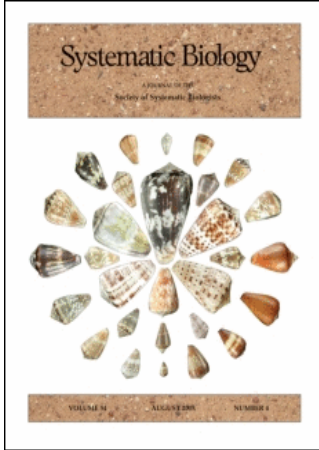


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Systematic Biology

Publication details, including instructions for authors and subscription information:
<http://www.informaworld.com/smpp/title~content=t713658732>

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First Published on: 01 August 2007

To cite this Article: Adl, Sina M., Leander, Brian S., Simpson, Alastair G. B., Archibald, John M., Anderson, O. Roger., Bass, David, Bowser, Samuel S., Brugerolle, Guy, Farmer, Mark A., Karpov, Sergey, Kolisko, Martin, Lane, Christopher E., Lodge, Deborah J., Mann, David G., Meisterfeld, Ralf, Mendoza, Leonel, Moestrup, Øjvind, Mozley-Standridge, Sharon E., Smirnov, Alexey V. and Spiegel, Frederick (2007) 'Diversity, Nomenclature, and Taxonomy of Protists', *Systematic Biology*, 56:4, 684 - 689

To link to this article: DOI: 10.1080/10635150701494127

URL: <http://dx.doi.org/10.1080/10635150701494127>

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First submitted 11 January 2006; reviews returned 6 June 2006;

final acceptance 2 May 2007

Associate Editor: Ron DeBry

Syst. Biol. 56(4):684–689, 2007
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 ISSN: 1063-5157 print / 1076-836X online
 DOI: 10.1080/10635150701494127

Diversity, Nomenclature, and Taxonomy of Protists

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The new classification of protists from the International Society of Protistologists (Adl et al., 2005) could not apply both the International Code of Botanical Nomenclature and the International Code of Zoological Nomenclature because the two are incompatible. The classification designated one name for each clade where multiple names from different codes had previously existed, traced authorities, and provided a classification based on nameless ranks. Here we review important issues that remain to be resolved. Current rules governing validation of new species, from various codes of nomenclature, have become an impediment to naming of new protists. Standard requirements for protist species descriptions and type specimens need to be modernized to accommodate the rapid discovery of new species made possible by modern microscopic and molecular techniques. Although we agree with the criticisms of

the botanical and zoological codes made by proponents of the Phylocode, we did not all agree that the current Phylocode is the solution, nor does it currently address species typification. Accordingly, new guidelines are needed to govern standards in protist species descriptions and classification.

Over the past 25 years, molecular phylogenetic studies have led to extensive modification of traditional classification schemes for eukaryotes. The most dramatic changes have occurred within protists, from which multicellular organisms evolved. The names of many protist groups and the genera they include have been changed so many times that the classification scheme is unclear, and it is difficult to determine which names apply. Two recent reviews have provided a modern phylogenetic perspective on the overall organization of eukaryote clades (Keeling et al., 2005; Simpson and Roger, 2004).

A necessary extension of this phylogenetic research was to establish a new classification that reflected the general consensus on the taxonomic names and their authorities (Adl et al., 2005). This classification scheme for protists breaks with tradition by not using either the International Code of Botanical Nomenclature (ICBN) (Greuter et al., 2000) or the International Code of Zoological Nomenclature (ICZN; International Commission on Zoological Nomenclature, 1999) regarding ranks, because neither of these codes are presently adequate for protists. The decision to do so was primarily practical. Where possible, well-known names referring to recognized monophyletic groups were retained. Although it did not try to follow the Phylocode, groups of named lineages were defined by apomorphies (derived characters) as much as possible, but node-based and stem-based definitions were used as necessary, even though they were not identified as such in the final presentation. In this classification, name endings that conveyed hierarchical information in a traditional code (e.g., -idae, -inae, -ales, -aceae) were retained to avoid unnecessary name changes but are not intended to convey hierarchical information. We believe this scheme to be more utilitarian as it recognizes one name for each clade where multiple names for the same clade were used previously. Furthermore, the classification is intended to facilitate future modification in light of improved phylogenetic information, without requiring a cascade of name changes. Further changes to the classification will no doubt be necessary given that our knowledge of some groups and our geographical sampling are still far from complete. Several critical issues remain to be resolved and we must continue to work towards a practical consensus.

