THE NEED FOR A NEW LOOK AT THE TAXONOMY OF THE PROTISTS*

La necesidad de un nuevo enfoque a la taxonomía de los protistas

John O. Corliss **

* This paper is dedicated to the memory of the late Professor Enrique Beltrán, a collegue and friend without peer in areas of both general protistology and the history of biology. I am indebted to him for the inspiration and stimulation he kindly to me over the years of our long acquaintance.

** P. O. Box 53008, Albuquerque, New Mexico 87153, USA. Miembro Honorario de la Sociedad Mexicana de Historia Natural.

ABSTRACT

As the research literature on the protists continues to grow, new data -- especially of an ultrastructural or molecular nature -- are accumulating that bear directly on the systematics (as well as evolution and phylogeny) of these biologically diverse forms of life. In this paper, the conclusion is drawn that the microbial eukaryotes now require assignment to multiple kingdoms within the empire EUKARYOTA. A six-kingdom system is endorsed here, with 34 protistan phyla assigned to them. Three of the kingdoms also contain phyla of plants, fungi, and animals.

RESUMEN

Dado que la literatura sobre la investigación de los protistas continúa aumentando, nuestros datos especialmente de naturaleza ultraestructural o molecular siguen acumulándose, e inciden sobre la sistemática (también sobre la evolución y filogenia) de esas diversas formas de vida. En este trabajo se concluye que los eucariotes microbianos requieren ser asignados a múltiples reinos dentro del imperio EUKARYOTA. Es propuesto un sistema de seis reinos con 34 phyla de protistas asignados a ellos. Tres de los reinos también contienen phyla de plantas, hongos y animales.

Brief Introduction and Considerations

After many decades of high-level taxonomic neglect, the diverse eukaryotic organisms best known as "the protists" (mostly microscopic, single-celled forms of algal or protozoan life occurring ubiquitously in all kinds of habitats on Earth) have become of increasing interest to research biologists of many persuasions, not only because of their practical importance to human beings in multiple ways but particularly because of the growing recognition of their great phylogenetic significance in the evolution of all life on this planet. Some 25 years ago, fundamentally following the original iconoclastic views of E. Haeckel (1866,1878), a unique kingdom PROTISTA was (re) recognized as a taxonomic bridgegapper between the prokaryotes (essentially the bacteria *sensu lato)* and the well-known "higher" eukaryotes (the multicellular, often multitissued groups formally recognized as the Plantae, Animalia, and Fungi). Much credit for this neoHaeckelian or "protistan prospective" properly goes to Dr. Lynn Margulis, who widely and stimulatingly publicized such a revolutionary and heuristic approach during the 1970s and the 1980s (e.g., see Margulis, 1970, 1974;Margulis *et al*., 1990; Margulis and Schwartz, 1982, 1988; Whittaker and Margulis, 1978).

Readers interested in more details concerning the background for the still widely held idea that these evolutionarily pivotal forms comprise a single kingdom PROTISTA are referred to several pertinent overviews by the author (Corliss, 1984, 1986, 1987, 1994a) and by others (e.g., Fernández-Galiano, 1990 and López-Ochoterena, 1991). And hypotheses concerning their specific role(s) as progenitors of the "higher" eukaryotic groups, a topic mostly beyond the scope of the present paper, have been discussed in recent reviews by Corliss (1989), Denis and Mignot (1994), López-Ochoterena (1994), and Wainright *et al.* (1993).

How are we to treat the overall highest-level systematics of the phylogenetically diverse assemblage of "lower" eukaryotes -that is, the protists- in light of the most uptodate information concerning their comparative taxonomy and their evolutionary interrelationships based largely on ultrastructural and molecular data? That is the formidable challenge facing us today, as we find ourselves in the closing years of the twentieth century.

