Published in Biological Journal of the Linnean Society 107, 469-476, 2012
which should be used for any reference to this work

Time to regulate microbial eukaryote nomenclature

DANIEL J. G. LAHR[1]*, ENRIQUE LARA[2] and EDWARD A. D. MITCHELL[2]

[1]*Department of Zoology, University of São Paulo, Rua do Matão, Travessa 14, #101, 05508-090 São Paulo, Brazil*
[2]*Laboratory of Soil Biology, University of Neuchâtel, Rue Emile-Argand 11, CH-2000 Neuchâtel, Switzerland*

Nomenclature of microbial eukaryotes has been historically relegated to secondary importance. This is a legacy of the traditional classification of life into the most studied multicellular forms (plants, fungi, and animals). Despite the revolution in an understanding of eukaryotic diversity and relationships that has been achieved as a result of the use of molecular techniques, the description of microbial eukaryote genera and species is more difficult today than in the past. Researchers are at liberty to choose between the botanical (in the traditional sense) and zoological codes of nomenclature, although there is no obligation to comply with either. We demonstrate that, by combining the foci of different nomenclature codes with the current knowledge of relationships, a large number of genera and species end up being regulated by two codes (Patterson's ambiregnal taxa) and, in some cases, may even be regulated by none. We briefly present historically proposed types of solutions to this problem, and propose that an elaboration of authoritative guidelines to regulate the nomenclature of microbial eukaryotes by the community of researchers is most appropriate at this time. Most importantly, we plead to the community of researchers to resolve this centuries old outstanding issue.

ADDITIONAL KEYWORDS: algae – biological names – codes – integrative taxonomy – protozoa – protistan.

INTRODUCTION

Carolus Linnæus revolutionized biology by introducing a binomial nomenclature system for plants and animals, in his famous *Systema Naturæ*. This major landmark led to the present systems of biological nomenclature, which developed largely throughout the 19th Century (Knapp *et al*., 2004). A little known fact about the *Systema Naturae* is that it largely ignored microbial eukaryotes, lumping the known diversity into a single genus, *Volvox* (Linnæus, 1758), even though a reasonable number of other organisms had been described by then. Noteworthy among these are the remarkable descriptions of genera made by John Hill, including *Paramecium* and *Cyclidium* (Hill, 1752); the many then-unnamed forms described by A. Leeuwenhoek [thoroughly reviewed in Dobell, (1932)]; and, later, the dozen or so ciliates described by Müller (1773) which were not included in subsequent editions of the system.

Contemporarily, microbial eukaryotes are recognized as an assemblage of many disparate lineages. For nomenclatural purposes, taxonomists treat each different protist lineage either as a 'plant' or an 'animal', and follow their respective codes (Corliss, 1992). One well known consequence of this system are the 'ambiregnal' organisms, which may be treated under both codes (Patterson, 1986; Patterson & Larsen, 1992). We advocate that the challenge today is to modify or rethink this system to make it compatible with modern knowledge and tools.

Biological nomenclature is regulated by codes designed to stabilize and standardize naming of biological entities (Knapp *et al*., 2004). In this manner, plants (together with fungi and algae), animals, bacteria, and viruses (as well as their respective fossils, fossil tracks, and other vestiges known as ichnotaxa) are regulated by different codes and follow slightly different rules, which broadly seek the same goals (Patterson & Larsen, 1992). Unregulated nomenclature may lead to confusion and imprecise naming, which is generally caused by two principal problems: using the same name for different taxa (homonymy) and using different names for the same taxa (synonymy). The solution for these two problems came with the elaboration of two key concepts: (1) typification, where a name is attached to a single taxon by a single designated specimen (in special cases, an illustration) that is the 'name-bearing type', in an exclusive relationship; and (2) the Principle of Priority, where the first name properly described provides the only correct name for a given taxon, and all subsequent names are synonyms. These two principles are at the core of type-based codes of nomenclature, with the remainder dealing mostly with legalistic measures to guarantee that these two principles are followed tidily.

Until recently, all codes were type-based in that they required the assignment of type specimens as a means of anchoring the imaginary human construction (the name) to reality (the name-bearing type). The Phylocode (Cantino & de Queiroz, 2010), a recent proposition aiming to deal with higher-level nomenclature, suggests that nomenclature can be based on phylogenetic hypotheses, and proposes that a number of 'identifiers' can be used instead of types (Cellinese, Baum & Mishler, 2012). The Phylocode has not been widely accepted and, at present, does not have regulatory power (Nixon, 2003).