DIVERSITY OF PROTISTS

Adl et al. (2005) defined protists as eukaryotic organisms with unicellular, colonial, filamentous, or parenchymatous organization that lack vegetative tissue differentiation, except for reproduction. Metazoa Haeckel 1874, Plantae Haeckel 1866, and some Phaeophyceae Hansgirg 1886 are recognized as being truly multicellular. The current number of described protist species, including fungi, is widely acknowledged to be a fraction of the total diversity in nature (Table 1; May, 1988; Corliss, 2002). Many geographic regions have not been sampled at all and most regions and habitats are insufficiently sampled. The rate of discovery of new species from environmental samples remains high. Indeed, most soil, freshwater, or marine samples collected contain a multitude of undescribed species (Foissner, 1999, 2006; Slapeta et al., 2005) that are found through microscopy or environmental DNA samples. Owing to insufficient environmental sampling and re-isolation, the geographical distribution of most species remains unknown. A meta-data statistical analysis of species richness indicated that unicellular organisms showed high relative local species richness, which is consistent with most species being locally rare (Hillebrand et al., 2001). Species composition for protists was statistically less similar between samples with geographical distance, suggesting a region-

TABLE 1. Approximate number of described species and estimated total number of species in each group.*

Group name	Number of known extant species	Potential number of species
Amoebozoa		
Lobose, naked	180	600
Arcellinida	1100	10 ³ to 10 ⁴
Myxogastria	>900	1200 to 1500
Dictyostelia	>100	300
Protostelia	36	150
Eumycetozoa	655	10,000
Other Amoebozoa	35	50
Opisthokonta		
Fungi (excluding Zygomycota)	335,000	$n \times 10^6$
Zygomycota	70,000	1.5 $\times 10^6$
Chytridiomycetes	1000	<2000
Microsporidia	1200	10,000
Mesomycetozoa	47	$n \times 10^3$
Choanomonada	120	300
Rhizaria		
Cercozoa	<500	$n \times 10^3$
Haplosporidia	31	$n \times 10^2$
Foraminifera	>10,000	15,000
Acantharia	160	<200
Polycystinea	700 to 1000	1,500
Nucleohelea	160 to 180	200
Archaeplastida		
Glaucophyta and Rhodophyceae	4000 to 6000	20,000
Chloroplastida, excluding Charophyta	8000 to 10,000	1–2 $\times 10^5$
Charophyta		
Charophyta, excluding Plantae	4300	5000
Chromalveolata		
Cryptophyceae	70	200
Haptophyta	350	<400
Phaeophyceae	1500 to 2000	2000
Actinophryidae	5	<10
Opalinata	400	500
Bicosoecida	72	100
Labyrinthulomycetes	40	<100
Hyphochytriales	25	$n \times 100$
Peronosporomycetes	676	10 ³ to 10 ⁴
Chrysophyceae	1000	2000
Dictyophyceae	15	30
Eustigmatophyceae	15	30
Pelagophyceae	12	20
Phaeothamniophyceae	25	40
Pinguicophyceae	5	20
Raphidophyceae	20	40
Synurophyceae	200	350
Xanthophyceae	600	800
Bacillariophyta	1–2 $\times 10^4$	2 $\times 10^5$
Apicomplexa	6,000	1.2–10 $\times 10^6$
Dinzoa	2000	<3000
Ciliophora	3500	30,000
Excavata		
Fornicata	146	<200
Parabasalia	466	500
Preaxostyla	96	<120
Jakobida	10	200
Heterolobosea	80	200
Euglenozoa	1520	2000
Incertae sedis		
Eukaryota		
Apusomonadida	12	20

*Potential number of species were estimated by authors for each group based on number of unknown DNA sequences found in environmental samples.

ally restricted distribution for some or many species, likely due to limitations to protist dispersal over long distances. Interpretation of these results is complicated, however, because species identification is typically based

on morphology, which often may not distinguish between species with similar or identical morphologies (Hillebrand et al., 2001; Adl and Gupta, 2006; Foissner, 2006).

WHICH CLASSIFICATION?

