RESEARCH ARTICLE

A Higher Level Classification of All Living Organisms

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Abstract

We present a consensus classification of life to embrace the more than 1.6 million species already provided by more than 3,000 taxonomists’ expert opinions in a unified and coherent, hierarchically ranked system known as the Catalogue of Life (CoL). The intent of this collaborative effort is to provide a hierarchical classification serving not only the needs of the CoL’s database providers but also the diverse public-domain user community, most of whom are familiar with the Linnaean conceptual system of ordering taxon relationships. This classification is neither phylogenetic nor evolutionary but instead represents a consensu view that accommodates taxonomic choices and practical compromises among diverse expert opinions, public usages, and conflicting evidence about the boundaries between taxa and the ranks of major taxa, including kingdoms. Certain key issues, some not fully resolved, are addressed in particular. Beyond its immediate use as a management tool for the CoL and ITIS (Integrated Taxonomic Information System), it is immediately valuable as a reference for taxonomic and biodiversity research, as a tool for societal communication, and as a classificatory “backbone” for biodiversity databases, museum collections, libraries, and textbooks. Such a modern comprehensive hierarchy has not previously existed at this level of specificity.

Introduction

Biological classification (taxonomy) aims to simplify and order the immense diversity of life into coherent units called taxa that have widely accepted names and whose members share important properties. It synthesizes information concerning a great variety of characters (e.g.,
morphological; molecular: genes, metagenome, and metabolome; etho-ecological). There is currently no consensus among the world’s taxonomists concerning which classification scheme to use for the overall hierarchy of life, in part because of the confusion resulting from Hennig’s \[1\] redefinition of previous terminology of classification, which has not been universally accepted; the separate goals of cladification and classification \[2\]; and conflicting or unresolved evidence for phylogenetic relationships. The continuing advances in the use of specialized analytical tools from many different fields and their resulting conclusions and assumptions require regular updates as advances in knowledge are made.

Biological classification can integrate diverse, character-based data in a phylogenetic framework, which allows a broad user community to utilize the disparate knowledge of shared biological properties of taxa. Phylogeny is, therefore, the basis for these biological classifications but there is still strong debate over their accounting for evolutionary divergence or information content other than the branching pattern \[3\]. Accordingly, classifications have often been labeled either phylogenetic or evolutionary, depending mainly upon whether or not they reject paraphyletic groups \[3, 4\].

While the type of classification to be used to support further exploration and analysis of any biological scenario may be important, it is not the subject of this paper. The proposed classification does not address detailed phylogenetic questions and, while hierarchical and reflective of phylogeny, is not itself a phylogenetic tree. The aim of this classification is to be a pragmatic means of managing the ever-increasing knowledge of the diversity of life, its relationships, characteristics, and properties. Indeed, the past two decades have witnessed an explosion in biodiversity research and informatics, emphasizing the need for a quality list of accepted scientific names of the more than 1.9 million described living species \[5\] and for greater consensus on how to classify them at higher taxonomic ranks. Since 2001, Species 2000 and the Integrated Taxonomic Information System (ITIS) have worked with their respective contributors to complete a comprehensive species list, called the Catalogue of Life (CoL). The CoL Annual Checklist (http://www.catalogueoflife.org/annual-checklist/2014/) already contains more than 1.6 million valid or accepted species names provided by more than 140 taxonomic databases involving more than 3,000 taxonomists \[6\]. More than 82% of the global species databases are provided at the rank of class or below (includes 1.3 million species), and more than 63% are provided at the rank of order or below (includes 1.0 million species). Owing to the heterogeneity in higher level classification among the contributed databases, the CoL managers sought a practical and coherent hierarchical classification that could serve as a framework for data integration. Here we explain the rationale behind the consensus higher level classification that we propose for CoL use.

Our goal, therefore, is to provide a hierarchical classification for the CoL and its contributors that (a) is ranked to encompass ordinal-level taxa to facilitate a seamless import of contributing databases; (b) serves the needs of the diverse public-domain user community, most of whom are familiar with the Linnaean conceptual system of ordering taxon relationships; and (c) is likely to be more or less stable for the next five years. Such a modern comprehensive hierarchy did not previously exist at this level of specificity. In this sense it summarizes overarching aspects of the tree of life, including both paraphyletic and monophyletic groups, both being important in facilitating meaningful communication among scientists and between the scientific community and society.

