

Concepts in protistology: Species definitions and boundaries

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Abstract

This paper summarises the Symposium ‘Concepts in Protistology’, during the VI European Congress of Protistology, Berlin, 25–29 July 2011. There is an increasing focus on cataloguing the number of species on earth, species barcoding initiatives, and the increasing need to reconcile molecular with morphological data in protists within a taxonomic framework. We identify several obstructions to defining species in protists, including the high incidence of asexuality, high levels of both morphological conservation and evolutionary convergence, high levels of genetic diversity that cannot so far be correlated with phenotypic characters, conflicting signals between both genetic and phenotypic taxonomic markers, and different requirements and challenges of species definition in different protist groups. We assert that there is no species ‘category’ for protists, and recommend that a working definition of species is clarified on a case-by-case basis. Thus, a consensus approach may emerge within protist groups, but any one approach is unlikely to encompass a wide phylogenetic range. However, as long as clarity of intent and method is maintained, the utility of the term ‘species’ in protists will also be maintained as a reproducible and convenient (if artificial) way of referring to particular lineages within a tightly defined context.

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Introduction

Although the high-level taxonomy of protists is a well-grounded (although not resolved) area of research, the opposite end of the taxonomic spectrum, alpha-taxonomy, and what constitutes protist species are issues fraught with uncertainty and disagreement. The fact that there is no generally accepted basis for delimiting species in protists has many unfortunate consequences, prime among them being (1) a

lack of basic communicability about fundamental biological units (with obvious negative implications for barcoding), (2) lack of clarity regarding their evolutionary and ecological significance, and (3) a drastic underestimation of protist diversity and importance in more general biodiversity papers. A good example of the latter is shown by Mora et al. (2011), in which (by no fault of theirs) estimates of species numbers of protists (in particular) are unrealistically depressed, in part because of the problem with defining ‘species’ and also because of the rapidly changing and relatively unstructured nature of protist taxonomy overall.

The ECOP workshop did not set out to ‘decide’ on the ‘best’ species concept to apply to protists, but rather to assess

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to what extent such a concept is possible, or even desirable, and what the best working bases for protist alpha-taxonomy should be. The main body of this paper summarises the issues and outcomes of the interactive process culminating in the oral presentations. The individual contributions of the authors are reproduced in the three supplementary files.

The historical context: shifts in the conception of megasystematics and species

The era of protistology has seen major methodological advances starting with the invention of simple microscopes, which allowed the first visualization of individual microbes by Leeuwenhoek in 1674 (cf. Dobell 1932). Early observers lumped the small microorganisms into broad categories, for instance as “*Vermis punctiformis*” (cf. the genus *Monas* Müller 1773), as “Punktthierchen”, “Kugelthierchen” and “Ovalthierchen” (von Gleichen and Freiherr 1778; compare also *Monas punctum* Ehrenberg 1838), or in the genus *Chaos* (Linnaeus 1758). The general system achieved by the end of the 19th century (cf. Bütschli 1880–89; Doflein 1916; Kent 1880–81; Pascher and Lemmermann 1914) remained in place for most of the 20th century. The general quality of the taxon diagnoses of protists improved little during this time and was largely based on light microscopy, even though the invention of electron microscopy in the 1930s (cf. Agar 1996) further increased taxonomic resolution.

The advent of molecular methods in the 1990s provided a very different perspective on microbial eukaryotic diversity. Many new genetic lineages were detected, a substantial number of which were highly distinct from those previously known, suggesting novel elements of biodiversity at high taxonomic ranks. At the other end of the scale, very high levels of genetic diversity were found within and around already known lineages, suggesting an abundance of cryptic species and sister taxa. Another revelation was that protist morphology is highly and often surprisingly convergent – for example ‘amoebae’ are found over most of the tree of life, classical Heliozoa and Radiolaria are several fold polyphyletic, and many lineages that were thought to be fungal were shown to branch elsewhere on the tree when placed by molecular phylogenetics (fungal analogues such as oomycetes, plasmodiophorids, labyrinthulids, etc.). Thus another layer of poorly resolved complexity was added to the already muddled story emerging from earlier morphological studies.

A recent approach for overcoming the drawbacks of insufficient taxonomic coverage of the studied diversity is the use of operational taxonomic units (OTUs) (e.g. Green et al. 2004). Especially in sequence-based diversity studies, such OTUs are defined by using sequence similarity or distance thresholds (e.g., Schloss and Handelsman 2005). In many cases these OTUs were treated synonymous to species, and were used, for instance, for the estimation of species richness data. The taxonomic power of lumping together organisms in OTUs based on sequence similarities was never evaluated

for eukaryotic microorganisms. However, in the case of prokaryotes the underestimation of real species numbers by approaches defining OTUs based on 16S rRNA sequences is obvious (Stackebrandt and Ebers 2006).

A consistent species concept for protists?

Biodiversity research and ecology rely on safe identifications of species and on reproducible species counts, but often this requirement is not met. Various problems result from partially inconsistent species concepts, insufficient taxonomic coverage (undersampling), and uncertainty about which characters should best be used as bases for deciding species boundaries. Recent methodological progress has highlighted severe inconsistencies between the conceptual and the practical historic approaches to species and biodiversity. The dispute is currently stirred up by inconsistencies between molecular phylogenies on the one hand and morphological species denominations and traditional classification concepts on the other.

The conceptual conflict embraces the differences between zoological, botanical, and microbiological concepts of species. Due to ambiguous, contradictory and/or inconsistent species descriptions, species numbers obtained from biodiversity surveys using the traditional morphospecies concept are not comparable to those obtained from environmental DNA. As different methodological approaches are – in part – linked to different concepts of species and of diversity the dispute on protist species, protist diversity, and protist systematics often fails to differentiate differences in the conceptual basis from methodological limitations and real variation. For instance, the existence of newly revealed cryptic species obviously results in increasing biodiversity estimates. By contrast, taxon-independent (OTU-based) diversity studies as often applied for microorganisms tend to fail to resolve species and thus tend to underestimate biodiversity. This basic problem has many consequences, and represents a serious obstacle to understanding key aspects of protist biology and ecology, for example the ‘everything is everywhere’ debate and the perception of protist biodiversity.

In this paper we review the difficulties and challenges of alpha-taxonomy and species delineation. We do not attempt to review each protist group in an attempt to decide how the basic taxonomic units in each group should be defined; that is up to the experts working on them. However, examples are given from some of the groups in which the authors do have expertise, and the inclusion of some very well-studied metazoa provides a phylogenetically distant but conceptually relevant and informative perspective on issues which are often thought to be particularly problematic in protists. A significant element of our discussion is not associated with any organismal group, but considers the ‘problem’ from a philosophical/logical standpoint, which we feel offers perhaps the strongest direction and encouragement for alpha-taxonomy. We see the key issues in protist alpha-taxonomy to be:

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