by Robert Whittaker (Whittaker, 1969).
1977	Discovery of the Archaea/Bacteria dichotomy based on molecular analysis using 16 S rRNA (Woese & Fox, 1977).
1980	Official introduction of kingdom Fungi (*cf.* much earlier work by Ernst Haeckel* and Robert Whittaker) (Moore, 1980).
1987	Taxon Opisthokonta proposed by Thomas Cavalier-Smith based on taxonomically informative eukaryotic subcellular structures (Cavalier-Smith, 1987).
1990	Publication on the tripartite system (Archaea, Bacteria, and Eucarya) with taxonomic rank name domain, and introduction of kingdoms Crenarchaeota and Euryarchaeota (Woese *et al.*, 1990).
1999	Proposal of a web of life (based on analysis of lateral gene transfer); (Doolittle, 1999).
2003	Environmental genomics results in the discovery of the uncultured majority of microbial organisms and expanded knowledge of the tree of life [see e.g. Battistuzzi *et al.* (2004) and Hug *et al.* (2016)].
2010	Animals and plants are shown to be far apart in the eukaryotic domain (see e.g. Burki *et al.*, 2007).
2013	Discussion of the central role of viruses in the evolution of life: an independent, crucial, taxonomic group mirroring cellular life (Koonin & Dolja, 2013).
2015	Discovery of Asgardarchaea, with implications for eukaryogenesis (Spang *et al.*, 2015; Koonin, 2015).
2021	Greatly extending the analyses of Battistuzzi *et al.* (2004), Coleman *et al.* (2021) identify Terrabacteria, Gracilicutes, and Fusobacteria as the main groups of Bacteria.

*In the 19th century, Haeckel had already moved the Fungi out of Plantae into Protista when revising an earlier classification. Robert Whittaker recognized an additional kingdom for the Fungi.

plants and animals were expanded by the addition of the kingdom fungi, see (Moore, 1980) and the Protista (single-celled eukaryotes), resulting in the influential, but informal and now largely abandoned, five kingdoms classification, with the prokaryotic 'Monera' constituting the 5th kingdom (Whittaker, 1969). Analysis of 18 S rDNA data confirmed the plants, animals, and fungi as valid taxonomic groups (although many algae were removed from the plants, all protozoa were taken out of the animals, and oomycetes and slime moulds were taken out of the fungi), but indicated that the Protista contain multiple groups that are of equal taxonomic rank. In addition, electron microscopy was used to identify major taxonomic groups in the eukaryotes based on sub-cellular structures (Cavalier-Smith, 1981, 1998), later on also including groups above the kingdom level (see Section VII). Initially, the plants, animals, and fungi were identified as clustering closely in the eukaryotic domain, but this proved to be erroneous (Burki *et al.*, 2007; Burki, Shalchian-Tabrizi & Pawlowski, 2008). Current eukaryote trees containing the phylogeny of all eukaryotic lineages now shows the bulk of diversity comprising microbial unicellular species. The new trees contain a minimum of eight supergroups, with many new kingdom-level lineages of protists (Adl *et al.*, 2019; Burki *et al.*, 2020). These phylogenetic clusters show animals and fungi indeed to be closely related, while the kingdom plants is located in a very different part of the eukaryotic tree. However, the process of introducing additional eukaryotic kingdoms and of eukaryotic groups with a taxonomic rank above kingdom is still ongoing.

(iv) New developments in the taxonomy of the Bacteria and Archaea have not been integrated. Analysis of 16 S rDNA data resulted in the proposal that the Archaea consist of two kingdoms (Crenarchaeota and Euryarchaeota; Woese *et al.*, 1990). This research regarding the fundamental archaeal groups and its taxonomical implications remains uncodified [i.e. formally dealt with by the International Committee on Systematics of Prokaryotes (ICSP)], while current work has progressed to identify additional (also not yet broadly recognized) archaeal kingdoms. One of these newly identified archaeal kingdoms (or superphyla) is the Asgardarchaeota, a group of organisms that has revolutionized insights into the evolutionary origin of the eukaryotes, which is further discussed in Section V.2 (Spang *et al.*, 2015). This area of research is still developing rapidly, but apart from the Asgard taxon, fundamental groups such as Diapherotrites/Parvarchaeota/Aenigmarchaeota/Nanohaloarchaeota/Nanoarchaeota (DPANN), Proteoarchaeota and Methanotecta are taking form [see e.g. Adam *et al.* (2017) for an overview]. An overhaul of higher-level classifications of the Archaea should also incorporate insights from the recent analyses and phylogenomic considerations in Tahon, Geesink & Ettema (2021) and Moody *et al.* (2022). Whether further research will support both the existence and ancient divergence of two main archaeal clades, with the proposed names Ouranosarchaea and Gaiarchaea (Aouad *et al.*, 2022), is still to be decided.

The identification of kingdoms in the bacteria proved to be highly challenging because of lateral gene transfer (LGT; see also Section V.3) and profoundly ancient splits, giving rise to the notion of 'Early evolution without a tree of life', as Martin (2011) titled a review. The concept of a disappearing tree entails that we can distinguish valid domains as well as valid phyla, but that the branching order in between has been irretrievably erased by LGT. However, recently, exciting progress has been reported (Coleman *et al.*, 2021). An earlier analysis grouping three major bacterial lineages together as Terrabacteria, reflecting their association with the ancient colonization of land (Battistuzzi, Feijao & Hedges, 2004), turned out to be robust (Coleman *et al.*, 2021), although Moody *et al.* (2022) consider Terrabacteria to be paraphyletic. The deep divide in outer membrane tethering systems between Terrabacteria and Gracilicutes recently helped microbiologists to make sense of the multiple diderm-to-monoderm transitions occurring during bacterial evolution (Witwinowski *et al.*, 2022); for further discussion, see Section IX.2.

In practice, the identification of many novel prokaryotic lineages and their relationships are still addressed using groups with ranks such as superphylum. The issue of grouping different bacterial phyla [surprisingly, only recently formally adopted as a rank by the ICSP (Oren *et al.*, 2015, 2021)], into higher-order taxa has been exacerbated by the identification of many novel phylum-level groups (Oren & Garrity, 2021). The results of metagenomic (i.e. culture-independent) techniques (Rappé & Giovannoni, 2003; Lloyd *et al.*, 2018) can be analysed by the Genome Taxonomy Database (GTDB; https://gtdb.ecogenomic.org) for prokaryotic genomes, which attempts objectively to calibrate evolution of successive taxonomic ranks (Parks *et al.*, 2021). The outcome of these studies has contributed to the current discussion regarding recent changes in the names of taxa which have long-standing informal names (leaving untouched uncertainties over the taxonomy of new, often uncultured, archaea and bacteria) by the ICSP [see e.g. the ongoing arguments in Lloyd & Tahon (2022), Sutcliffe *et al.* (2022), Panda, Islam & Sharma (2022) and Oren, Göker & Sutcliffe (2022)]. We envisage groupings reflecting the deepest splits in both the archaea, and the bacteria (such as the Gracilicutes), to be afforded the rank of empire. We will mostly leave the construction of bacterial and archaeal phylogenies to the experts working in these respective fields (being fully aware of the specific prokaryotic challenges), but will revisit these questions in section IX. However, we hope that the usefulness of the higher-level ranks kingdom and empire in the prokaryotic realm has become evident from our discussion.