In brief, then, what are the options available to us for solving this rather pressing problem, an answer to which is badly needed by teachers, students, and researchers alike, as well as by persons responsible for setting up biological information retrieval systems and for organizing slide and culture collections? An overall useful and usable taxonomy of protists and their relatives represents an inevitable pragmatic need, despite our continuing lack of additional data required to resolve debatably controversial points. An absolutely *ideal* hierarchical classification system can, obviously, never be achieved. Any tentatively adopted scheme must allow for sufficient flexibility to absorb (future) changes dictated by fresh data and new analyses. Four options are considered in this paper, solutions slightly modified and updated from those presented by Corliss (1994b).

A Single Kingdom Protista

This solution is still considered an ideal one by a number of workers. And it is the one most convenient for teachers of biology at many educational levels, since it properly emphasizes recognition of a vast assemblage of diverse forms that appear to lie, evolutionarily, in an intermediate position between the bacteria (the prokaryotes) and the so-called "higher" eukaryotes, the latter groups so familiar to students everywhere. This view emphasizes the "protist perspective," properly focusing our attention on the role of protists in the overall phylogeny of life on Earth. It stresses the importance of the use of protists in research on such major phenomena as endosymbiosis, crucial in evolution but largely neglected until recently (Margulis, 1993).

A separate kingdom PROTISTA is described as a salient part of a five-kingdom system (Margulis and Schwartz, 1988), an appealing textbook oriented treatment that will likely y remain pedagogically popular for many years to come, as mentioned above. Unfortunately (in a way), this otherwise neat approach fails to give proper recognition to the accumulating evidence that the protists, overall, are simply *too* diverse an assemblage phylogenetically to be forced taxonomically into a *single* kingdom.

A number of research biologists have been aware of this fact for some years but have seemed reluctant to express it clearly in print or to offer alternative solutions to the vexatious problem (see section: Multiple Kingdoms in a Hierarchical System, below). Assigning all protists to a single high-level group, while taxonomically convenient, cannot be considered a satisfactory solution, in view of the pertinent evolutionary data now available to us.

Protistan Groups as Evolutionary Grades

This proposed solution of how to treat the protists, popular among a number of evolutionary biologists, holds that present-day "lower" eukaryotes represent simply remnants of forms once serving as phylogenetic links between prokaryotic progenitors and our current more complex metazoan and metaphytan assemblages. The importance of protists as (a) pivotal group(s) is, in a way, emphasized by the hypothesis; and underscoring the structural continuity in the evolutionary sequence of life forms is commendable (unicellularity preceding multicellularity, etc.).

The major disadvantage of this approach is that it denies taxonomic *integrity* to the protists. It allows no independent hierarchical arrangement of the microbial eukaryotes into high-level taxa equivalent to those recognized for plants and animals. Furthermore, there appear to be major assemblages of protists that are totally separate from or independent of other groups of organisms, living or fossil. That is, by no means have all the unicellular taxa recognized today served only the function of being temporary phylogenetic way-stations enroute to evolutionarily "higher" forms of life.

Thus, while this hypothesis for the protists --grades without formal taxonomic status -- may merit consideration and might indeed, hold true in certain cases, it seems to beg the question of the major place or role of protists over time in the entire biotic world.

Un-Ranked, Non-Hierarchical Clades

In very recent years, the concept that diverse groups of protists represent separate evolutionary lines or diverging lineages (i.e., clades) which may have no discernible *taxonomic* relationship to each other has become popular with several schools of protistology (e. g., see Leipe and Hausmann, 1993; Lipscomb, 1991; Patterson, 1994; Patterson and Sogin, 1993; Schlegel, 1991: Sogin, 1989, 1991; Sogin *et al.,* 1989). Ideally, such clades are *monophyletic* in nature -- that is, groups/taxa included within such a lineage are all those derived evolutionarily from a single ancestral group, which is also a member of the clade (Wiley, 1981). To date, strict monophyly has been difficult to demonstrate or prove in numerous cases of clusters of protists species; however, the number of successful instances is rapidly increasing with the rigorous application of ultrastructural and molecular techniques and the use of sophisticated methods of analysis of the data so obtained (reviewed in Patterson, 1994).