With these simple guiding principles in mind, it is hard to consider that there are multiple type-based codes of biological nomenclature ruling at the same time, divided by discipline. This separation is based on tradition, an intellectual legacy of a time when major gaps separated biological taxa. In an age where unprecedented integration of knowledge is envisioned (Godfray, 2002; Garrity & Lyons, 2003; Godfray *et al.*, 2007; Clark *et al.*, 2009), it is truly intriguing that rules of nomenclature are specific for different organismal groups, which represents a major obstacle in the path of achieving a unified nomenclatural system that will benefit all of biology (Scoble, 2004; Patterson *et al.*, 2010; Deans, Yoder & Balhoff, 2012).

To evaluate the pertinence of existing systems, it is perhaps useful to ask the following question: if we were to create a nomenclatural system of all biological organisms taking into account all knowledge available to us today, would we create the systems that we now have or would we not rather create a single unified system for all organisms? What then is keeping us from taking the necessary action to unify the nomenclatural systems? The debate drags on for decades: the BioCode (Greuter *et al.*, 2011; Hawksworth, 2011), comprising the most serious initiative to install a unitary code, has not yet achieved full compliance subsequent to its conception in the mid-1990s, despite the many admirable features that it contains. We consider that one of the main reasons for this is the resistance against change from an already established community of researchers who are able to proficiently use their respective codes (Flann, 2011).

WHY CURRENT CODES ARE INADEQUATE FOR THE DESCRIPTION OF MICROBIAL EUKARYOTES

There are three major type-based codes: the 'Botanical code', formerly called International Code of Botanical Nomenclature (ICBN) and now called International Code of Nomenclature for algae, fungi, and plants (ICN) (Knapp, McNeill & Turland, 2011); the 'Zoological code', called International Code of Zoological Nomenclature (ICZN, 1999); and the 'Bacterial code', the International Code of Nomenclature of Bacteria (ICSP, 1990). There are further codes that deal more specifically with subsets or juxtapositions of the organisms already regulated by these three codes. For example, there is a code for cultivated plants [the International Code of Nomenclature for Cultivated Plants Brickell *et al.*, 2009], which regulates a subset of organisms already regulated by the ICN; and the Phylocode (Cantino & de Queiroz 2010), which attempts to regulate nomenclature of all organisms, including those that already have a regulatory code. This list is not exhaustive.

However, there are more types of organisms. Fungi are regulated by the ICN, despite the fact that we have known for at least for 20 years that they are phylogenetically closer to animals than to plants (Baldauf & Palmer, 1993), and have considered them a separate evolutionary entity since the inception of the five kingdom systems, more than 40 years ago (Whittaker, 1969). Viruses, for which there is an ongoing debate about their very organismal nature (Koonin, Senkevich & Dolja, 2009; Moreira & Lopez-Garcia, 2009; Navas-Castillo, 2009), are regulated by a specific nomenclatural code, the International Code of Virus Classification and Nomenclature (ICTV, 2005).

Yet, there are even more types of organisms. How should we deal with the diversity of single celled eukaryotes? The two classical codes ('Zoological' and 'Botanical') of taxonomic nomenclature are the legacy of a time when known biodiversity was mostly restricted to macroscopic plants, animals, and fungi (Rothschild & Heywood, 1988; Corliss, 1992; Patterson & Larsen, 1992). Microorganisms were starting to be described, although they were considered by most natural historians to be primitive animals or plants, and thus were assigned to either of the existing codes (Patterson, 1986).

THE PROBLEM OF TYPIFICATION OF MICROBIAL EUKARYOTES

One additional difficulty is that assigning name-bearing types to microbial eukaryotes is not as straightforward as in macro-organisms. Preservation is one problematic issue because most standard techniques yield non-usable or unrecognizable specimens (Bandoni & Duszynski, 1988). As a result, many genera and species were described without specific determination of a name-bearing type, as is the case for the heterotrophic flagellates *Katablepharis* and *Leukocryptus* (explained in Patterson & Larsen, 1992) and the majority of lobose testate amoebae (a thorough study is presented by Lahr, Bergmann & Lopes, 2008).

Alternatives to standard specimen-based typification have been proposed: photographs as name-bearing types (Duszynski, 1999), genomes, frozen cell lineages, etc. The current codes deal with this particular difficulty only to some extent (ICZN's hapantotypes), hence justifying the need for specific rules dealing with microbial eukaryotes. In practice, most modern mycologists and protistologists comply with the rules dictated by the ICNB (the 'bacterial code'), which requires that 'Whenever possible, the type of a species or subspecies is a designated strain' (Rule 18a). This strain has to be maintained in pure culture in a collection and made accessible to researchers. However, if a species has not been maintained in culture, or if the type strain does not exist, it is possible to use a description, preserved specimen or illustration as the type.