(v) Viruses have not yet been placed within the taxonomic system. Viruses have now been identified as a major reservoir of sequence diversity on Earth (Suttle, 2007), and it has been proposed to recognize the viruses as a distinct taxon, with its own hierarchical taxonomy (Koonin *et al.*, 2020). However, currently the issue of how to integrate the taxonomy of cellular organisms with that of viruses remains unclear, and the International Committee on Taxonomy of Viruses (ICTV) still faces many challenges. In a step aimed at harmonisation with the Linnaean system, the ICTV recently ratified the standard two-part binomial nomenclature for naming virus species (Zerbini *et al.*, 2022). However, it is far from clear whether this is helpful. We will return to the many specific problems of viral taxonomy in Section VIII.

This summary indicates that great progress in understanding of biological diversity has uncovered many key building blocks for a revised Natural System (see Table 1). However, that revision remains to be presented in a coherent manner (see Section X). Here we aim to formulate proposals intended to serve as the starting point for a broad scientific discussion regarding such a modernization of the Linnaean system.

IV. TAXONOMY IS NEVER JUST ABOUT TAXONOMY

Taxonomic considerations are not just about semantics, but carry important implications for biological understanding and subsequent research (van der Gulik *et al.*, 2017). A correct taxonomy should mirror our best scientific insights at every consecutive level. But, crucially, at the same time it also shapes our scientific interpretations and experimental interests. This important point was explicitly formulated by Woese (1998, p. 11046): 'A biological classification is … an overarching evolutionary theory that guides our thinking and experimentation, and it must be structured … to reflect evolutionary reality'.

Only referring rather abstractly to 'organizing biological information' can obscure problems caused by what one might call 'getting lost in a giant muddle of unstructured taxonomic groups'. We will illustrate this issue with some examples. Regarding the singular nature of eukaryogenesis and the unaddressed taxonomy of mitochondria, we are still often confronted with students asking: 'So do bacteria contain mitochondria to generate ATP?' A proper understanding of the evolution of eukaryotes would immediately identify mitochondria as organelles derived from bacteria (but highly altered and containing strongly reduced genomes). Thus, of course, bacteria do not contain mitochondria, and any ATP-producing membrane potential is associated with their cell membranes instead. Medically useful antibiotics often specifically target prokaryotic characteristics (e.g. of ribosomes). Thus, they distinguish between bacterial ribosomes (inhibited) and eukaryotic ribosomes (not inhibited). However, without a clear taxonomical framework it is easy to forget that mitochondria contain ribosomes that were derived from bacterial ribosomes. Therefore, the effect of such antibiotics on mitochondrial ribosomes needs to be determined to ensure that mitochondrial translation is not also inhibited.

Regarding the placement of plants within the eukaryotes: if plants and animals could be placed very closely in this tree (as was the case in various influential phylogenetic trees), one might suspect that embryogenesis in plants and animals could be traced back to molecular processes in the last common ancestor of plants and animals. Now that it is clear that plants and animals are very distantly related eukaryotes, the implication is that these two groups evolved embryology entirely independently. On the other hand, since animals and fungi are more closely related eukaryotes, one might reasonably expect studies on fundamental molecular processes in fungi such as yeast to have clinical relevance for animals, although there remain many pitfalls. The corollary of animals and fungi being related eukaryotes can be seen in the difficulty of producing anti-fungal drugs without significant side-effects (Tverdek, Kofteridis & Kontoyiannis, 2016). Last but not least, integrating viruses into Linnaean taxonomy can be expected to empower a deeper understanding of their tremendous contribution to the history of life (Koonin & Dolja, 2013).

V. IMPORTANT CHALLENGES TO THE LINNAEAN SYSTEM

In addition to the important unaddressed aspects listed above, many recent research findings have led to challenges to foundational aspects of the Natural System introduced by Linnaeus. There are three major issues: (*i*) the multitude of novel higher-order lineages being uncovered by DNA sequencing and bioinformatics approaches – combined with the complication of subjective judgements needed to decide what taxonomic groups in the three domains are on equal footing – has led to the proposal to focus only on the structure of the phylogenetic tree, while abandoning the use of taxon levels with specific names (see e.g. Adl *et al.*, 2019). (*ii*) Recent strong evidence that the domain eukaryotes arose from a merger of an Asgard archaeon and an alphaproteobacterium (Spang *et al.*, 2015; Zaremba-Niedzwiedzka *et al.*, 2017; Imachi *et al.*, 2020) represents a unique, and, to our minds, insurmountable challenge (see Section V.2) to strictly cladistic taxonomy (van der Gulik *et al.*, 2017). Such cladistic purity has resulted in calls for the domain Eukaryotes to be abandoned (Williams *et al.*, 2013; Raymann, Brochier-Armanet & Gribaldo, 2015; Doolittle, 2020; Williams *et al.*, 2020). More generally, should this discovery of such non-cladistic evolution cause a break with the Linnaean system? (*iii*) The discovery that LGT is a major contributor to molecular evolution has resulted in proposals in which phylogenetic trees are abandoned altogether in favour of various alternatives such as pattern pluralism and/or a web of life (Doolittle & Bapteste, 2007).

Our proposed solutions to these three issues (described in more detail in the subsections of Section V) are, respectively: (*i*) revising current taxonomic groupings based on novel insights and formalizing the extra named taxonomic level of empire, (*ii*) accepting an instance of non-cladistic behaviour at the base of the eukaryotes, and (*iii*) assimilating new insights that show prokaryotic tree reconstruction to be perfectly feasible.

The above summary indicates that major researchers, representing different fields of biological scientific endeavour, have proposed the abandoning of core tenets of the Natural System as introduced by Linnaeus. Below we review the main arguments that form the basis of these proposals and indicate a way forward by addressing these concerns in a manner that retains the value of an updated Linnaean Natural System.

(1) Challenge 1: a taxonomy based on nameless ranked systematics

Recently, some biologists studying protists (unicellular eukaryotes) have proposed that we stop using the (higher) Linnaean ranks when describing unicellular eukaryotes, replacing them by a 'scheme that is based on nameless ranked systematics' instead (Adl *et al.*, 2005, p. 399). Of note, ranking in hierarchical categories is still retained. Taken strictly, this proposal amounts to abandoning the use of the terms: domain, kingdom, phylum, class, order, and (possibly) family, genus, and species in protist taxonomy. Part of the reasoning for this is based on the fact that the continuous name changing that has afflicted protistology over recent decades is effectively undermining knowledge regarding unicellular eukaryotes, as illustrated by the following quote: 'Perhaps the most serious consequence of not having had a classification with name stability for protists over the past decades has been the gradual omission of protists from biology textbooks. Without a classification with stable names to teach students, or to search the literature, the significance of the diversity of protists to the biology community has been diminishing'. (Adl *et al.*, 2007, p. 688). The authors make a strong case arguing that this is severely detrimental for the research community (and humanity as a whole), e.g. pointing out that unicellular organisms include a wide range of deadly pathogens as well as many organisms capable of devastating essential food crops. Another ostensibly forceful argument in support of the abandonment of named ranks is the difficulty in objectively determining which taxa are to be assigned a specific rank (especially when comparing ranks in distinctly unrelated parts in the Natural System). For example, how do we determine if the colloquially named taxon Proteobacteria is taxonomically equivalent to the phylum Chordata (the slightly extended group of organisms previously known as Vertebrata; see also Fig. 3)?