The most recent higher level classification to this level was published more than 30 years ago, before the advent of modern molecular analysis \[7\]. Beyond the immediate use for CoL, the hierarchy is valuable as a reference for taxonomic and biodiversity research, as a tool for societal communication, and as a stable classificatory "backbone" for biodiversity databases, museum collections, libraries, and textbooks, to name a few applications.
Approach

When Linnaeus introduced his novel “system of nature” in the mid-18th century, he recognized three kingdoms of nature: Regnum Vegetabile (plants), Regnum Animale (animals), and Regnum Lapideum (minerals) that has long since been abandoned. However, as is evident from the title of his work, he introduced lower level taxonomic categories (named class, order, genus, and species), each successively nested within higher ranked categories. Linnaeus’ system has proven to be robust for more than 250 years (see the comprehensive discussion and suggestions for dealing with potential conflicts in Vences et al. [8]). In modern-day classifications, the starting point for botanical names is Linnaeus’ Species Plantarum [9] and for zoological names it is the tenth edition of the Systema Naturae [10]. Since Linnaeus, the expansion of knowledge and the increase in the number of described species has required an expansion of the number of hierarchical levels (ranks) within the system. The categories of family and phylum (or division) were introduced in the early 19th century and many intermediate categories have been added since. There is currently little agreement about the general names for categories above that of kingdom; here we use superkingdom rather than empire or domain. In addition, there are three separate codes that govern the assignment and use of scientific names, each with different requirements and terminology and consequences for their classifications. For algae, fungi, and plants (ICN: International Code of Nomenclature for algae, fungi, and plants), the principle of priority does not apply above rank of family; for animals (ICZN: International Code of Zoological Nomenclature), priority does not apply above the family-group ranks; and for prokaryotes other than Cyanobacteria (ICNB: International Code of Nomenclature of Bacteria), only the categories ranked as class and below are covered by the code. A recent paper by the International Committee on Bionomenclature compares terminology among six current nomenclatural codes and makes recommendations for their use in improving communication [11].

In 2005, on behalf of the International Society of Protistologists, Adl et al. [12] presented a nested eukaryote-only cladification that used the names of six supergroups—Amoebozoa, Opisthokonta, Rhizaria, Excavata, Chromalveolata, and Archaeplastida (= Plantae) [13–17]—as the highest ranked eukaryote groups. Their schema was updated in 2012 [18], with Rhizaria and Chromalveolata replaced by SAR plus four small hacrobian groups. Although these taxa are nested, and ranked by a “bulleted” system, Adl et al. avoided the use of Linnaean higher category names (phylum, class, order, family) that would have more usefully denoted rank. Insofar as the nested groups comprise a mix of taxon names based on priority (i.e., according to the year of introduction of the name), many individual genera as well as traditional taxon names (family through class) end up having the same rank in the Adl et al. hierarchy, while at the same time having different suffixes or none at all. The ranks assigned therein often seem to reflect our present partial ignorance of relationships more than careful assessment of relative phenotypic disparity as in Linnaean taxonomy. This is very confusing when these “group names” (genus to kingdom) are used in isolation without regard to phylogenetic relativity.

Two of the great benefits of Linnaean-ranked categories and their standardized suffixes are that they instantly relativize taxa that are otherwise unknown to the non-specialist and also indicate the relative degree of phenotypic distinctiveness amongst groups. The overarching higher level classification used by the CoL, therefore, uses the standard formal categories, as it is intended to be simultaneously pragmatic and informative of both evolutionary relatedness and relative phylogenetic subordination. A classification should be biologically well-grounded and widely useful. In its simplicity, it provides less detail about relationships than a complete phylogeny but is still congruent with it [19]. Our classification is not intended to compete with a cladification such as Adl et al.’s—both are valid ways of ordering the living
world—but we would argue that their’s is less comprehensible to many in the public-domain user communities.

These actual complexities of phylogenetic history emphasize that classification is a practical human enterprise where compromises must be made [20]. We have therefore named only groups generally considered to have had a monophyletic origin, even though some of them may be paraphyletic (i.e., do not include all descendants of their last common ancestor) and others, e.g., Euglenozoa, Rhizaria, Cercozoa, include subgroups (such as Euglenophyceae, Chlorarachnea, and Paulinella) that evolved by the symbiogenetic merger of two fundamentally different lineages [21], while others have had infusions of genes from elsewhere [22] and therefore do not conform to any purely formal definition of monophyly. We have not adopted the view that one should never accept paraphyletic groups in a classification but rather have evaluated each case of paraphyly on its practicability and usage. In some cases (e.g., classical bryophytes) we accepted the splitting of paraphyletic taxa into holophyletic groups (groups with a monophyletic origin that also include all descendants of their last common ancestor, i.e., clades). In others we retained ancestral (paraphyletic) taxa when it seemed beneficial to do so (e.g., Prokaryota, Protozoa, Crustacea, Sarcophterygii, Reptilia). For practical purposes we treat Proteobacteria and Cyanobacteria as holophyletic phyla even though both exclude their mitochondrial and chloroplast descendants, neither of which is now a bacterium but an evolutionarily chimaeric cell organelle. We have conservatively retained several groups where evidence for paraphyly or holophyly is contradictory, such as Archaea (Archaebacteria).