For historical reasons, protists traditionally fell under the jurisdiction of the ICBN if they were "algae" or "fungi" and under the jurisdiction of the ICZN if they were "protozoa." This system has been unraveling for several decades, as a number of groups were described in parallel by zoologists (ICZN) and by botanists (ICBN) each with distinct names (Corliss, 1995). To give just one example, *Diatomea Dumortier* 1821 and *Bacillariophyta Haeckel* 1878 both describe the same clade: the diatoms. The ranks within this group received a parallel series of names independently by zoologists and botanists to accommodate rank endings appropriate for each code (the so-called ambireginal classification). These unnecessary duplications introduced a double language throughout protist classification schemes that resulted in confusion.

The situation was exacerbated from the 1960s onward, as many genera were reclassified to accommodate new research and discoveries of new taxa. The traditional classification of protozoa and algae collapsed during the 1970s and 1980s as many groups were subsequently shuffled. Many ranks contained genera that were described under one code and other genera under the other code. More dramatically, it became evident through molecular phylogenies that fungi (governed by the ICBN) are a sister lineage of animals (governed by the ICZN), and novel protists discovered at the base of both of these clades were described following ICZN rules (Mendoza et al., 2002; James et al., 2006).

Lastly, 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. These issues were elaborated fully elsewhere and will not be repeated here (Cantino, 2004; Pleijel and Rouse, 2003). Previous attempts at synthesis of a classification for eukaryotes, based on identifying successive evolutionary steps and providing a Linnaean name for each rank in the hierarchy, required numerous novel rank names (Cavalier-Smith, 1993) and never became widely used by protistologists. In part, this valiant effort was premature because most of the molecular phylogenetic information necessary became available subsequently. Several alternative classifications were proposed in this new light, with new competing names for the same groups of organisms (Cavalier-Smith, 1998; Patterson, 1999, 2002), with accompanying changes in ranks and authority as required by the ICBN or the ICZN. As a result, authors resorted to selecting one of several possible names for each group or, more commonly, used informal names without specifying an authority or a definition. This further added to the confusion. Without a memory of the history of changes associated with a taxon name,

rank, and clade, identifying a group and its composition became very difficult for professionals, and almost impossible for those entering the field of protistology. There was simply no common rationale for deciding which name and which classification to use.

HOW DID WE GET INTO THIS MESS?

The purpose of classification is to arrange biological diversity in such a way as to facilitate communication and accurate information retrieval. This system must operate within a phylogenetic context and must be able to accommodate modification while retaining name stability. This is a particularly onerous task as there are millions of phylogenetic entities at different hierarchical levels, with thousands more being discovered annually (May and Nee, 1995). The mess that arose in the classification of protists attests to the failure of the ICBN and ICZN to arrive at a mutually satisfactory accommodation, at accommodating changes in the classification, and providing unambiguous name stability in a modern evolutionary context.

The ICBN and ICZN were created based on preevolutionary principles laid out by Aristotle and Linnaeus, using a species binomial nomenclature of *Genus epithet*. Binomial nomenclature is responsible for much of the instability in the classification, as each time a taxon is moved, its generic name is changed (Cantino, 1998). This is not problematic for a small number of taxa, but the extent of change required to the classification was unforeseen. The fundamental division of life into plants versus animals appeared distinct and stable enough at the time, but protists blurred that distinction. The flexibility that would later be required of the traditional schemes, with the rapid expansion of protist taxa and extensive reclassification, simply could not be accommodated while retaining name stability.

Other problems with the Linnaean rank-based nomenclature have been the subject of many papers over the past 15 years (de Queiroz and Gauthier 1992, 1994; Cantino et al., 1997; de Queiroz, 1997; Kron, 1997; Hibbett and Donoghue, 1998; Pleijel and Rouse, 2003; Cantino, 2004). Some of the more problematic issues raised are that (1) rank dictates priority and synonymy under separate codes, instead of clades; (2) rank changes cause a cascade of name changes following even minor changes in phylogenetic hypotheses (shifting to a new rank changes both the name, and the authority of a group, even though the organisms it describes and the clade remains the same); (3) the codes are essentially silent on what is considered today to be the overriding concern in classification—the principle of common descent. It is permissible for the members of well supported clades to be separated into paraphyletic categories, even if doing so introduces misleading information about evolutionary relatedness; and (4) more emphasis is placed on who named or moved a group than the group and its name. Several other issues concern outdated approaches to describing species. For example, the requirement for Latin descriptions in the ICBN and what is acceptable as a type specimen

and holotype under both codes are impractical for protists and need modernizing, as discussed below. Unfortunately, the Phylocode is not much help on this point. Although it has attempted to introduce “tree-thinking” from molecular phylogenies into its rules of nomenclature, it deals only with rules governing clades and not with naming species.