But what would be the consequences of abandoning named ranks? First, this proposal appears to abolish over 250 years of ground-breaking taxonomic work in the biological sciences. Second, as such, nameless ranked systematics would not guarantee stability, as the groupings themselves might still have to be revised in light of new evidence. Third, and of greater importance, partly abolishing the roadmap into the living world provided by the system of named taxonomic ranks poses a real risk that students and researchers in the biological sciences will no longer being able to traverse biological diversity easily without getting lost in an ocean of relatively unstructured complexity. Taxa with a named rank provide conceptual anchoring points for organizing and working with biological data. Another key aspect in favour

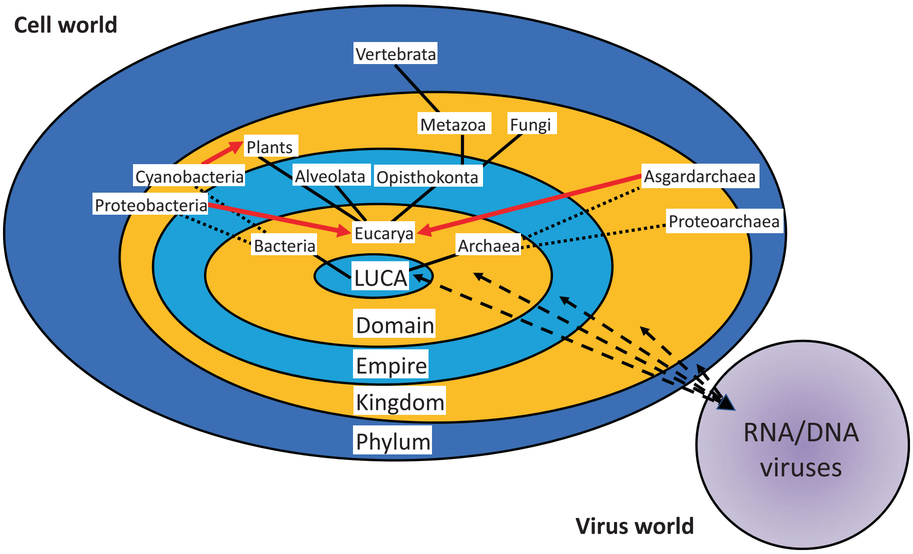

Fig. 3. Cell and Virus worlds. The contours of the Cell world depicted as a bird's eye view of selected groups at the highest taxonomic levels. The newly proposed taxonomic level empire is indicated, together with two proposed empires: Opisthokonta and Alveolata. Vertical descent is indicated by solid black lines. Crucial, primary, merger/endosymbiosis events (eukaryogenesis and the acquisition of cyanobacteria to give rise to plants) are indicated by red arrows. Dotted black lines indicate parts of the tree of life in the Cell world that have not yet been completely resolved. Note: only two bacterial kingdoms and two archaeal superphyla are depicted. For clarity, we use popular vernacular (e.g. Plants, Fungi, and Vertebrata instead of Chordata; see Section V.1). The Virus world is indicated as a separate world outside of the cellular one, distinct but strongly interacting with the Cell world, most likely already at the last universal common ancestor (LUCA) level as explained in e.g. Krupovic *et al.* (2020). This is schematically illustrated by bi-directional dashed black arrows. Relative sizes of the areas are arbitrary.

of a ranked system is the overarching goal that the Natural System (ordering groups forming part of the tree of life) should, as far as possible, reflect the history of organismal evolution. A carefully considered and well-argued selection of a rank for a taxonomic group would reflect the important observation that some bifurcations can be considered more consequential than others. This touches upon a crucial point, i.e. that there will always be some arbitrariness in what one considers consequential. It is our contention that careful consensus building in the scientific community would allow the retention of classical ranked taxonomy, reflecting a deeper understanding of life's evolution.

So how can we decide on the taxonomic rank of a taxon? Which branches on a phylogenetic tree fall just outside or just within this taxon? The example of geographical maps might be illuminating. For instance, consider Central-America. Does Panama belong to the North or the South? There is some arbitrariness in such decisions, but it appears that they are an intrinsic, unavoidable part of a messy biological reality. We argue that the price of abandoning named ranks is much higher than the cost of living with an acceptable (and likely unavoidable) level of arbitrariness in naming biological taxa. While we agree with the comments in Adl *et al.* (2005) that the neglect of knowledge of unicellular organisms is a troubling development, we strongly disagree with the idea that the abolishment of Linnaean ranks would in any way improve the situation. Quite the contrary: biology students and researchers of the future would find it difficult to traverse the mire of biological diversity, being faced with a bewildering amount of relatively unstructured biological diversity, unmoored from essential bifurcation points (such as changes leading to successful radiations).

As a final point here, we also stress that our comparison to geographical maps helps to illuminate the question of taxonomic equivalences. The states of California, Henan, or Uttar Pradesh do not reach country level while Luxemburg or the Maldives do, although in terms of area, economic output, and number of inhabitants this makes no sense. However, due to a combination of historical accidents of a political and governmental nature, as well as human conventions, this is the present situation. The essential point here is that some degree of absence of equivalence is implicitly understood and does not interfere with a proper use of taxonomy. This also implies that questions such as 'Is the taxon Vertebrata taxonomically equivalent to the taxon Proteobacteria (e.g. at phylum level)?' are misdirected.

It would appear that the practice of only rarely updating major groups, i.e. only when substantive progress in the field mandates such updates, can avoid most of the issue of a prohibitively high level of instability in the naming of groups. This approach would likely result in very infrequent, but robust and well-supported, changes in the names of groups with a named taxonomic rank, thus making it unlikely that future developments would necessitate further changes. The grouping phylum Chordata/subphylum Vertebrata, introduced and developed during the nineteenth century, was based on extensive supporting data, and remains valid and valuable up to today (Nielsen, 2012). It is based on five shared primary anatomical characteristics (synapomorphies) and supported by molecular data (e.g. analysis of rRNA, highly conserved protein genes and genomic synteny). A correction arose as a result of, amongst others, the discovery of organisms with notochords instead of vertebrate spines, which was addressed by the change from phylum Vertebrata to phylum Chordata/subphylum Vertebrata [however, we note that this 'downgrading' of the phylum Vertebrata is still being debated (Irie, Satoh & Kuratani, 2018)].

Current complications in the taxonomy of the group of organisms colloquially referred to as Protista, do not seem to warrant the elimination of the Phylum level, in light of its flexible nature (with use of prefixes such as super-, sub-, and infra-), as exemplified by the Vertebrata taxon. The inherent subjective aspects of the choices of organisms as belonging to a specific phylum can be achieved *via* careful consideration by the scientific community to arrive at agreed-upon groups with named taxonomic rank that are of practical and conceptual value. Instead of accepting a nameless ranked systematics, we argue that modernization of Linnaean systematics based on well-established new insights is the way forward. We will set out the principal elements of such a modernization from Section VII onwards. For biologists, the 10-rank system we propose below will provide a much-needed, recognizable map of the living world. When biologists debate certain specific areas of that living world map in specialized technical literature, they can of course depart from this coarse-grained map using an expert level of nameless ranked systematics, if required.

(2) Challenge 2: eukaryogenesis and the three domains of cellular life

The second challenge stems from a curious and important fact: Eucarya is a most unusual taxon, in that it represents the result of a *merger* of an archaeon and a bacterium. Herein we use the generally accepted term 'eukaryote', unless we refer to the group in a strict taxonomic sense (Eucarya) to honour priority (Woese *et al.*, 1990). When we consider the tree of life and focus on the eukaryotic branch, we encounter a highly uncommon situation: two entirely separate major taxonomic branches united to form a new branch of organisms, identifiable by a unique set of characteristics. The published work on this symbiogenic (Martin & Muller, 1998; Doolittle, 1998) merger (Speijer, 2015; Lane & Martin, 2010; Novoa *et al.*, 2012; van der Gulik *et al.*, 2017) shows that it should not be viewed as a form of LGT on a more massive scale, since the integration of two living organisms poses completely different challenges when compared to integrating gene products on their own. A range of considerations indicate that eukaryotes combined biochemical and cellular features from Bacteria and Archaea, and achieved important innovations in these features, including aspects of DNA replication and transcription, ribosome and genome composition, organelle structures, lipid biochemistry, transfer RNA (tRNA) anticodon modifications, electron transfer chains, cytoskeletal proteins, and histones (Barry & Bell, 2006; Fouqueau *et al.*, 2018; Novoa *et al.*, 2012; Speijer, 2017; Speijer *et al.*, 2020; van der Sluis *et al.*, 2015; Gould, 2018; Brunk & Martin, 2019). A schematic overview, stressing the hybrid and biochemically innovative character of eukaryotes due to a merger of archaeal and bacterial prokaryotes is provided in Fig. 1. However, a merger of two lineages resulting in great molecular and evolutionary innovation appears to represent an insurmountable challenge to a strictly cladistic approach to taxonomy. We previously defended the position that the Eukaryotes represent a merging of cells from the two primary domains, representing a clearly distinct third one: the three-domain system thus remains intact and essential to biology (van der Gulik *et al.*, 2017).