The major problem here is that, generally, cladistic "trees" are not easily transformable into hierarchical *classification* schemes of the conventional type. In fact, as Patterson (1994, page 11) candidly states, representing the cladistic point of view, "Ranks are irrelevant to phylogenetic insights and, being a source of confusion, are excluded" (from his schemes). Yet there remains wide demand for hierarchical systems in which groups/taxa are clearly assigned appropriate (high-level) rank-names (reviewed in Corliss, 1994a). If/when the exact phylogenetic relationship (e.g., of two classes or phyla) is not (yet) known, it is temporarily/tentatively *assumed,* on the basis of data available, in order to present a single unified scheme useful to numerous biologists, as pointed out above (in the last paragraph of my introductory remarks).

In theory, the time should come when the criterion of monophyly *can* be used, almost exclusively, in support of a proposed system of high-level classification of protists plus other eukaryotic groups. That time has been predicted as around the turn of the twenty-first century, a fitting date for offering robust new taxonomies that clearly represent improvements over past hierarchical schemes inevitably based on inadequate data (Corliss, 1994a; Patterson, 1994; Patterson and Sogin, 1993).

Multiple Kingdoms in a Hierarchical System

The last major option, in my opinion, is to recognize discrete high-level, ranked groupings of protists and (other) eukaryotes arranged in a "typical" hierarchical scheme which is more or less *conventional* in its appearance. Unlike solution number 1 (above), species of protists would be assigned to, or found in, more than a single kingdom, in proper recognition of their ultrastructural and genetic diversity. Unlike options 2 and 3 (above), protozoan and algal phyla would have their own integrity as well as showing degrees of relatedness to other eukaryotic phyla; and while demonstrating monophyly where possible, they might also tentatively and undeniably, in selected cases, represent instances of paraphyly or even polyphyly. The resulting overall classification may be considered flexible in that changes can be effected as reliable new data become available. Ignorance would eventually be replaced by knowledge.

By use of a more or less conventional arrangement of taxa, one can produce an overall classification system that can serve as a helpful link with the past. I consider this to be an important feature of this fourth option, because many persons -teachers, students, and researches alike from diverse fields of biology- who may not be in a position to keep abreast of the very latest developments in evolutionary protistology have been depending on various earlier taxonomies, including ones treating protists as either mini-plants or mini-animals (Corliss, 1983), and would be royally confused by the totally different (strange!) approach of the cladists (option 3).

The idea of multiple kingdoms of protists within an empire or domain is not a new one: several workers have suggested such an arrangement during the past 30 years, from Leedale (1974) to Möhn (1984) to Cavalier-Smith (1981, 1983, 1989a, b, 1993) and the author (Corliss, 1993, 1994a, b). Möhn's treatment of the entire eukaryotic assemblage of organisms was the most unusual, with the protists alone comprising 10 of his total of 16 kingdoms. In general, for various reasons, the protistological community has not accepted such proposals with much enthusiasm. But seldom have the suggestions, denying, as they do, support for the concept of a *single* kingdom for the protists, offered detailed alternative taxonomic schemes, with the notable exceptions of those by Cavalier-Smith and by Corliss.

In the remainder of this paper, a condensed presentation of the macrosystematics of the empire EUKARYOTA recently published by the author (Corliss, 1994a) is offered, with limited discussion beyond that given in preceding sections. In adopting the fourth option for treatment of the (mostly) microbial eukaryotes (the former protozoa, algae, and "lower" fungi), however, the following considerations are worthy of special note:

1) The eukaryotes are divided into the six kingdoms endorsed by Cavalier-Smith (1993), all of which -- although controversially in the case of the Animalia -- are considered by me to contain one or more phyla of protists.