These rules are well-suited to eukaryotic micro-organisms: culture collections such as the American Type Culture Collection in the USA (ATCC) or the Centraalbureau voor Schimmelcultures in the Netherlands (CBS); and the Culture Collection of Algae and Protozoa in the UK (CCAP); already host large assemblages of microbial eukaryotes, and many are already designated as name-bearing types. Inorganic remains such as shells (tests) may also be used as type material by deposition in museums: for example, approximately 16 000 types of Foraminifera are stored in the Smithsonian collection. More fragile organisms (such as ciliates) are mounted and stained in permanent slides. Organisms that cannot be cultured and that leave no exploitable remains can still be described on the basis of drawings, micrographs and/or molecular sequences (*'Candidatus'* status), as allowed by the ICNB.

CODES AND THE ORGANISMS THEY REGULATE

We now highlight and comment on relevant portions in each of the different codes that determine the natural objects that each one regulates.

1. The International Code of Nomenclature of Bacteria, ICNB (ICSP, 1990) states the following in **General Consideration 5**: 'This *Code of Nomenclature of Bacteria* applies to all bacteria. The nomenclature of certain other microbial groups is provided for by other Codes: fungi and algae by the Botanical Code, protozoa by the Zoological Code, and viruses by the Virological Code when it is approved'. Hence, the International Committee on Nomenclature of Prokaryotes does not regulate in any way the nomenclature of single-celled eukaryotes.
2. The International Code of Virus Classification and Nomenclature, ICVCN (ICTV, 2005) deals very specifically only with viruses, and makes no claim or provides no overlap for the nomenclature of microbial eukaryotes.
3. The International Code of Botanical Nomenclature, recently renamed International Code of Nomenclature of algae, fungi and plants, *ICN* (Knapp *et al*., 2011) states in **Preamble 7** that: 'The rules and recommendations apply to all organisms traditionally treated as fungi, algae or plants, whether fossil or non-fossil, e.g. blue–green algae (*Cyanobacteria*), fungi (including chytrids, oomycetes, and slime moulds, but excluding *Microsporidia*), and photosynthetic protists with their taxonomically related non-photosynthetic groups'. Hence, the botanical code also partly regulates the nomenclature of bacteria.
4. The International Code of Zoological Nomenclature, *ICZN* (ICZN, 1999) includes microbial eukaryotes stating in **Article 1.1.1** that 'For the purposes of this Code the term "animals" refers to the Metazoa and also to protistan taxa when workers treat them as animals for the purposes of nomenclature'. There is even a further specification in case the taxon ends up classified as a different kind of organism in **Article 2.2**: 'Names of taxa at some time but not later classified as animals. Any available name of a taxon that has at any time been classified as animal continues to compete in homonymy in zoological nomenclature even though the taxon is later not classified as animal'.

The rules set by the codes of the two major macroscopic groups are in conflict when we consider modern knowledge of organismal classification. We will provide examples of four deep lineages, which present problems in terms of nomenclature. First, the Amoebozoa and the Alveolata, which present problems with legacy names, and then the Billiphytes and the Breviata, which present problems with new names.

Most organisms in the Amoebozoa (Fig. 1) were treated at some time as 'primitive' animals (protozoa), and hence fill the prerequisite for inclusion in the ICZN. Both major types of slime molds are within the Amoebozoa, although relationships between them are still debated. The slime molds are explicitly included in the ICN. Hence, the nomenclature of some members of Amoebozoa is regulated by both codes (i.e. a dictyostelid slime mold species name is regulated at the same time by the ICZN and the ICN) and the Amoebozoa, as a single evolutionary lineage, has different members regulated by two different codes.

Similarly, the dinoflagellates are regulated by the ICN because they were traditionally treated as plants (as dictated by Preamble 7). However, they belong to the same deep lineage (Alveolata) as the ciliates, which are regulated by the ICZN code. The Alveolata thus have different members regulated by different codes. Indeed, the same reasoning can be applied to many higher-level groupings of Eukaryotes (Fig. 1). An even more dramatic case occurs when different life stages of the same organism may be ruled by different codes: the amoeboflagellate taxon *Hyperamoeba*, traditionally treated within the ICZN, turned out to be the solitary stage of several disparate myxogastrids (i.e. slime molds) that are ruled by the ICN (Dykova *et al*., 2007).