Another way of looking at this conundrum is that most researchers have tended to treat mitochondria as if they were still alpha-proteobacteria. However, this approach results in a taxonomic paradox. Mitochondria of different eukaryotic species have evolved to be quite different, and when treated as proteobacteria, logic dictates that mitochondria of different eukaryote species should be described as a plethora of new species of proteobacteria. But the conception of such a bacterial tree mirroring the host tree is likely ill-advised: the evolution of mitochondrion and cytoplasm is fully integrated. A more coherent view appears to be that eukaryogenesis gave rise to a fundamentally new type of cell containing two kinds of ribosomes (mitoribosomes and cytoplasmic ribosomes), and both types should be viewed as eukaryotic (i.e. not archaeal or bacterial) ribosomes. Both diverged far away from the prokaryotic types they started out as. The biogenesis, larger size and increased complexity of cytoplasmic ribosomes in eukaryotes has been extensively studied (Wilson & Doudna Cate, 2012; Baßler & Hurt, 2019). Mitoribosomes have undergone similarly substantial modifications compared to the bacterial ribosome. Notably, chloroplast ribosomes [ancestral cyanobacteria arriving after the last eukaryotic common ancestor (LECA) had already evolved] remained much more 'bacterial' in structure, without the destabilizing rRNA mutations (van der Sluis *et al.*, 2015) and with only a few so-called supernumerary subunits (Smits *et al.*, 2007) that characterize mitoribosomes (Yamaguchi & Subramanian, 2000; Yamaguchi, von Knoblauch & Subramanian, 2000). Recently, another striking example of the unique trajectory of mitoribosomes was found in the green alga *Chlamydomonas reinhardtii*, where the mitochondrial rRNA component is assembled from 13 non-contiguous encoded rRNA fragments. Single-particle cryo-electron microscopy has revealed additional proteins in this mitoribosome that are necessary for stable assembly (Waltz *et al.*, 2021). Thus, mitoribosomes exquisitely illustrate the many fundamental mutual adaptations during this transition (the merger giving rise to LECA), as well as later more individual variations [for further details, see van der Sluis *et al.* (2015) and Speijer *et al.* (2020)].

This remarkable aspect of the tree of life, due to the singularity of eukaryogenesis, is, in our opinion, best reflected by having *three* cellular taxa: Archaea, Bacteria and Eucarya. As mentioned above, we previously argued that biology involves three different types of cells: the archaeal cell, the bacterial cell, and the eukaryotic cell. This is best recognized by describing each of them as a taxon, with the rank of domain. These domains represent taxa above the (currently) highest Linnaean levels (but see Section VIII). Eukaryogenesis has surprising cladistic implications (see the next paragraph) for the 'primary domains' Archaea and Bacteria (which can conveniently be referred to as prokaryotes, to contrast with the 'secondary domain' of the eukaryotes; Eucarya). The 'secondary' character is reflected in their distinctive molecular characteristics (see also Fig. 1).

This position is an important, but necessary, departure from the position of Carl Woese. He proposed that all three types of cells arose independently from a primordial consortium without cellular and genomic identity. In his body of published work, the three domains are pure and separate taxa. This view has become increasingly untenable in light of the accumulating evidence for a eukaryotic origin starting with merging archaea and bacteria approximately 2 billion years ago. The maintenance of a three-domain taxonomy is an important, but unavoidable, departure from cladistics. Of note, the acceptance of a Eukaryotic domain leads to problems regarding the description of the other domains as monophyletic: the domains archaea and bacteria become paraphyletic, as the eukaryotes are excluded. Since the evolutionary origin of the eukaryotes is a merger of two lineages, it is a taxon that inescapably leads to problems with the classical cladistic approach. In justification of this departure from cladistics in the description of three domains, we invoke the key consideration that the Natural System should accurately reflect both the phylogenetic relationships between organisms and their evolutionary origin. Thus, we propose to retain the three-domain structure introduced by Woese *et al.* (1990) even in the light of recent discoveries concerning Asgardarchaeota as the archaeal component in eukaryogenesis. The retention of the three-domain structure for cellular life is the *first* deviation from strict cladistic taxonomy we propose here.

(3) Challenge 3: a tree of life or a web of life?

The aspect of merging of two organisms during endosymbiosis in general, and more specifically during eukaryogenesis, brings us to a final point of contention that does not involve merging at a cellular level, but involves genome fragments: the phenomenon of LGT. Its rampant, extensively described, presence (especially well documented in prokaryotes and profuse when viruses are involved) has been argued to make the whole Linnaean system unviable. As evidence was uncovered for massive LGT, particularly in prokaryotes, an argument was formulated that this process indeed abolishes the classical tree phylogenetic structure for describing biological diversity, to be replaced by a web of life (Doolittle, 1999; Doolittle & Bapteste, 2007; Olendzenski & Gogarten, 2009). Now that genomics has developed into a mature field, this issue can be evaluated more thoroughly, and a few important findings have emerged that should allay fears regarding its threat to the Linnaean system. Gene transfer has been extensively documented, both between different prokaryotes and between different eukaryotic organisms (Van Etten & Bhattacharya, 2020). In addition, prokaryote to eukaryote transfer is more common than previously thought (Matriano, Alegado & Conaco, 2021), while some instances of combinations of eukaryotic donors and prokaryotic acceptors have also been described (Koonin, Makarova & Aravind, 2001). There have been estimations that only one-third of the gene content might be linearly inherited in prokaryotes (Puigbò, Wolf & Koonin, 2010), but certain central constituents (such as rRNAs) are known to be rarely, if ever, replaced by gene transfer. Thus, closely related prokaryotic species can have, overall, quite different gene contents. But prokaryotes also contain a collection of ubiquitous and highly similar genes (representing their core genomes), different from the large set of flexible, more dispensable genes (the auxiliary genes). Genomics in prokaryotes is being performed at an ever-increasing rate and shows that reconstructing the archaeal and bacterial branches of the tree of life is perfectly feasible. For further details, see e.g. Vernikos *et al.* (2015), Bobay (2020) and Hugenholtz *et al.* (2021). In a recent analysis for bacteria, the last bacterial common ancestor gives rise to a fundamental split occurring between Gracilicutes (containing familiar taxa such as Proteobacteria and Bacteroidota) and Terrabacteria (including e.g. Firmicutes and Cyanobacteria). In this analysis average gene transmission is estimated to be two-thirds vertical, and only one-third horizontal (Coleman *et al.*, 2021). Such analyses of the deepest branches of the prokaryotic domains are complicated specialist undertakings, in which the selection of a well-chosen and well-curated set of ancient vertically evolving genes is of central importance (Moody *et al.*, 2022), together with carefully selected methods for phylogenetic tree reconstruction based on sequence alignments of these genes.