A panel of experts representing the major taxonomic disciplines was convened to review, revise, and update the existing incomplete CoL hierarchy. These authors consulted more than 200 sources (see S1 Appendix), most of which were from recent taxonomic publications and websites. The product is a current and practical classification that meets the panel’s established goal. In achieving a consensus, the panel was required to make some compromises that may require future revision as the related issues are resolved. While all of these individuals made contributions to the hierarchy, not all necessarily endorse every aspect of it. The CoL classification will undergo review and revision at five-year intervals to consider changes as necessary.

Results and Discussion

We are proposing a two-superkingdom (Prokaryota and Eukaryota), seven-kingdom classification that is a practical extension of Cavalier-Smith’s six-kingdom schema [19]; the latter has been used, for example, in the compendious checklist of marine biota of Chinese seas [23] and in the first comprehensive national inventory of biodiversity for New Zealand [24–26]. For each of these kingdoms we had to exercise our taxonomic judgment and reach a practical compromise among diverse opinions and usages and conflicting evidence about certain phylogenetic questions important for defining the boundaries between and ranks of major taxa, including kingdoms. Our schema includes: the prokaryotic kingdoms Archaea (Archaebacteria) and Bacteria (Eubacteria), and the eukaryotic kingdoms Protozoa, Chromista, Fungi, Plantae, and Animalia. We have retained 14 ranks from superkingdom to order (Table 1). Several key taxonomic issues, some not fully resolved, are discussed below.

Prokaryota

The higher classification of prokaryotes is still somewhat unsettled. Woese and Fox [27] treated Archaebacteria (Archaea) and Eubacteria (Bacteria) as separate kingdoms. Margulis and Schwartz [28] recognized the superkingdom Prokarya, containing one kingdom Bacteria that
included a subkingdom Archaea; Cavalier-Smith also treated Archaebacteria and Eubacteria as prokaryote subkingdoms [19, 29]. Commonly used sources of prokaryote names, such as the List of Prokaryotic Names with Standing in Nomenclature (LPSN) [30] and the Taxonomic Outline of Bacteria and Archaea (TOBA) [31] treat Bacteria and Archaea as separate domains but are silent about the category of kingdom. While these sources list the names of phyla in common use as a service to the user, they are not validly published under the ICNB. We have not placed phylum names in quotation marks as they have but we have so designated a few prokaryote names at lower ranks that are in common use but not (or not yet) valid. As no prokaryote names above the ranks of class are covered by ICNB rules, there is no official higher classification of prokaryotes [32] and any attempt at such is necessarily difficult. We have chosen to adopt the classification in current use by the Catalogue of Life. It is derived from the TOBA and recognizes Bacteria and Archaea as equivalent in rank to the eukaryote kingdoms. We treat them as de facto kingdoms until there is a better resolution of their status. The number of negibacterial "phyla" currently recognized [30] is probably excessive compared with eukaryotes and mainly reflects uncertainty about the true relationships of many small phyla, probably exaggerating the significance of their biological disparity. Greater use of multigene trees rather than over reliance on rRNA gene trees alone may eventually allow further simplification by grouping them into fewer phyla, possibly only about half the present number [28].

Protozoa and Chromista

Unicellular eukaryotes, usually called protists, comprise a polyphyletic group of eukaryotes that do not undergo tissue formation through the process of embryological layering. They include ancestrally unicellular eukaryotes directly descended from bacteria by the origin of the nucleus, endomembrane, cytoskeleton, and mitochondria. Assigning them to separate kingdoms was historically difficult when only light microscopy was available but is now

Table 1. List of ranks used in the hierarchy with the number of taxa per rank.

<table>
<thead>
<tr>
<th>Rank</th>
<th>Number of Taxa</th>
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<tbody>
<tr>
<td>Superkingdom</td>
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<td>Kingdom</td>
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</tr>
<tr>
<td>Subkingdom</td>
<td>11</td>
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<tr>
<td>Infrakingdom</td>
<td>8</td>
</tr>
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<tr>
<td>Infra phylum</td>
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<td>Infraclass</td>
<td>23</td>
</tr>
<tr>
<td>Superorder</td>
<td>52</td>
</tr>
<tr>
<td>Order</td>
<td>1,467</td>
</tr>
</tbody>
</table>

Main ranks are in bold type; unnamed taxa are not counted.