The newly-described Billiphyta (or Picobiliphyta) present difficulties regarding the creation of new names. These organisms have been tentatively placed in the lineage Hacrobia (Okamoto *et al*., 2009), although their precise phylogenetic position still remains to be confirmed. Their very existence was acknowledged by environmental DNA screening (Romari & Vaulot, 2004). They were later suggested to be photosynthetic (Not *et al*., 2007), thus being considered algae and claimed by the ICN. However, a single-cell genomic study on three distantly-related biliphyte cells failed to find plastid DNA or nuclear-encoded plastid genes, thus demonstrating the existence of non-photosynthetic species in the group (Yoon *et al*., 2011). If biliphytes turn out to be primarily heterotrophic, researchers who discover new genera and species in this group are at liberty to either: treat them as 'relatives of photosynthetic organisms' under Preamble 7 of the ICN, or follow ICZN's Article 1.1.1 and treat them as 'nomenclatural animals', thus giving rise to yet another ambiregnal taxon.

Concurrently, there are groups for which no code needs to be applied, for example, the newly-described Breviata (Fig. 1). Although there is still some uncertainty about their exact phylogenetic position, the breviates are either within Amoebozoa or basal to the Amoebozoa + Opisthokonta clade. Hence, neither code explicitly regulates breviate names, although researchers may choose to follow the ICZN, in accordance with Article 1.1.1. The descriptions of the two existing breviate genera are in general agreement with the ICZN (Walker, Dacks & Martin Embley, 2006; Katz *et al*., 2011). However, further researchers are not required to comply with the rules of the ICZN, which may lead to confusion. Additionally, novel deep, non-photosynthesizing lineages may be discovered that do not permit designation of name-bearing types that the ICZN considers valid. In this hypothetical case, the lineage cannot be described in accordance with any code.

The inadequate treatment by different nomenclature codes results in confusion for the description of microbial eukaryotic taxa, principally at the basic levels of genera and species. Descriptions of genera and species form the foundation upon which classification systems are built. The names assigned in these descriptions are the currency with which biological information is traded (Patterson *et al*., 2010). Without explicitly tailored rules for microbial eukaryote genera and species, we expect confusion to permeate all taxa. This difficulty in establishing proper names is routinely faced by researchers, although it often remains concealed in backstage discussions between authors, reviewers, and editors.

One solution is to follow recommendations in more than one code of nomenclature to ensure that the newly-described genus or species is valid. A current example is the description of novel acrasid species by Brown, Silberman & Spiegel (2012). Acrasids in the strict sense are Heterolobosea, which are phylogenetically nested within the Excavata (Parfrey *et al*., 2010). They were once considered slime molds, and hence regulated by the ICN as are all fungi. The novel positioning has made the authors describe a series of new species seeking to comply with both the ICZN and ICN (including the now revoked ICN requirement of a Latin diagnosis). Besides being an unfair burden to be born by researchers of microbial eukaryotes, the necessity to observe regulations in multiple codes will likely lead to reduced compliance.

NO SIMPLE SOLUTION

Over the years, a number of different ideas have been presented aiming to deal with this problem. The solutions suggested so far fall into three main categories: (1) creating a unified system of nomenclature (Scoble, 2004); (2) creating a separate nomenclatural system for microbial eukaryotes only (Rothschild & Heywood, 1988) or; (3) finding a way to 'fit' microbial eukaryotes