Finally, a fundamental aspect to be considered is that, as far as we know, ever since the emergence of the first cells on Earth, all subsequent cellular evolution proceeded by cell divisions and mutations (with the notable exception of eukaryogenesis, where two cells lines merged): *omnis cellula e cellula* (Virchow, 1858). The present challenge is to map this (several billion year long) uninterrupted chain of divisions and diversifications in a taxonomic system. Horizontal gene flow can most definitely make the task of correctly reconstructing the tree of life more difficult. However, the underlying cell tree of life remains unchanged, with gene transfer being one of the types of mutations that contribute to the process of cellular evolution. Of note, later instances of secondary endosymbiosis also do not fundamentally challenge this picture.

VI. MODERNIZATION OF THE LINNAEAN SYSTEM IS NOT WITHOUT PRECEDENT

The rank of phylum was never used by Linnaeus. In the kingdom of animals, Linnaeus recognized several classes, such as mammals, insects, fishes and birds. That mammals, fishes and birds share the characteristic of having vertebrae was a seminal discovery made in the surge of biological research occurring, in part, as a result of the introduction of the Linnaean system. This system provided scientists with a framework to order the living world, and research could develop further aided by its introduction. The discovery of the existence of vertebrates, such as mammals, fishes and birds, and invertebrates, such as insects and 'worms' (Lamarck, 1794), was formalized by introducing a new rank in the system, the phylum (Haeckel, 1866), and recognizing Vertebrata and Invertebrata as new taxa in the Linnaean system. Thus, the practice of introducing novel named taxa within the Linnaean system based on extensive evidence has a long and productive history.

The next development came with the realization that the Invertebrata was a highly heterogeneous group. Instead of the phylum Invertebrata, a series of new phyla came into focus. Insects became a class of the phylum Arthropoda. Spiders and crustaceans were recognized as arthropod classes in their own right. Mollusca became a new phylum, with bivalves, gastropods and cephalopods becoming new classes. Many more invertebrate phyla (e.g. representing fundamentally different 'worms' such as Annelida, Platyhelminthes, and Nematoda, to name but a few) followed. Of course, the use of the terminology 'fundamentally different' implies choices and interpretations to represent life's complexity. These choices are based on careful consideration of the phylogenetic trees of the organisms involved, their structural and functional properties, and consideration of previously established groups at a similar taxonomic level.

Thus, any system purporting to provide an overview of life necessarily is a simplification, in the following sense. Since Darwin, we have understood that the multitude of living animals (or Metazoa, as we now call them) reflects a history of diversification, of numerous forks in a tree of life. However, when every fork receives equal attention, the number of ranks quickly becomes so huge as to be utterly impractical, and problems in terms of different numbers of branching events, as well as reconstructing their precise temporal sequence in the lineage under study, often arise. As a result, in the first approximation, which taxa are more closely related (again using the examples of molluscs: cephalopods and gastropods *versus* bivalves, or cephalopods and bivalves *versus* gastropods, or gastropods and bivalves *versus* cephalopods) can be temporarily ignored to achieve a valuable insight. They are all recognized as being part of the phylum Mollusca, and the reconstruction of the actual evolutionary diversification sequence within the phylum remains an issue for specialists (for the case of molluscs, see e.g. Wanninger & Wollesen, 2019). Analogous considerations (e.g. described in Section IX) bear directly on the proposal outlined here.

VII. HISTORY REPEATS ITSELF WITH THE DISORDER AMONG PROTISTS: INTRODUCING EMPIRES

Interestingly, the upheaval experienced during the development of the taxonomy of invertebrate metazoans finds a modern parallel in the current taxonomic instability with respect to the 'protists' that we alluded to in Section III. Adl *et al*. (2007) considered strong molecular and cytological evidence that the kingdom of animals and the kingdom of fungi belong to a taxon of higher order within the eukaryotes. In an important example, one distinguishing characteristic cytological feature of this group is a single posterior flagellum. But instead of introducing a new rank for this new taxon of great parochial importance (e.g. the realization that *Saccharomyces cerevisiae* is in fact clearly more closely related to *Homo sapiens* than *Arabidopsis thaliana* has medical implications), they opt to drop all rank names. We contend that by doing so, they did not make a scientifically beneficial choice. We think the obvious solution for the problem of having the kingdom of animals and the kingdom of fungi being part of the opisthokonts (Cavalier-Smith, 1987), is to introduce a new named rank. This rank would be inserted between the Linnaean rank of kingdom and the Woesian rank of domain. The introduction of the Woesian rank of (three) domain(s) releases the rank empire from the previous two-empire system championed, amongst others, by Mayr (1998). We here propose the empire rank for Opisthokonta.

A second eukaryote taxon which, in our estimation, deserves empire rank is Alveolata. Microscopical and cytological research indicates that three previously recognized groups [Apicomplexa (e.g. *Plasmodium* and *Toxoplasma*), Ciliophora (also known as ciliates), and Dinozoa (also known as dinoflagellates)] together belong to a common group that is distinct from other unicellular eukaryotes (Cavalier-Smith, 1991). In the Alveolata a distinguishing characteristic cytological property is the presence of cortical alveoli that appear as flattened vesicles (sacs) just under the membrane. One way to incorporate these recent insights is to recognize Apicomplexa, Ciliophora, and Dinozoa as separate kingdoms in the empire Alveolata. This view of a group, such as the dinoflagellates, constituting a whole kingdom in itself, may be initially bewildering for biologists used to such groups as being relatively low-level taxa – but it illustrates the kind of change in mindset we need to achieve to modernize the Linnaean description of the remarkably diverse unicellular eukaryotes. We will not discuss the long history of taxonomic debate regarding the Alveolata clade (see e.g. Cavalier-Smith, 2018), but simply state that the problem of the rank of the three long-recognized groups within it can be dealt with in a formal taxonomic manner, using the revised Linnaean system that we propose.

One important feature to assess if the hierarchical taxonomy we propose has objective merit, is the obvious fact that higher-level taxa, overall, need to incorporate older bifurcations. This simple, but important, concept is illustrated in Fig. 2, linking cellular evolution to Linnaean nomenclature. For instance, Bayesian estimates indicate that the last alveolate common ancestor branched off more than ~850 million years ago, while its opisthokont counterpart did so approximately a billion years ago (Berney & Pawlowski, 2006). Returning to our geographical map metaphor: identifying continents, instead of just listing the countries we find on them, allows us to look back (much) further in time. As a side note: Fig. 2, in using biological timescales, illustrates some important facts. For a very long period of time there were only Prokaryotes. Their two domains sprang into existence early on, while the eukaryotes came much later. Considerably later again, macroscopic multicellular organisms arose. Plants and animals are thus fairly recent additions to the tree of life, which already had an enormously rich and complex evolutionary history. We should stress that we are discussing relative timing in the broadest sense here, and do not propose in any way that one might time evolution by looking at rank levels.

In light of the abundant new data, numerous kingdoms of unicellular eukaryotes can probably be recognized, and when they can be joined into higher taxa based on cytological and genetic characteristics, the empires representing all of eukaryotic diversity will be delineated. Just as a flurry of invertebrate phyla arose during the 19th and 20th centuries, now is the time to bring forth a similar flurry of (mostly) unicellular taxa of higher order. We frequently encounter instability in taxonomic groupings for eukaryotic groupings of the highest level. For example, Excavata, Unikonta and Chromalveolata remain heavily debated. Given this phenomenon, we conclude that the time has not yet come to formalize combinations of eukaryote empires to taxa of even higher level. Thus, this is not part of our current proposal. Molecular phylogeny at many of these levels of the eukaryotes, especially the highest ones, is still progressing. However, it is time to start formalizing the kingdoms and empires of unicellular eukaryotes.