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considerably facilitated because of advances in electron microscopy and gene sequencing. Formerly, the unicellular amoeboid group Myxozoa with multicellular spores was included in Protozoa but these protists are now firmly within the animal kingdom, having been proven to be greatly simplified parasitic animals. Yeasts are unicellular fungi that evolved polyphyletically from multicellular filamentous ancestors and are assigned to one of three higher fungal phyla. Microsporidia are highly reduced intracellular parasites traditionally considered to be Protozoa, but they have been known for two decades to be related to Fungi. At one time it was thought microsporidia had evolved from Fungi and therefore were placed in that kingdom [19, 33]. For several years multigene trees were contradictory about whether microsporidia branched within or diverged from Fungi. The latest evidence is that they are most closely related to rozellids [34], which also have been treated either as Fungi or Protozoa. If this recent phylogeny [34] is correct, both should be in the same kingdom. Here we take the view that the best demarcation between Protozoa and Fungi lies immediately before the origin of the chitinous wall around vegetative fungal cells and associated loss of phagotrophy [33]. We therefore include microsporidia and rozellids in Protozoa (vegetatively wall-less, typically phagotrophs) not Fungi (vegetatively walled osmotrophs).

For decades, taxonomists have debated the boundary between Protozoa and Plantae. We accept the view that it should be placed just prior to the evolutionary origin of chloroplasts and that Plantae should comprise all eukaryotes with plastids directly descending from the initially enslaved cyanobacterium, i.e., Viridiplantae (green plants), Rhodophyta (red algae), and Glaucophyta (glaucophyte algae), but exclude those like chromists that got their chloroplasts from plants secondarily by subsequent eukaryote-to-eukaryote lateral transfers. Therefore, all green algae are included in Viridiplantae and Plantae and are excluded from Protozoa. The only photosynthetic Protozoa are Euglenophyceae, which obtained their chloroplasts subsequently from an enslaved green alga [21].

The boundary between Protozoa and Chromista has been more controversial. Chromista was established to include all chromophyte algae (those with chlorophyll c, not b) considered to have evolved by symbiogenetic enslavement of another eukaryote (a red alga) as well as all heterotrophic protists descended from them by loss of photosynthesis or entire plastids [35]. With phylogenetic advances it has become clearer that alveolates (once considered Protozoa) are related to chromistan heterokont algae (and related heterotrophic heterokonts) and more distantly to Rhizaria, the three together forming the major group Harosa (equivalent to SAR). Consequently, Chromista has been greatly expanded to include all Harosa as well as other former protozoa that turned out to be related to haptophytes or cryptophytes. Chromista now includes many groups once treated as Protozoa [19], an expansion followed here. In multigene trees, this expansion is the most difficult part of the entire eukaryote tree to resolve. They sometimes show one or both of Plantae and Chromista as a clade but often their major subgroups are intermingled in contradictory ways [36, 37]. This may be a consequence of the eukaryote-eukaryote chimaeric history of chromists that acquired some genes from red algae or of the very rapid basal radiation of the robust corticate clade (i.e. Plantae plus Chromista). Because of this, some question whether Chromista represents a clade, yet trees are still too poorly resolved to eliminate the likelihood from cell evolutionary considerations that Chromista and Plantae are genuinely distinct sister clades. Evidence that Harosa is a clade is very strong. Evidence that Haptista plus Cryptista are a clade Hacrobia is strong on some trees but questioned by others [37].

Protozoa, like Prokarya, is certainly a paraphyletic taxon [38]; Animalia, Fungi, Plantae, and Chromista all evolved from it. In our hierarchy Protozoa comprises seven phyla, of which
four are probably clades and three paraphyletic. We do not consider it useful in a general classification to subdivide the paraphyletic phyla into numerous smaller ones, often with only a handful of species that most have never heard of, even though a few specialists might favor that despite their constituent subgroups not differing radically in cell structure. For both Protozoa and Chromista we have favored large groups with shared body plans, analogous to extremely diverse animal phyla like Chordata and Arthropoda. The higher proportion of ancestral (paraphyletic) phyla in Protozoa compared with terminal groups like animals and plants is unsurprising because they were the first eukaryotes and they diverged early on but with many fewer associated major changes in body plan than occurred during the much later radiation of bilateral animals. Distinct early diverging protozoan clades can be remarkably similar morphologically and biologically [39].

Fungi
As stated earlier, we take the view that the best demarcation between Protozoa and Fungi lies immediately before the origin of the chitinous wall around vegetative fungal cells and associated loss of phagotrophy. We use an updated version of the higher classification presented in the 10th Edition of the *Dictionary of Fungi* [40]. The evolutionarily convergent Oomycetes such as the serious pest *Phytophthora*, formerly treated as Fungi, belong instead in phylum Pseudofungi of the heterokont Chromista.

Plantae
As with the other kingdoms, Plantae is classified in a variety of ways. Margulis and Schwartz [28] restricted Plantae to land plants (embryophytes or higher plants) and popularized the use of kingdom Prototista to include lower plants (green, red, and glaucophyte algae) and lower Fungi as well as chromists with classical protozoa. Many now consider such a kingdom too broad and heterogeneous and the associated separation of lower and higher plants in different kingdoms to be undesirable. Now taxonomists almost universally classify lower and higher plants together in the single kingdom Plantae and lower and higher fungi within the single kingdom Fungi. We have adopted this delimitation of Plantae here [19, 35] (for which Archaeplastida [12, 18] is a less familiar recent synonym). The structure of plastid genomes and the derived chloroplast protein-import machinery support a single origin of glaucophytes, red algae, green algae, and embryophytes (land plants). The ancestral embryophyte is thought to have originated from relatives of the Charales (stoneworts) or Coleochaetales (Charophyta). Jeffrey [41] first grouped charophytes and embryophytes as a clade Streptophyta, which was later validated as a superphylum [42] and reduced to phylum by Bremer [43].