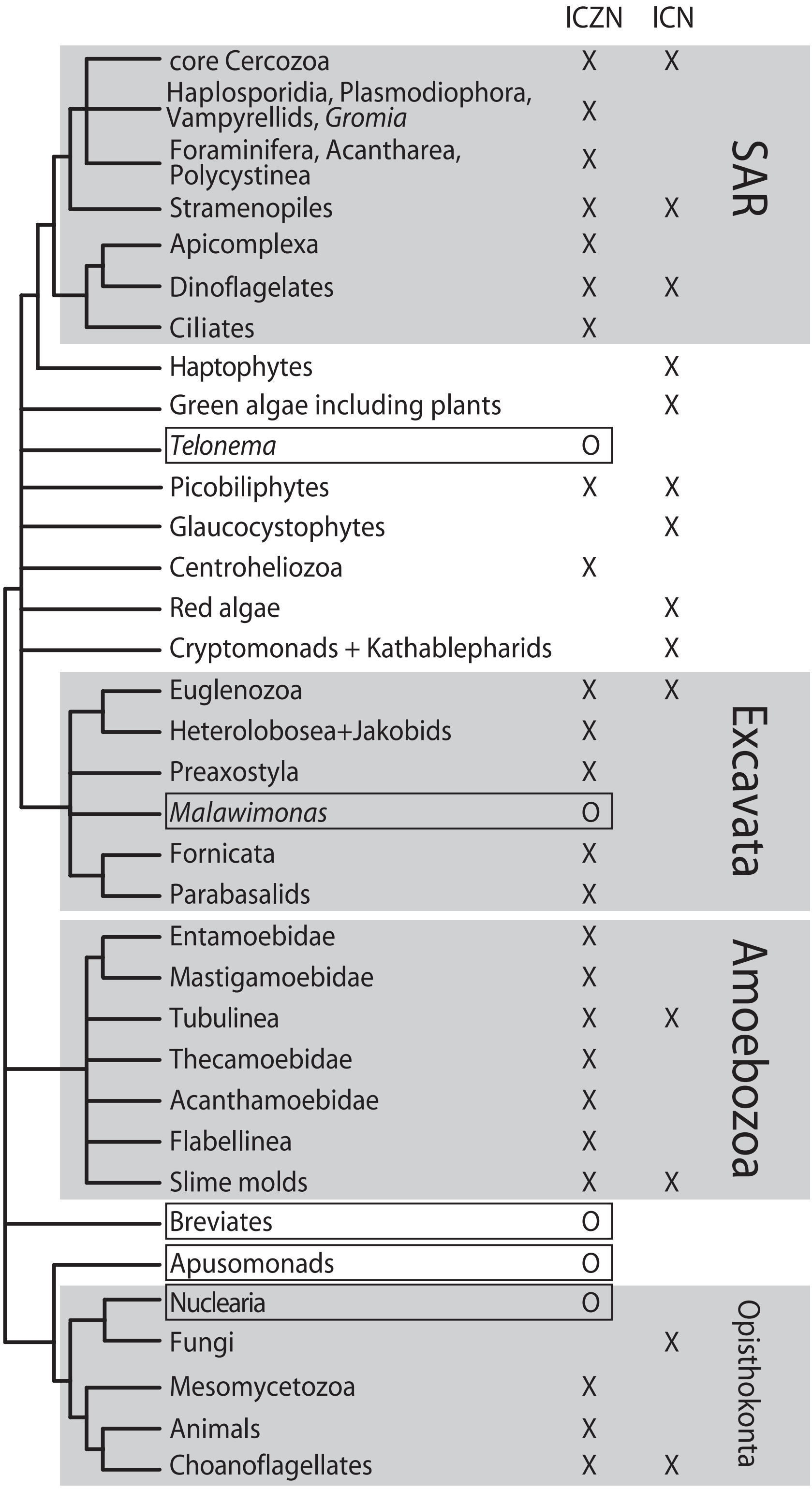

Figure 1. A summary of current code claims, plotted on a consensual tree of eukaryotes, modified from Parfrey *et al*. (2010). X, respective code officially regulates nomenclature for the group; O, possible regulation according to Article 1.1.1 of the International Commission on Zoological Nomenclature (ICZN) . Under this article, any organism may be treated as an animal for nomenclatural purposes, if the author so chooses; hence, we regard this regulation as optional (O). ICN, International Code of Nomenclature for algae, fungi, and plants.

into existing systems, which is currently the case. A number of additional issues associated with organisms potentially treated by multiple codes, such as difficulty in establishing priority of a name, have been discussed elsewhere (Corliss, 1992; Patterson & Larsen, 1992), and these will need to be dealt with specifically regardless of what kind of solution is adopted. It is important to emphasize that these are very present issues that need solutions.

We advocate that the best solution, for a number of reasons, is the adoption of a single code. The advantages of this approach have been extensively discussed elsewhere, and a very mature proposition is available in the form of the BioCode (Greuter *et al*., 2011). This has not been widely adopted (yet), and hence does not solve the immediate problem of microbial eukaryote nomenclature.

A more pragmatic solution would be to elaborate the long delayed Code for Nomenclature of Microbial Eukaryotes (CNME). Such a code would need to acknowledge the existence of other codes, and be non-independent, to achieve the goal of stability. The CNME should be designed so as to enable integration of the ICZN and ICN, with a typification protocol derived from the ICBN, pending some adjustments (at the very least solving homonyms resulting from a fusion). Further desirable features will likely be similar to those previously outlined by Patterson & Larsen (1992).

However, generating yet another code of nomenclature, which repeats the same rules of both *the ICZN and ICN*, could also be redundant. A more direct solution can be considered. This may not be the silver bullet that we all are hoping for, although it can solve problems relating to day-to-day taxonomic work.