VIII. THE STRUCTURE AT THE HIGHEST LEVEL: THE TWO WORLDS AT THE TOP

Ongoing research (Koonin & Dolja, 2013; Krupovic, Dolja & Koonin, 2019, 2020) has continued to reveal the remarkable diversity (Schulz *et al.*, 2017), and biological importance of viruses and their interactions with cellular organisms. The world of viruses has been coming increasingly into focus during the last 130 years. They have also become visible to wider society as a result of viral diseases such as polio, AIDS and the Covid-19 pandemic. These biological entities are very different from pathogens such as bacteria or amoebae, in a broad sense because they are not cellular, do not reproduce by cell division, and are not capable of synthesizing protein in the absence of a cellular host entity. However, they represent a major fraction of genomic diversity on Earth and should be part of a Natural System describing life on Earth (Harris & Hill, 2021). As others (especially Eugene Koonin) have argued, ignoring them taxonomically seems untenable. As abundant entities in the biological world, they deserve a place in our Linnaean system. However, viruses are still not a formal part of the Natural System.

Table 2. Proposed ranks in the updated Natural System, using the Tibetan sand fox as an example.

Taxonomic rank	Taxon	Other taxa of this rank
World[a]	Cells	Viruses
Domain[a]	Eucarya	Archaea, Bacteria
Empire	Opisthokonta	Alveolata, others to be determined
Kingdom	Metazoa	Plants, Fungi, others to be determined
Phylum	Chordata[b]	Many, e.g. Mollusca
Class	Mammalia	Many, e.g. Aves
Order	Carnivora	Many, e.g. Rodentia
Family	Canidae	Many, e.g. Felidae
Genus	*Vulpes*	Many, e.g. *Canis*
Species	*ferrilata*	Many, e.g. *lagopus*

[a] These two highest ranks contain groups (the Eucarya and the Viruses) that are by necessity not monophyletic, making the proposed Natural System a mixture of cladistic and non-cladistic components, as explained in more detail in Sections V.2 and VIII.
[b] Subphylum: Vertebrata.

Viruses do not have an equivalent of *omnis cellula e cellula*, and are entirely distinct from cellular life. Therefore, in order to include viruses coherently into the Natural System, we propose a rank above domain: next to the world of cells, there is a world of viruses. Since cells and viruses do not share a common ancestor in any usual sense of the word, this proposition forms the second instance where the hybrid system proposed here deviates from strict cladistic rules. The final addition gives us all the proposed ranks in the updated Natural System, as illustrated in Table 2, using the Tibetan sand fox *Vulpes ferrilata* as an example. An overview of the proposed modernizations of the Natural System is illustrated in Fig. 3.

Why do the viruses deserve their own world next to the cellular world? A number of foundational properties distinguish between the cellular and viral worlds. All organisms in the three domains are cellular organisms. They multiply by cell division and form a membrane-enclosed compartment that produces ATP, either by using a membrane gradient or substrate-level phosphorylation, or both. Cells operate according to the Central Dogma of Molecular Biology: they have DNA as an information database, transcribe this information in an RNA format, and make proteins on their own ribosomes, translating the information present in the messenger RNA (mRNA) part of their transcriptome. Viruses also contain information in a nucleic acid genome, but they do not divide and can only propagate in a host cellular compartment capable of producing ATP and synthesising proteins. They are not like cells at the most fundamental level. However, they are not just molecules either. They carry genetic information and evolve. In fact, because they have to reproduce by infecting host cellular organisms, deregulating and often killing them, their rapid massive production and ensuing parasite–host arms races cause them to evolve very quickly. This is due to high levels of mutation and/or appropriation of cellular genomic information, leading to a steady flow of new genetic combinations in the virosphere (Harris & Hill, 2021), for instance in the form of regular gene exchanges between viruses (Gorbalenya & Lauber, 2017). Thus, viruses evolve, and because they evolve, they dissociate into phylogenetic groups. However, their origins are debated, and their evolution is characterized by processes that make analysis according to cladistic principles highly challenging. Like cells, they have probably existed for billions of years (Krupovic *et al.*, 2020), and interact continuously with the cellular world in biologically consequential ways. In addition to attacking all cellular organisms, from prokaryotes and protists to plants and animals, viruses have had a major influence on cellular evolution, apart from constituting an important selection force as cellular parasites. They have a crucial role in LGT, which represents a fundamental and innovative mechanism during biological evolution (Kunin & Ouzounis, 2003; Koonin, 2016). All these interactions require their proper inclusion into our new taxonomic structure, sidestepping contentious issues such as whether they can only have evolved after the emergence of cellular life, or whether they can even be considered as living entities at all, and should *thus* be excluded (Moreira & López-García, 2009). The latter issue is addressed here by excluding viruses from the world of cells.

We mentioned that a cladistic analysis of the viral world would be highly challenging (or even inherently impossible). However, a hierarchical, all-inclusive taxonomy of the virus world has recently been proposed (Koonin *et al.*, 2020). Some authors believe that sequencing of viral genomes allows viral phylogenies to be built in the same manner as cellular phylogenies, even though viral genomes, as mentioned, have much higher mutation and gene exchange rates, as found in an analysis of bacteriophages (Hatfull & Hendrix, 2011). However, just as prokaryotic genomes, viral genomes can also be differentiated with regard to the stability of their genetic structures: structural and replication gene clusters co-evolve as single evolutionary units much more often than less-essential parts of viral genomes. The latter are swapped more frequently, giving rise to differential gene mobility (Hatfull & Hendrix, 2011). Whether structural and/or replication clusters are indeed mostly vertically inherited (allowing them to play pivotal roles in viral tree reconstruction, emulating rRNA genes in the reconstruction of cellular gene trees) or move more regularly between viral species, remains to be seen. Indeed, in contrast to the cellular world, viruses do not have any genes that are common to all of them, meaning that a single viral phylogenetic tree cannot be produced. Recent evidence also suggests viruses to be polyphyletic in origin, following complex evolutionary scenarios, e.g. with different types of primordial replicons becoming viruses by recruiting host proteins for virion formation and new groups of viruses emerging all the time upon displacement of ancestral structural or even replication genes (Krupovic *et al.*, 2020, 2019). Still, many of the evolutionary issues of the virus world will be more amenable to analysis with ever-expanding sample analyses and the increasing speed of the metagenomics revolution of virus discovery. To provide one example: a new petabase-scale sequence alignment tool has allowed a ~10-fold increase in identified RNA virus sequences (Edgar *et al.*, 2022). As this exciting research on the fundamental properties and evolution of viruses proceeds, it is urgent that they have a place in the Natural System.

An effective way to deal with the inclusion of viruses was pointed out by Koonin (2011): by introducing a rank above domain. Because empire is used herein for the rank directly above kingdom (see Section VII), we do not follow Koonin's use of the term 'empire' for this level (Koonin, 2011), but instead propose the description 'world' for this rank. Thus, there is a world of cells, and there is a world of viruses. When Woese *et al.* (1990) introduced the rank 'domain', they also provided the Latin word *regio*, in order to make their contribution as formal as possible. We here do the same, and formally suggest the word *mundus* for the world rank as well as *imperium* for the rank empire.

In conclusion, to illustrate our proposal for the modernization of the long-cherished Linnaean system, in Table 2 we use the example of the Tibetan sand fox. This species belongs to the world of Cells, and to the domain of Eucarya, empire Opisthokonta, kingdom Metazoa, phylum Chordata (subphylum Vertebrata), class Mammalia, order Carnivora, family Canidae, genus *Vulpes*, and species *ferrilata*. Thus, the proposed modernization of the Natural System combines a practical structure and order for the myriad living entities, while at the same time reflecting evolutionary descent in a proper fashion.