Chase and Reveal [44] published a phylogenetic classification of land plants, reasoning that “If the major clades of green algae are recognized as classes, then all land plants, the embryophytes, should be included in a single class, here recognized as Equisetopsida.” This argument, however, overemphasizes cladistic level compared with phenotypic disparity, and is contrary to traditional assignment of phylum (or division) status to the main bryophyte, “pteridophyte” and seed-plant subgroups. This latter treatment was exemplified in the 2008 Annual Checklist of the CoL, which listed three bryophyte phyla, four pteridophyte phyla, and five seed-plant phyla, reflecting the arrangement found in many university textbooks of the late 20th century and in Margulis and Schwartz’s *Five Kingdoms* [28]. Here we recognize four embryophyte phyla—three of bryophytes (liverworts, hornworts, and mosses) and a single phylum Tracheophyta for vascular plants—with all species characterized by a diploid phase having xylem and phloem. Bryophyte specialists tend to treat each of the three major bryophyte groups as phyla—Marchantiophyta, Anthocerotophyta, Bryophyta [45, 46]. We have chosen a
conservative approach to the higher classification of plants, largely consistent with Mabberley [47] for the embryophyte ranks above class, while using Chase and Reveal [44] and Stevens [48] for the lower ranks.

Animalia (Metazoa)

The numbers of phyla and classes with extant species in kingdom Animalia differ according to molecular and morphological partitioning in phylogenies [49–59] as well as the preferred treatments of specialists of particular traditional phyla and where to “draw the line” between related taxa and how to rank them—the ranking of phylum versus subphylum is sometimes rather subjective. Based on the contributions of taxonomic experts to an outline of higher level classification and survey of taxonomic richness [60, 61], as many as 39 animal phyla might be recognized (more, if Porifera were abandoned as a phylum and constituent major clades given higher rank [62]). Below we discuss some issues encountered in arriving at decisions for our proposed classification, which accepts 34 animal phyla.

(1) Porifera—One phylum or three? Nielsen [62] argued that ‘The three apparently monophyletic sponge groups Silicea, Calcarea, and Homoscleromorpha do not constitute a monophyletic group, and the “phylum Porifera” thus has to be abandoned.’ More recent studies alternatively support paraphyly [63] or holophyly [58, 64] of sponges. Until the issue is resolved, we will follow the Porifera community [65–67] in retaining one phylum Porifera with four classes.

(2) Status of Myxozoa. Recent work on the vermiform myxozoan Buddenbrockia has demonstrated conclusively that myxozoans are extremely simplified Cnidaria, possibly Medusozoa [68, 69]. We classify Myxozoa as a subphylum of Phylum Cnidaria.

(3) Flatworms—Monophyletic or not? In 1995, Nielsen [70] wrote “The delimitation of the phylum [Platyhelminthes] is not much in question,” but recent molecular analyses, combined with a careful reconsideration of morphology and anatomy, have confused the classification of Platyhelminthes, affecting particularly Acoela, Xenoturbella, and Nemertodermatida. Egger et al. [71] reviewed the evidence, noting the contrast between morphological and phylogenomic data. Whereas the stem-cell system and the mode of replacing epidermal cells unite both Acoela and Rhabditophora and are not found in any other bilaterian lineage, phylogenomic data support a separation of these two groups, a conclusion reached by Philippe et al. [72] based on mitochondrial genes, a phylogenomic data set of 38,330 amino-acid positions, and miRNA complements. We follow Philippe et al. [72] and Tyler and Schilling [73] in uniting Acoela, Xenoturbella, and Nemertodermatida as the deuterostome phylum Xenacoelomorpha. The remaining internal classification of Platyhelminthes is also somewhat problematic. We propose a classification that is based in part on Riutort et al. [74] and Tyler [75].