Our proposition is that the research community of microbial eukaryotic taxa come together and generate a list of 'Guidelines for the Nomenclature of Microbial Eukaryotes'. One suitable stage for this discussion is the yearly meeting promoted by the International Society of Protistologists (ISoP). After discussion with the broad community, a smaller committee of experts in diverse areas of eukaryotic microbiology should generate a document with guidelines that will be commonly accepted by the entire community. This list of guidelines may either be formally adopted by the Society with the publication of an independent document (online or otherwise), or suggested as an authoritative annex to the Biocode with the International Union of Biological Sciences/International Union of Microbiological Societies International Committee for Bionomenclature (the reasoning for this is that the Biocode is the suggested universal code of nomenclature). A non-exhaustive list of urgently needed guidelines to be discussed is given below:

1. Separate treatment between legacy and new names to ensure future stability at the same time as dealing with inconsistencies of the past.
2. Definition of code-organism relationship: an authoritative list that supersedes decisions made by each individual code, and assigns which set of rules should be followed for description of new names by researchers of different groups of microbial eukaryotes.
3. Non-independence of codes: for the purposes of microbial eukaryote nomenclature, the ICN and ICZN Codes cannot be independent. The consequences of this action both to protistan nomenclature and to plant and animal taxa will need to be evaluated carefully.
4. Establishment of different start dates for new and legacy microbial eukaryote names.
5. Definition of rules to deal with multicode homonyms – decisions will need to be adopted by users of other codes, and this might be problematic. For novel names, full compliancy with both codes should be required. Legacy names may be fully compliant with both codes, as well as a homonym. A specific decision needs to be made in these cases, whether homonymy will be accepted or a number of well-known names should be changed.
6. Periodic publication of a list of approved microbial eukaryotic names.
7. Accepted methods of typification.
8. All other minutiae to be dealt by specific rules in each code, except the following five serious issues, which will need to be specifically dealt with: (1) tautonimy (use of same word for both genus and species epithets); (2) allowed Latin words for name formation; (3) allowed ranks and rank names, if any; (4) formation of family- and genus-group names; and (5) ichnotaxa.

There are further issues where the study of microbial eukaryotes would benefit from having a specifically regulated nomenclatural system. Taxa discovered using culture independent molecular analyses are a significant and important part of modern microbial eukaryote systematics, from deep level lineages (Dawson & Pace, 2002) to lineages within alveolates, stramenopiles (Massana & Pedros-Alio, 2008), basal fungi (Lara, Moreira & López-García, 2010), and foraminifera (Habura *et al*., 2008). Breviates themselves were originally identified molecularly from environmental samples (Walker *et al*., 2006). Additionally, the contemporary issue of *e*-publication may be addressed because many of the relevant journals that contribute to microbial eukaryote systematics are only published electronically.

CONCLUSIONS

We would like to conclude by pointing out that, although comprising a heated topic of discussion during the 1980s (Corliss, 1992), three decades have passed and no solid solution has been proposed for the nomenclatural problem in microbial eukaryotes. This is a problem with potentially large consequences. First, it is now clear that biological diversity is composed of a large (perhaps dominant) microbial component (López-García *et al*., 2001; Pedrós-Alió, 2006). We argue that this component is not compatible with the existing categories of organisms for which nomenclatural systems were designed. Second, major research initiatives such as the barcoding of life and the use of massive sequencing are revealing huge unknown diversity that overwhelms all previous expectations (Caron *et al*., 2012). Unless a unified (and simple) system of nomenclature is established quickly, we face the risk that a very large number of species [estimates are conservatively in the thousands (Mora *et al*., 2011) but may reach millions (Decaëns, 2010)] fundamental to earth's processes (Field *et al*., 1998) will never be properly described and remain in a 'grey zone' of taxonomic knowledge.

ACKNOWLEDGEMENTS

We thank Antonio Carlos Marques for many useful discussions on this issue. We are also very appreciative of the many insightful comments and criticisms received from Malcolm J. Scoble and four anonymous reviewers. Their work enabled a great improvement over an earlier version of this manuscript. This work was supported by a CNPq Post-Doctoral Fellowship (501089/2011-0) to D.J.G.L., a SNSF (Swiss National Science Foundation) Ambizione fellowship (PZ00P2-122042) to E.L., SNSF projects no. 205321-109709/1 and 205321-109709/2 to E.A.D.M., and Science and Technology Cooperation Program Switzerland – Russia grant IZLR Z3_128338 to E.L. and E.M.

REFERENCES

Baldauf SL, Palmer JD. 1993. Animals and fungi are each other's closest relatives: congruent evidence from multiple proteins. *Proceedings of the National Academy of Sciences of the United States of America* **90:** 11558–11562.

Bandoni SM, Duszynski DW. 1988. A plea for improved presentation of type material for coccidia. *Journal of Parasitology* **74:** 519523.

Brickell CD, Alexander C, David JC, Hetterscheid WLA, Leslie AC, Malecot V, Jin X. 2009. *International code of nomenclature for cultivated plants*. Leuven, Belgium: International Society for Horticultural Sciences.