IX. DELINEATION AND NAMING OF HIGH-LEVEL PROKARYOTIC RANKS

(1) Background

In the preceding text we describe specific taxonomic proposals regarding the worlds of cells and viruses based on converging and solid evidence reported in the literature. We now return to taxonomy at the highest levels of the bacterial and archaeal domains of life, which both are under active study.

While a range of exciting and revolutionary results are appearing in the current literature (see Sections IX.2 and IX.3), many key questions and proposals still await answers and confirmation. By discussing these recent results and the novel challenges emerging from them, we stress that our ideas regarding high-level prokaryotic taxonomy remain tentative and separate from the proposals we made above for the restructuring and modernization of the Linnaean system as a whole. The reader can disagree with our position here but still be in favour of our overall proposal.

As a background to these considerations, we emphasize both the challenges of ensuring, and the importance of determining, the monophyly of groups of organisms at the superphylum, kingdom and possible empire levels in the prokaryotic domains. At every rank, groups derive from a common ancestor, and phylogeny in both domains should reflect the latest phylogenomic insights. Although applying this principle might be difficult in practice, the principle itself is not under debate. However, when it comes to *naming* the different higher-level taxa, opinion can be divided. This issue is illustrated by recent developments in bacterial taxonomy (see e.g. Oren & Garrity, 2021). In an important step forward, the ICSP officially included the rank of phylum in the International Code of Nomenclature of Prokaryotes (ICNP) (Oren *et al*., 2015, 2021). As a result, 42 phyla were renamed using the ending -ota after a stem taken from a member genus (preferentially the one that was first officially described). This approach to reducing the number of names needed to describe taxa using a standardized approach is comparable to an earlier development in botanical taxonomy. The use of fixed rules of nomenclature, and of favouring naming after the first genus described (thus honouring priority), which often is the best known as well, offers advantages in the form of clarity and standardization. But there are also drawbacks to be considered. Apart from consistent rules, taxonomy also has to take stability and considerations of priority into account. We encountered the issue of stability (in the context of eukaryotic microorganisms) already in Section VII. We concluded that removing names with a long and useful history (as well as their associated claims on priority) can be counterproductive. Thus one question is: how to balance these aspects in the naming of higher prokaryotic taxa? We propose a solution by using such important names for higher ranks. We will begin with our proposals for bacteria.

(2) Bacteria

We propose that the names Proteobacteria, Firmicutes and Cyanobacteria are the appropriate names for bacterial kingdoms. Based on 16 S rRNA studies, Woese (1987) introduced a phylum Purple Bacteria. Subsequently, this taxon received a formal description with the name Proteobacteria by Stackebrandt, Murray & Trüper (1988). This name has been used extensively and productively in the literature. We contend that removal of this name would violate the code of conduct for using Linnaean taxonomy. The Proteobacteria is a very diverse group, and its subgroups of delta- and epsilon-proteobacteria are now considered to be phyla in their own right (Campylobacterota and Myxococcota). The new name introduced for the taxon consisting of alpha-, beta- and gamma-proteobacteria is Pseudomonadota. Instead of considering the 'old' Proteobacteria as a polyphyletic taxon, we argue that it is better to take the view that Aquificota, a group of bacterial inhabitants of extreme environments (Huber *et al*., 1992), were mistakenly excluded from the taxon Proteobacteria. In our opinion Proteobacteria should be recognized as a bacterial kingdom containing all Myxococcota, Campylobacterota, Aquificota, and Pseudomonadota (plus any other bacteria of a monophyletic taxon containing these groups). This would do justice to both stability and priority. There is also an element of common sense in our approach: to base the name of the kingdom on the genus *Pseudomonas* would focus too much on this single genus, and divert attention from the enormous breadth of this taxon.

Applying such considerations would likely lead to the introduction of other bacterial kingdoms, such as a kingdom Cyanobacteria, making it likely that many of the newly named bacterial phyla will be properly assigned to a relatively small number of bacterial kingdoms. The names of these kingdoms would then reflect the properties of the organisms in each kingdom in a biologically useful manner while also respecting the priority of the researchers who originally described these taxa. In this proposal, when novel organisms [or metagenome-assembled genomes (MAGs)] are discovered, and a monophyletic group emerges that contains these together with a bacterial kingdom, stability can be maintained by amending the description of that kingdom to include this newly discovered lineage. The alternative, which we consider more disruptive and less desirable, would be to demote the kingdom in question to a superphylum and to introduce a novel name for the taxonomically expanded kingdom. A similar situation led to the demotion of the first described phylum: the vertebrates, which we described in Section V.1. Based on the discovery of invertebrates with a notochord, which were recognized as early branches of a monophyletic group also containing the vertebrates, phylum Vertebrata was replaced by phylum Chordata. This issue remains a point of contention in zoology (Irie *et al*., 2018), and the approach outlined here can avoid such issues. We are convinced that an approach of naming higher taxa after the genus first described should *not* be followed for taxa higher than phyla. Should this advice not be heeded, stability and vitality of microbiology could suffer.

When we compare the trees depicting prokaryotic diversity in recently published articles by Aouad *et al*. (2022) and Moody *et al*. (2022), and the tree of bacterial diversity from Coleman *et al*. (2021), we see that a monophyletic taxon containing the Proteobacteria (in the kingdom sense), the Bacteroidetes, the Chlorobi, the Chlamydiae, the Planctomycetes and the Spirochetes (all in the sense of Woese, 1987) is consistently present. This taxon with the name Gracilicutes therefore is clearly supported as a bacterial empire. The taxon with the name Terrabacteria, however, is not supported by all three studies. If we follow the tree in fig. 4 of Moody *et al.* (2022), Terrabacteria is paraphyletic when Gracilicutes is not included. Describing (1) the Fusobacteria, (2) the Thermotogae, (3) the *Deinococcus–Thermus* group, (4) the monophyletic taxon containing Cyanobacteria, Melainabacteria, Sericytochromatia and Marinamargulisbacteria, and (5) the monophyletic taxon containing 'candidate phyla radiation' (CPR), Chloroflexi, Actinobacteria and Firmicutes, each as an empire provides a structure which is stable independently of the outcome of the issue of probable non-monophyly of the Terrabacteria. Of note, the above names are taken from fig. 4 of Moody *et al.* (2022), and are open to possible further refinement. The approach of introducing these five empires next to the Gracilicutes empire is, in fact, the same approach we discussed earlier in this review with respect to the Bivalvia, Gastropoda and Cephalopoda forming parts of the Mollusca. This issue of probable non-monophyly of the Terrabacteria illustrates why we are much more doubtful about our ideas regarding high-level prokaryotic taxonomy compared to our earlier proposals in this review. However, the demonstration of the monophyly of Gracilicutes has been shown to be robust (Aouad *et al.*, 2022; Moody *et al.*, 2022; Coleman *et al.*, 2021).

(3) Archaea

Turning to the Archaea, when we compare the branching order in the relevant figures of Aouad *et al.* (2022) and Moody *et al.* (2022), a monophyletic taxon joining the Asgard superphylum with the TACK [Thaumarchaeota (now renamed Nitrososphaerota) plus Aigarchaeota plus Crenarchaeota (now renamed Thermoproteota) plus Korarchaeota] superphylum is consistently found. We propose to maintain the currently widely used superphylum rank (i.e. the accessory rank above phylum, below infrakingdom) for Asgard and for TACK, and to introduce a kingdom rank for the monophyletic taxon containing both. It is instructive to see how the TACK superphylum illustrates the current problems with name stability within prokaryotic microbiology. We argue here that the TACK superphylum has already received a formal name: Proteoarchaeota (Petitjean *et al.*, 2014). But, as in the case of Proteobacteria, some taxonomists in prokaryote biology retroactively consider this name to be informal. Woese *et al.* (1990) originally intended the Crenarchaeota to be a taxon of kingdom level. Thus, honouring priority, with the Crenarchaeota phylum having given way to Thermoproteota, we suggest the proper name for the archaeal kingdom uniting the superphylum Asgardarchaea and the superphylum Proteoarchaea (according to the recent rules the suffix -ota is used for phyla, *not* superphyla) is Crenarchaea.