(4) Phylum Gnathifera or phyla Acanthocephala, Gnathostomulida, Micrognathozoa, and Rotifera? Until recently, all four of these groups were commonly treated as separate phyla [28, 61, 76–80]. However, numerous recent molecular and morphological analyses nest Acanthocephala within Rotifera [81–86]. A syncytial epidermis links rotifers, Seison and Acanthocephala; Ahlrichs [87, 88] proposed Syndermata for this clade. As revealed by transmission electron microscopy [89] and scanning electron microscopy [90], the jaw apparatus of gnathostomulids and rotifers is remarkably similar. That of Seison is less obviously homologous [91] and the Seisonidea may have diverged from rotifers at an early stage of their evolution. On the other hand, Seison has similar sperm to acanthocephalans and the epidermis of both groups contains bundles of filaments. Limnognathia maerski, representing a new category of organism (Micrognathozoa) from cold fresh waters in Greenland and the Crozet Islands [92, 93], has a remarkable jaw apparatus (the most complicated known among invertebrates) with
clear homologies, in both the jaw elements and musculature, with the trophi in Rotifera and the jaws in Gnathostomulida. The jaw apparatus and musculature, as well as molecular analyses, unite these taxa as a clade known as Gnathifera (see [86, 92]). In the analysis by Giribet et al. [94], the issue remained unresolved, as Micrognathozoa appeared independent of Gnathostomulida and Rotifera, with unclear affiliation. Edgecombe et al. [59] and Nielsen [95] retain phylum status for Gnathostomulida, Micrognathozoa, and Rotifera but not Acanthocephala. We treat each of the major gnathiferan groups as a phylum, including Acanthocephala, following Monks and Richardson [79], though some of us think that the number of gnathiferan phyla ought to be substantially reduced when their phylogeny, including ingroup relationships of Rotifera sensu lato, is more firmly established.

(5) The scaldidophoran phyla Adrianov and Malakhov [96] erected phylum Cephalorhyncha for Kinorhyncha, Loricifera, Priapula, and Nematomorpha. The first three of these phyla have in common an eversible snout (introvert) with scald spines and inner and outer retractor muscles, a similar excretory filter (protonephridium), and similar sense organs, providing strong justication for uniting them in a single clade, the Scaldidophora [97]. There is also molecular support, though not unanimity, for a clade of Kinorhyncha, Loricifera, and Priapula, known as Scaldidophora. On the other hand, Kinorhyncha has internal and external body segmentation lacking in the other groups. Neuhaus and Higgins [98] noted that conflicting evidence exists for every one of the possible sister-group relationships among these phyla and prefer to keep them separate in a superphylum Scaldidophora (which is preferred over Cephalorhyncha, the latter name originally including the Nematomorpha). We recommend separate scaldidophoran phyla, though the number might be greatly reduced when the phylogeny becomes clearer.

(6) The chordate subphyla Cephalochordata and Urochordata Some sequence analyses have questioned the monophyly of Chordata [99, 100]. Nielsen [95] maintains Urochordata (or Tunicata) and Cephalochordata as separate phyla, whereas the group Urochordata is closer to Vertebrata (craniates), in a clade Olfactores, than Cephalochordata. We retain all three groups as traditional chordate subphyla.

Many users of classifications would prefer a stable, unchanging system. Yet classifications are syntheses of biological knowledge, particularly contemporary phylogenetic understanding of taxa, that must be regularly updated in accord with new scientific discoveries. Taxonomy must therefore navigate between the dual perils of ignoring important advances and making premature or unnecessary changes. We seek stability in nomenclature at the species level but at higher levels the concepts and compositions of major taxa, and therefore the scope of well-known names, must inevitably shift as new organisms are discovered and evolutionary affinities are better understood. The fact that we have been able to agree on a practical unified classification shows that taxonomists can broadly agree, despite the diverse experiences, viewpoints, and to some extent, differing philosophies of classification represented on our panel. The present classification (as, indeed, all classifications) should be regarded as interim, and it will inevitably change in certain respects, some hinted at above. However, we suspect that the recent torrent of radical re-evaluations (resulting especially from the application of DNA sequencing and other new techniques) may lessen as time passes. We hope that this unusually comprehensive classification will be widely useful and provide a sound basis for further improvement.

A complete proposed classification from superkingdom to order is provided in Table 2 and is available for download at <http://www.catalogueoflife.org/col/>. Below the rank of infra-kingdom, we have followed the convention used in the Catalogue of Life and listed taxon names alphabetically. This allows easier searching by those not familiar with the phylogenies of
Table 2. Proposed hierarchical classification from superkingdom to order.

<table>
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<tr>
<th>SUPERKINGDOM PROKARYOTA</th>
<th>KINGDOM ARCHAEA [= ARCHAEBACTERIA]</th>
<th>Phylum Crenarchaeota</th>
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<td>Order N.N. (&quot;Ca. Caldiarchaeum&quot;)</td>
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<td>Class Thermoprotei [= Crenarchaeota]</td>
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SUBKINGDOM POSIBACTERIA

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**SUBKINGDOM SARCOMASTIGOTA**

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**SUBKINGDOM SARCOMASTIGOTA**

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SUBKINGDOM HAROSA [= "Supergroup SAR"]

INFRAKINGDOM HALVARIA

Superphylum Alveolata

Phylum Ciliophora

Subphylum Intramacronucleata

Class Armophorea

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Subclass Coleotaphia

Order Coleotaphiida [= Protococcida]

Subclass Hematozooa

Superorder Aconoidia

Order Nephromycida
Order Piroplasmida

Superorder Haemosporidia

Order Hemosporida

Class Gregarinomorpha

Subclass Cryptogragaria

Order Cryptogregarida (Cryptosporidium)

Subclass Histogregaria

Order Histogregarida

Subclass Orthogregarinia

Order Arthrogregarida
Order Vermigregarida

Class Paragregarea

Order Archigregarinida
Order Stenophorida
Order Velocida

Infra phylum Dinozoa

Superclass Dinoflagellata

Class Dinophyceae

Subclass N.N.