TOWARD A SOLUTION

It has been argued that the traditional codes can be revised to accommodate some of the problems mentioned above, and that many of the identified problems are not serious (Barkley et al., 2004). That may be true for extant Animalia and Plantae, although some disagree (Cantino, 2004), but for protists that is simply not the case. An example of the many profound difficulties that can be encountered was recently provided for *Pneumocystis*, a pathogen that was traditionally treated as a protozoan under the ICZN but is now known to be a fungus and must be treated by the ICBN (Redhead et al., 2006). These difficulties are encountered with well-known isolates that exist in many laboratories. The problem is insurmountable with isolates that can be fully described but cannot be cultured or cryopreserved. To place the issue in perspective, imagine a situation where plant species descriptions would be acceptable only if the new specimen was domesticated enough to be cultivated! For example, a protist specimen that is digitally photographed and then used to obtain DNA for phylogenetic information will no longer physically exist to be deposited as a holotype. However, the resulting digital images, sequence data, and DNA sample—which are all necessary, sufficient, and more useful than a microscope slide for subsequent identification—continue to exist. At some point, so much modification is needed that the original code is no longer the same code but becomes something new (Cantino, 2004). It is impossible to be familiar with the diversity and classification of protists on the one hand and to claim that the ICBN and the ICZN have been stabilizing and accommodating on the other.

In our view, the following issues need to be addressed in the formulation of articles for a code that would be useful for the classification of protists and all eukaryotes. Below we highlight several approaches that would help in species typification by working towards standardized rules. We emphasize parameters that are useful to protist species delineation using a variety of biological and molecular approaches. Next, we discuss nomenclatural issues that would provide name stability.

Standardized Data Acquisition

Fundamentally, there is widespread acceptance that identification of protist species using light microscopy alone is no longer sufficient or adequate. Many well-studied morphotypes, including those with sufficient biogeographical sampling, are known to represent a variety of morphologically indistinguishable species (see Adl and Gupta, 2006; Foissner, 2006). These cryptic

species can be distinguished by mating types if sexual, by feeding preferences, from DNA sequences, from excystment requirements, and from temperature or habitat optima. Descriptions based on microscopy and holotypes deposited in designated institutes as fixed slide preparations or photographs can help to describe a morphotype but fail to identify species. Accurate identification of morphotypes by microscopy depends on the array of morphotypes known to the microscopist. Identification errors are common because type specimens generally have limited accessibility, being kept inside “designated institutes” far away, or are not useful, and older published drawings and photographs are often of poor quality and insufficient on their own. We therefore recommend adoption of some combination of standardized requirements for microscopy that include using digital still-images of live specimens or digital video showing patterns of motility (in motile specimens), scanning or transmission electron micrographs, DNA sequence information, habitat and feeding preferences, and, where possible, a description of life cycle stages. For reference material, both the images and the sequence information must be freely available in electronic public databases.

Use of Molecular Data

DNA sequence information is commonly used both for understanding relatedness between clades as well as for identifying species. The most commonly used DNA sequences for phylogenetic reconstruction of eukaryotic groups, such as small subunit ribosomal DNA (18S rDNA), may underestimate intrageneric diversity in some clades but may be less conserved in others (Keeling et al., 2005; Simpson and Roger, 2004). Careful consideration is required to supplement the 18S rDNA data with sequence information from other genes, such as the mitochondrial *cox1* or from the ribosomal ITS regions. Choices about the number and identity of genes necessary for sufficient resolution may be different for different clades, and this needs to be established by experts. The sequence information should be compared with similar isolates from across the geographical range of morphotypes to obtain a sense of how much variation or diversity is represented by each morphotype. It is only with repeated isolation and comparison at a variety of locations that intrageneric protist diversity can be described adequately.

When comparing sequence differences, a recurring issue has been to ask, how much sequence divergence warrants a new species or genus? If a fixed amount of sequence difference is preset and applied uniformly, would many of the large primates, antelopes, or the brown kelps in the *Laminariales* converge to a small number of species and genera? Solving this question by setting a number, even with a more complicated formula, would be an arbitrary delineation of isolates into categories. We do not advocate a standardized and uniformly applied fixed amount of sequence difference to delineate species. Rather, the emphasis for species delineation would be placed on the combination of phylogenetic analysis of sequence data plus physiological

adaptations to a multidimensional niche space (i.e., an ecologically relevant parameter; Whittaker, 1972). These would include parameters described above in obtaining a standard set of information in species delineation. This shift in emphasis would require more species characterization than is currently done in describing isolates, a problem that will no doubt intensify as molecular data become cheaper and easier to acquire. A practical solution will have to be accommodated.