Again comparing Aouad *et al.* (2022) and Moody *et al.* (2022), we find agreement for joining the Diaforarchaea and the Methanotecta into one monophyletic taxon of very high rank. We propose considering this taxon as a second kingdom in the Archaea. With regard to the position of the Methanomada, however, these studies disagree. In Aouad *et al.* (2022), the Methanomada form a monophyletic group with Thermococci and the group we suggested above as kingdom Crenarchaea. However, in Moody *et al.* (2022), the Methanomada, Methanotecta and Diaforarchaea form a monophyletic group. Traditionally, Methanomada, Methanotecta, Diaforarchaea and Thermococci were considered constituents of the kingdom Euryarchaeota (Woese *et al.*, 1990). To provide stability we suggest the elevation of both Methanomada and Thermococci to kingdom status, and to leave the question of the exact branching of the four groups to future investigators. All four kingdoms, however, belong to an empire of classical archaea, as opposed to the empire of DPANN archaea. However, this last group is considered an artefact by Petitjean *et al.* (2014). This last controversy regarding the DPANN taxon is another reminder of the state of flux of higher-level prokaryotic taxonomy, and explains our doubts and restraint in this section of our review.

X. CONCLUDING REMARKS AND PRACTICAL CONSIDERATIONS

In Table 1 we listed some of the most salient historic developments in taxonomy from the introduction of the Linnaean system to the present. One emerging trend seen in this historic overview is an overall shift from a focus on macroscopic diversity (large eukaryotes such as animals and plants) to one on microscopic diversity, found both within and outside the eukaryotes. These developments necessitate a revision of Linnaean taxonomy that is broad in scope.

A number of decisions in obtaining a taxonomic system of life appear at least in part arbitrary. So how do we compare which groups in the Eukaryotes or Bacteria have equal taxonomic status, and how do we circumscribe a taxonomic rank (the difficulty of which is likely to vary in different cases)? It appears to us that these types of issues are unavoidable when describing many aspects of the natural world. With the 10-rank system of species, genus, family, order, class, phylum, kingdom, empire, domain and world, it will be no different. Some researchers studying protists have stimulated this discussion by arguing that '… the recognition of monophyletic groups based on modern phylogenetic concepts forces us to do things that are awkward with the traditional codes. For example, we would be forced to place classes within classes, and kingdoms within kingdoms, or invent many new ranks.' (Adl *et al.*, 2007, p. 686). Rather than inventing such a multitude of ranks, these researchers opt out of the classic Linnaean system. But by basing their taxonomic procedures on considerations like these, they run the risk of throwing away Linnaeus's *Systema Naturae* that has served the biological community extremely well, and, as we have argued, is endowed with adequate flexibility to integrate current biological insights successfully. We consider that doing away with that system would be neither prudent nor acceptable. The 'awkwardness' referred to in the quote above, is solved by raising the protistan taxa to their rightful kingdom level, and introducing not many, but only a very few, new formally named ranks in the Natural System: empire, domain and world. These three additional named ranks provide important tools that appear quite capable of capturing and organizing current knowledge of the tree of life. Some might argue that three new named ranks constitute too much change. However, multiple authors have already published specific proposals for each of these ranks, based on large bodies of published data. In addition, in our estimation three new named ranks is the minimum needed to accommodate properly the wealth of novel information that has been accumulating. The introduction of these new named ranks also appears justified based on the greatly increased time window of evolutionary change (see Fig. 2) when considering plants and animals (approximately 0.8 billion years) *versus* all genome-based evolving entities (approximately 4 billion years). The way forward is then to agree upon reasonable decisions that match phylogenetic information and capture the reality of biological history. Thus, we acknowledge the presence of one instance of a fused structure, representing eukaryogenesis, as well as LGT and a separate world of viruses. All of this is perfectly compatible with the proposed 10-rank Natural System for the tree of life. We propose that this system represents the optimal biological way of integrating and structuring our knowledge of all of evolution.

The difficulties of being 'forced to place classes within classes, and kingdoms within kingdoms, or invent many new ranks' impel us to address these challenges in the manner that best captures the complexity of biological diversity. These considerations illustrate two important practical challenges for taxonomy that have resulted in proposals to abandon aspects of the Linnaean system. The first is the issue of arbitrariness in assigning a group of organisms to a specific named taxon rank such as phylum or kingdom. It appears that these difficulties can be kept within quite narrow bounds by using a taxonomic triangulation approach, as explained below.

In general, when considering related groups of organisms, unambiguous taxonomic descriptors both at the higher and lower ends can be identified. Thus, for example, when a novel species of (unicellular) eukaryotes is identified, the placement of such a species within the eukaryotic tree is to be determined. This placement is informed by established ranked taxa as anchor points. However, this approach can be challenging when the organism seems to represent a previously unknown deep branch in the phylogenetic tree (for example around the phylum level or kingdom level). A pragmatic approach can help resolve such issues. For example, consider the historic debate around whether sponges are animals which ended with their recognition as an early-diverging phylum (Porifera) in the animal kingdom. That kingdom is now known as Metazoa, partly as a result of the inclusion of this new phylum. Upon identifying a new 'deep' protist, different taxonomic outcomes could occur. Either, a previously existing high taxon level might be expanded to include the newly identified group. Another outcome might be that evidence accumulates that the newly identified group of unicellular eukaryotes exhibits considerable diversity and unique distinguishing features. As such evidence accumulates, at some point the introduction of a novel group at that taxon level becomes sufficiently strongly supported. In turn, this can have effects on still higher levels. Thus, the introduction and combination of clades has led to the group Opisthokonta at the ranked taxonomic level empire.

Here we approached the discussion of ranks from an extended, updated taxonomic perspective (the Natural System), which is of course linked to the Linnaean nomenclatural framework. Consequently, the changes we propose would require changes to multiple Codes of Nomenclature, including the International Code of Zoological Nomenclature, the International Code of Nomenclature for algae, fungi and plants (the Botanical Code), the International Code of Virus Classification and Nomenclature, and the ICNP. Such Code revisions are of course the responsibility of the respective scientific bodies. We can only strongly recommend that future amendments of these multiple Codes of Nomenclature are structured along the lines of the overall scheme we have described here.

We hope to have convinced the biological community that the Linnaean system can, and should, be updated for the 21st century, not because it fits the natural world perfectly (no classification system ever will), but because it shows itself to be highly useful and sufficiently adaptable in light of recent scientific developments and challenges.

XI. CONCLUSIONS

(1) Recent important (phylo)genomic discoveries reorganizing and extending biological diversity have not been integrated yet into a formal, coherent taxonomic system.
(2) Because of taxonomic challenges and conflicts, a number of proposals are being made to abandon key aspects of the Linnaean Natural System or restrict its application.
(3) Upon careful consideration of arguments against and in favour of these proposals, we conclude that an updated version of the Linnaean system is the optimal way forward.
(4) A relatively small number of amendments to the Linnaean Natural System that include: (*i*) the named rank of world (Latin alternative *mundis*) formally to include non-cellular entities (viruses), (*ii*) the named rank of empire (Latin alternative *imperium*) to accommodate the recently uncovered depth of diversity in (unicellular) eukaryotes, (*iii*) formal acceptance of the three-domain structure of cellular life (Archaea, Bacteria and Eucarya), is sufficient to retain an effective Linnaean Natural System, applicable to all biological entities.

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