Brown MW, Silberman JD, Spiegel FW. 2012. A contemporary evaluation of the acrasids (Acrasidae, Heterolobosea, Excavata). *European Journal of Protistology* **48:** 103–123.

Cantino PD, de Queiroz K. 2010. *International code of phylogenetic nomenclature*, Version 4c. Available at: http://www.ohio.edu/phylocode/.

Caron DA, Countway PD, Jones AC, Kim DY, Schnetzer A. 2012. Marine protistan diversity. *Annual Review of Marine Science* **4:** 467–493.

Cellinese N, Baum DA, Mishler BD. 2012. Species and phylogenetic nomenclature. *Systematic Biology*. doi: 10.1093/sysbio/sys035.

Clark BR, Godfray HCJ, Kitching IJ, Mayo SJ, Scoble MJ. 2009. Taxonomy as an eScience. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* **367:** 953–966.

Corliss JO. 1992. Should there be a separate code of nomenclature for the protists? *Biosystems* **28:** 1–14.

Dawson SC, Pace NR. 2002. Novel kingdom-level eukaryotic diversity in anoxic environments. *Proceedings of the National Academy of Sciences of the United States of America* **99:** 8324–8329.

Deans AR, Yoder MJ, Balhoff JP. 2012. Time to change how we describe biodiversity. *Trends in Ecology & Evolution (Personal edition)* **27:** 78–84.

Decaëns T. 2010. Macroecological patterns in soil communities. *Global Ecology and Biogeography* **19:** 287–302.

Dobell C. 1932. *Antony van Leeuwenhoek and his 'Little animals'*. New York, NY: Harcourt, Brace and company.

Duszynski DW. 1999. Revisiting the code: clarifying name-bearing types for photomicrographs of protozoa. *Journal of Parasitology* **85:** 769–770.

Dykova I, Lom J, Dvorakova H, Peckova H, Fiala I. 2007. Didymium-like myxogastrids (class Mycetozoa) as endocommensals of sea urchins (*Sphaerechinus granularis*). *Folia Parasitol (Praha)* **54:** 1–12.

Field CB, Behrenfeld MJ, Randerson JT, Falkowski P. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* **281:** 237–240.

Flann CM. 2011. Biocode: third time lucky? *Zootaxa* **2874:** 38–40.

Garrity GM, Lyons C. 2003. Future-proofing biological nomenclature. *OMICS* **7:** 31–33.

Godfray HCJ. 2002. Challenges for taxonomy. *Nature* **417:** 17–19.

Godfray HCJ, Clark BR, Kitching IJ, Mayo SJ, Scoble MJ. 2007. The web and the structure of taxonomy. *Systematic Biology* **56:** 943–955.

Greuter W, Garrity GM, Hawksworth DL, Jahn R, Kirk PM, Knapp S, McNeill J, Michel E, Patterson DJ, Pyle RL, Tindall BJ. 2011. Draft BioCode (2011): principles and rules regulating the naming of organisms. *Taxon* **60:** 201–202.

Habura A, Goldstein ST, Broderick S, Bowser SS. 2008. A bush, not a tree: the extraordinary diversity of cold-water basal foraminiferans extends to warm-water environments. *Limnology and Oceanography* **53:** 1339–1351.

Hawksworth DL. 2011. Introducing the draft BioCode (2011). *Taxon* **60:** 199–200.

Hill J. 1752. *An history of animals*. London: Thomas Osborne.

International Commission on Systematics of Prokaryotes. 1990. *International code of nomenclature of bacteria bacteriological code, 1990 revision*. Washington, DC: ASM Press.

International Commission on Zoological Nomenclature. 1999. *International code of zoological nomenclature*. London: International Trust for Zoological Nomenclature.

International Committee on the Taxonomy of Viruses. 2005. The international code of classification and nomenclature of viruses. In: Fauquet CM, Mayo MA, Maniloff J, Desselberger U, Ball L, eds. *Virus taxonomy: eighth report of the International Committee on Taxonomy of Viruses*. Amsterdam: Elsevier Academic Press, 1209–1214.

Katz LA, Grant J, Parfrey LW, Gant A, O'Kelly CJ, Anderson OR, Molestina RE, Nerad T. 2011. Subulatomonas tetraspora nov. gen. nov. sp. is a member of a previously unrecognized major clade of eukaryotes. *Protist* **162:** 762–773.

Knapp S, Lamas G, Lughadha EN, Novarino G. 2004. Stability or stasis in the names of organisms: the evolving codes of nomenclature. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **359:** 611–622.