Order Actiniscales
Order Blastodinales
Order Coccidinales
Order Dinamoebales
Order Lophodinales
Order Pyrocystales
Order Thoracosphaerales

Subclass Dinophysoidea

Order Dinophysidales
Order Nannoceratopsales

Subclass Gonyaulacoidia

Order Gonyaulacales
Order Gymnodiniales

Subclass Peridinoidia

Order Peridiniales
Order Prorocentrales

Subclass Suessioidia

Order Suessiales

Class Ellobiopsea

Order Ellobiopsida

Class Noctilucea

Order Noctilucida

Class Oxynheia

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Table 2. (Continued)

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**Class Boldophyceae**

- Order Parmales (= Bolidomonadales)

**Class Chrysomophyceae**

- Order Chrysoeridiales

**Class Chrysophyceae**

- Order Chloramoebales
- Order Chromuliniales
- Order Chryymphalaerales
- Order Heterogloeales
- Order Hydratales
- Order Ochrymonadiales
- Order Paraphysomonadida
- Order Synurales
- Order Thallochrysidales

**Class Eustigmatophyceae**

(Continued)
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**INFRASKINGDOM RHIZARIA**

**Phylum Cercozoa**

**Subphylum Endomyxa**

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**Class Gromiidea**

| Order Gromida       | Order Reticulosida    |

**Class Phytomyxea**

| Order Phagomyxida   | Order Plasmodiophorida|

**Class Vampyrellidea**

| Order Vampyrellida  |                       |

**Subphylum Monadofilosa**

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**Subclass Placoperla**

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**KINGDOM FUNGI**

**SUBKINGDOM DIKARYA [= NEOMYCOTA]**

Phylum Ascomycota

Subphylum Pezizomycotina

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**KINGDOM PLANTAE**

**SUBKINGDOM BILIPHYTA**

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| Superorder Polyneoptera               | Order Blattodea              |
|                                        | Order Dermaptera             |
|                                        | Order Embioptera             |
|                                        | Order Grylloblattodea        |
|                                        | Order Mantodea               |
|                                        | Order Mantophasmatodea       |
|                                        | Order Orthoptera             |
|                                        | Order Phasmdida              |
|                                        | Order Plecoptera             |
|                                        | Order Zoraptera              |
| **Class Protura**                     | Order Ephemeroptera          |
|                                        | Order Odonata                |
| **Subphylum Myriapoda**               | Order Acerentomata           |
|                                        | Order Eosentomata            |
|                                        | Order Sinentomata            |
| **Infraclass Helminthomorpha**        | Order Craterostigmomorpha    |
| Superorder N.N.                       | Order Geophilomorpha         |
|                                        | Order Lithobiomorpha         |
|                                        | Order Scolopendromorpha      |
|                                        | Order Scutigeromorpha        |
| **Class Chilopoda**                   | Order Julida                 |
|                                        | Order Spirobolida            |
|                                        | Order Spirostreptida         |
| **Subclass Chilognatha**              | **Superorder Juliformia**    |
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|                                        | Order Spirobolida            |
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| **Superorder Nematophora**            | **Superorder Merochaeta**    |
|                                        | Order Polydesmida            |

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| **Phylum Onychophora** | Order Triplonchida  
Order Tripylida  
Phylum Nematomorpha  
Order Gordioidea  
Order Nectonematoida |
| **Phylum Priapula (= Priapulida)** | Class Udeonycophora  
Order Euonyphora  
Phylum Priapula  
Class N.N. (e.g., Priapulidae) |
| **Phylum Tardigrada** | Class Eutardigrada  
Order Apochela  
Order Parachela  
Class Heterotardigrada  
Order Arthropodigrada  
Order Echiniscoidea |
| **Superphylum Spiralia (= Lophotrochozoa)** | Phylum Acanthocephala  
Class Archiacanthocephala  
Order Apororhynchida  
Order Gigantorhynchida  
Order Moniliiformida  
Order Oligacanthorhynchida  
Class Eoacanthocephala  
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Order Myzostomida  
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| Class Monogonta | Order Flosculariaceae |
| Class Bdelloidea (e.g., Adinetidae) | Order Ploima |
| Subclass Monogonta | |