Name Stability

In seeking unambiguous and stable names in biological classifications, the PhyloCode (Cantino and de Queiroz, 2006) proposed a shift from Linnaean rank based nomenclatures toward naming nested clades with stem-, node-, or apomorphy-based definitions (de Queiroz and Gauthier, 1994; Cantino, 2004). This approach, as the authors argued, separates naming clades from assembling nested hierarchies, in contrast to rank-based nomenclature, which treats these steps as part of the same process. Therefore, clade composition is determined by the interaction of a clade definition with a phylogenetic hypothesis. The names do not necessarily change when the phylogenetic hypothesis (the classification) changes. This goes a long way toward providing name stability while accommodating changes in the classification. We do not suggest that the current PhyloCode provides solutions to all of the problems of protist classification, but it is clearly a step in the right direction. As we work toward adopting rules that will work for protists, the criticisms made of Linnaean rank-based nomenclatures, and its benefits, ought to be considered seriously by the biological community. The danger with the current situation is that out of necessity, protist species descriptions will occur outside of the guidelines established by the existing codes, and thus without standards, as researchers continue to ignore them as unworkable. The ambiguous situation has now expanded beyond protists, as descriptions of animal species are also occurring according to PhyloCode (even though it has not been formally implemented) or the ICZN, creating an ambireginal situation in Animalia (Hillis, 2007; Dubois, 2007), where clades are named and described according to two different and parallel set of rules.

CONCLUDING REMARKS

The new classification of eukaryotes reflects our current knowledge of protist evolution, has reintroduced some formality with group names and their authority, and provides a point of reference for protist systematics (Adl et al., 2005). Unresolved cases remain where relationships between clades are unclear (Adl et al., 2005; Keeling et al., 2005; Patterson, 1999). Some of the most undersampled groups include the most diverse eukaryotes, such as red algae, fungi, and apicomplexan parasites (Table 1). The rate of new species description should be limited only by how fast individual cells can be collected, photographed, and their genes sequenced, not by antiquated codes of nomen-

clature. Using high-throughput methods developed for genomic studies, potentially hundreds of new species could be discovered weekly from environmental samples, with accompanying phenotypic information from microscopy. Images and sequence information need to be publicly available electronically in searchable databases, such as in Discover Life (www.discoverlife.org) or Microscope (<http://starcentral.mbl.edu/microscope/>). Ultimately, all species need to be transferred into digital searchable catalogues that contain both DNA sequence information and images, as well as additional biological information. (A task of this magnitude can be accomplished with sufficient resources. For example, it was accomplished for much of the published scientific literature of the last century in two decades, despite many pessimists claiming it would take an unreasonably long time to do so.) There has to be a shift away from the emphasis on authorities and ranks toward clade name stability. Possibilities for dealing with the *genus epithet* binomial ambiguity can be handled simply, by combining the two (*genus.epithet* or *genus-epithet* or *genusepithet*) into a single unambiguous name (Cantino et al., 1999). The rules to standardize the process must be simple, few, and practical.

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 (Adl, 2005). 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. This has dire consequences to research funding in protistology, as long as these organisms are considered few and unimportant despite their key role in ecosystems and the evolution of life. This is unfortunate because protists cause many of the world's deadliest human diseases and include the most damaging crop pathogens such as *Phytophthora* that caused the Irish famine. The World Health Report (2004) ranked respiratory tract infections, diarrheal diseases, and malaria respectively as first, fourth, and sixth in number of deaths caused by communicable diseases, maternal and perinatal conditions, and nutritional deficiencies. Each of these categories contains a variety of pathogenic protists (Corliss, 2002). Yet, most people remain unaware of the diversity and complexity of protist cell biology, which is necessary to prevent crop damage, maintain livestock health, and to save human lives.

ACKNOWLEDGMENTS

Several colleagues have contributed through responding to emails or in conversations at conferences and elsewhere. These include Robert A. Andersen, Louise Lewis, Richard M. McCourt, Robert Fensome, Timothy Y. James, Laura Katz, Georges Merinfeld, and Gary Saunders.

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First submitted 22 January 2007; reviews returned 31 March 2007;

final acceptance 1 May 2007

Associate Editor: Tim Collins

Editor: Jack Sullivan