Knapp S, McNeill J, Turland NJ. 2011. Fungal nomenclature. Changes to publication requirements made at the XVIII International Botanical Congress in Melbourne what does e-publication mean for you? *Mycotaxon* **117:** 509–515.

Koonin EV, Senkevich TG, Dolja VV. 2009. Compelling reasons why viruses are relevant for the origin of cells. *Nature Reviews Microbiology* **7:** 615–615.

Lahr DJG, Bergmann PJ, Lopes SGBC. 2008. Taxonomic identity in microbial eukaryotes: a practical approach using the testate amoeba centropyxis to resolve conflicts between old and new taxonomic descriptions. *Journal of Eukaryotic Microbiology* **55:** 409–416.

Lara E, Moreira D, López-García P. 2010. The environmental clade LKM11 and rozella form the deepest branching clade of fungi. *Protist* **161:** 116–121.

Linnæus C. 1758. *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis.* Tomus I. Editio decima, reformata. Salvius.

López-García P, Rodríguez-Valera F, Pedrós-Alió C, Moreira D. 2001. Unexpected diversity of small eukaryotes in deep-sea Antarctic plankton. *Nature* **409:** 603–607.

Massana R, Pedros-Alio C. 2008. Unveiling new microbial eukaryotes in the surface ocean. *Current Opinion in Microbiology* **11:** 213–218.

Mora C, Tittensor DP, Adl S, Simpson AGB, Worm B. 2011. How many species are there on earth and in the ocean? *PLoS Biology* **9:** e1001127.

Moreira D, Lopez-Garcia P. 2009. Ten reasons to exclude viruses from the tree of life. *Nature Reviews Microbiology* **7:** 306–311.

Müller OF. 1773. *Vermium terrestrium et fluviatilium, seu animalium infusoriorum, helminthicorum, et testaecorum, non marinorum, succincta historia*. Copenhagen and Leipzig: Havniae & Lipseae.

Navas-Castillo J. 2009. Six comments on the ten reasons for the demotion of viruses. *Nature Reviews Microbiology* **7:** 615–615.

Nixon KC. 2003. The phylocode is fatally flawed, and the 'Linnaean' system can easily be fixed. *Botanical Review* **69:** 111–120.

Not F, Valentin K, Romari K, Lovejoy C, Massana R, Tabe K, Vaulot D, Medlin LK. 2007. Picobiliphytes: a marine picoplanktonic algal group with unknown affinities to other eukaryotes. *Science* **315:** 253–255.

Okamoto N, Chantangsi C, Horak A, Leander BS, Keeling PJ. 2009. Molecular phylogeny and description of the novel katablepharid *Roombia truncata* gen. et sp. nov., and establishment of the hacrobia taxon nov. *PLoS ONE* **4:** e7080.

Parfrey LW, Grant J, Tekle YI, Lasek-Nesselquist E, Morrison HG, Sogin ML, Patterson DJ, Katz LA. 2010. Broadly sampled multigene analyses yield a Well-resolved eukaryotic tree of life. *Systematic Biology* **59:** 518–533.

Patterson DJ. 1986. Some problems of ambiregnal taxonomy and a possible solution. *Symposia Biologica Hungarica* **33:** 87–93.

Patterson DJ, Cooper J, Kirk PM, Pyle RL, Remsen DP. 2010. Names are key to the big new biology. *Trends in Ecology & Evolution* **25:** 686–691.

Patterson DJ, Larsen J. 1992. A perspective on protistan nomenclature. *Journal of Eukaryotic Microbiology* **39:** 125–131.

Pedrós-Alió C. 2006. Marine microbial diversity: can it be determined? *Trends in Microbiology* **14:** 257–263.

Romari K, Vaulot D. 2004. Composition and temporal variability of picoeukaryote communities at a coastal site of the English Channel from 18S rDNA sequences. *Limnology and Oceanography* **49:** 784–798.

Rothschild LJ, Heywood P. 1988. Protistan nomenclature: analysis and refutation of some potential objections. *Biosystems* **21:** 197–202.

Scoble MJ. 2004. Unitary or unified taxonomy? *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **359:** 699–710.

Walker G, Dacks JB, Martin Embley T. 2006. Ultrastructural description of breviata anathema, N. Gen., N. Sp., the organism previously studied as 'mastigamoeba invertens'. *Journal of Eukaryotic Microbiology* **53:** 65–78.

Whittaker RH. 1969. New concepts of kingdoms of organisms. *Science* **163:** 150–160.

Yoon HS, Price DC, Stepanauskas R, Rajah VD, Sieracki ME, Wilson WH, Yang EC, Duffy S, Bhattacharya D. 2011. Single-cell genomics reveals organismal interactions in uncultivated marine protists. *Science* **332:** 714–717.