**Phylum Sipuncula**

| Class Phascolosomatidea | Order Seisonacea |
| Order Aspidosiphoniformes | Order Golfiniflorines |
| Order Phascolosomatiformes | Order Sipunculiformes |
| Class Sipunculidea | |

**Phylum Chordata**

| Subphylum Cephalochordata | Order Amphioxiformes |
| Subphylum Urochordata | |
| Class Appendicularia | Order Copelata |
| Class Ascidiacea | Order Enterogona |
| Class Thaliacea | Order Pyrosomida |
| Subphylum Vertebrata [= Craniata] | Order Salpida |

**InfraKingdom Deuterostomia**

| Infraphylum Agnatha | |
| Class Cephalaspidomorphi | Order Petromyzontiformes |
| Class Myxini | Order Myxiniformes |

| Infraphylum Gnathostomata | |
| Superclass Actinopterygii | Order Acipenseriformes |
| Class Chondrostei | Order Polypteraiformes |
| Class Cladistia | Order Amiiformes |
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</tr>
<tr>
<td>Order Gaviiformes</td>
</tr>
<tr>
<td>Order Gruiformes</td>
</tr>
<tr>
<td>Order Leptosomiformes</td>
</tr>
<tr>
<td>Order Mesitornithiformes</td>
</tr>
<tr>
<td>Order Musophagiformes</td>
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</table>

(Continued)
Table 2. (Continued)

<table>
<thead>
<tr>
<th>Class</th>
<th>Order</th>
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<tbody>
<tr>
<td>Phylum Echinodermata</td>
<td>Subphylum Asterozoa</td>
</tr>
<tr>
<td>Class Asteroidea</td>
<td>Order Brisingida</td>
</tr>
<tr>
<td></td>
<td>Order Forcipulatida</td>
</tr>
<tr>
<td></td>
<td>Order Notomyotida</td>
</tr>
<tr>
<td></td>
<td>Order Paxillosida</td>
</tr>
<tr>
<td></td>
<td>Order Peripoda</td>
</tr>
<tr>
<td></td>
<td>Order Spinulosida</td>
</tr>
<tr>
<td></td>
<td>Order Valvatida</td>
</tr>
<tr>
<td></td>
<td>Order Velatida</td>
</tr>
<tr>
<td>Class Ophiuroidea</td>
<td>Order Euryalida</td>
</tr>
<tr>
<td>Subphylum Crinozoa</td>
<td>Order Ophiurida</td>
</tr>
</tbody>
</table>

(Continued)
### Table 2. (Continued)

<table>
<thead>
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<th>Order</th>
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<tbody>
<tr>
<td>Order</td>
<td>Cyrtocrinida</td>
</tr>
<tr>
<td>Order</td>
<td>Hyocrinida</td>
</tr>
<tr>
<td>Order</td>
<td>Isocrinida</td>
</tr>
</tbody>
</table>

**Subphylum Echinozoa**

**Class Echinoidea**

**Subclass Cidaroida**

Order Cidaroida

**Subclass Euechinoidea**

Infraclass N.N.

Order Echinothurioida

Infraclass Acroechinoidea

Order Aspidodiadematoida

Order Diadematoida

Order Micropygoida

Order Pedinoida

**Infraclass Carinacea**

Order Arbacioida

Order Camarodonta

Order Salenioida

Order Stomopneustoida

**Infraclass Irregularia**

Order Cassiduloida

Order Clypeasteroida

Order Echinolampadoida

Order Holasteroida

Order Spatangoida

**Class Holothuroidea**

Order N.N. (Thyone)

Order Apodida

Order Aspidochirotida

Order Dendrochirotida

Order Elasipodida

Order Molpadida

**Phylum Hemichordata**

Class Enteropneusta (e.g., Harrimaniidae)

Class Pterobranchia

Subclass Cephalodiscida (Cephalodiscus)

Subclass Graptolithina

Order Rhabdopleurida

**Phylum Xenacoelomorpha**

Subphylum Acoelomorpha

Class Acoela (e.g., Diopisthoporidae)

Class Nemertodermatida (e.g., Nemertodermatidae)

Subphylum Xenoturbellida

Class N.N. (Xenoturbellidae)

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Names below rank of infrakingdom are arranged alphabetically within each parent rank, except for taxa that are not named (N.N.). Brackets indicate synonyms. Quoted names are not validly published but in common use.

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the many taxa therein and provides for easier import and manipulation of data by information systems.

Supporting Information

S1 Appendix. List of sources consulted for proposed higher level classification of all living organisms. (PDF)

S1 Table. Proposed hierarchical classification from superkingdom to order. (XLSX)

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Author Contributions

Conceived and designed the experiments: MR DG NB TB RC-S MG PK TO. Analyzed the data: MR DG NB TB RC-S MG PK TO. Wrote the paper: MR DG NB TB RC-S MG PK TO.

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