2) Some 34 phyla, 83 classes, and numerous orders are assigned to these six kingdoms. The (resurrected) PROTOZOA and the mostly algal CHROMISTA (not entirely dissimilar to the chromophytes of the neoclassical literature or of the "stramenopiles" of Patterson, 1989, and Leipe *et al.*, 1994) embrace the greatest numbers of species and higher taxa formerly contained in the here no longer recognized "kingdom PROTISTA."

3) A primitive kingdom ARCHEZOA, totally composed of protists lacking mitochondria and certain other organelles, is considered to have given rise to the kingdom PROTOZOA, members of which, in turn, are postulated to have served as progenitors of the other four kingdoms, the CHROMISTA, the PLANTAE, the FUNGI, and the ANIMALIA.

4) With an eye to consistency, and to provision of some continuity with standard protozoan and algal classifications of past decades, the nomenclature (including pre- and suffixes) used stresses adoption of conventional, longknown names and authorships wherever reasonably appropriate. Fortunately, international codes of nomenclature seldom dictate choice of names above the familial level; but perhaps in the future, they should provide some uniform guidelines for the naming of such higher taxa (Corliss, 1995).

5) Further discussion of the above and additional points, many specific references to the burgeoning literature from areas of phycology, protozoology, mycology, and parasitology, as well as from fields of cell and molecular and evolutionary biology, and precise characterizations of supraordinal taxa (plus lists of major taxa including numerous representative genera) appeared in my full paper of last year (Corliss, 1994a) to which the reader is thus referred for such important details. And Cavalier-Smith (1993) should be consulted for taxonomic details, especially at the ordinal levels of classification. Here, space permits only a listing of phyla included within the recognized kingdoms, with an occasional comment or word of explanation when needed for the sake of clarity.

A Classification of the Microbial Eukaryotes

Included phyla of the Kingdom ARCHEZOA Haeckel, 1894

1. Archamoebae Cavalier-Smith, 1983

2. Metamonada Grassé, 1952

3. Microspora Sprague, 1977

Comment: Some workers include the phylum Parabasala (in my kingdom PROTOZOA, below) here, in which the missing mitochondria seem to have been replaced by hydrogenosomes.

Included phyla of the Kingdom PROTOZOA Goldfuss, 1818

1. Percolozoa Cavalier-Smith, 1991

2. Parabasala Honigberg, 1973

3. Euglenozoa Cavalier-Smith, 1981

4. Opalozoa Cavalier-Smith, 1991

5. Mycetozoa de Bary, 1859

6. Choanozoa Cavalier-Smith, 1989

7. Dinozoa Cavalier-Smith, 1981

8. Ciliophora Doflein, 1901

9. Apicomplexa Levine, 1970

10. Rhizopoda von Siebold, 1845

11. Heliozoa Haeckel, 1866

12. Radiozoa Cavalier-Smith, 1987

13. Ascetospora Spragua, 1978

Comment: A huge and diverse group, the PROTOZOA may represent a polyphyletic assemblage, The phyla Percolozoa, Opalozoa, and Rhizopoda, in particular, are in need of more study. Most of the species of the conventional former *"phylum* Protozoa" are assignable here, with the important exceptions of the haptophytes, the cryptomonads, and several smaller groups now placed in the kingdom CHROMISTA, the volvocids of the PLANTAE, and all the phyla of the primitive kingdom ARCHEZOA. A fourteenth phylum, the Myxozoa, was included above by both Cavalier -Smith (1993) and Corliss (1994a, b); but here it is removed to the kingdom ANIMALIA, based on the very recent findings of Smothers *et al.* (1994).

Included phyla of the Kingdom CHROMISTA Cavalier-Smith, 1981

1. Bicosoecae Cavalier-Smith, 1989

2. Labyrinthomorpha Page in Levine *et al.,* 1980

3. Dictyochae Haeckel, 1894

4.Raphidophyta Chadefaud, 1950

5. Phaeophyta Wettstein, 1901

6. Diatomae Agardh, 1824

7. Pseudofungi Cavalier-Smith, 1986

8. Haptomonada Cavalier-Smith, 1989

9. Cryptomonada Ehrenberg, 1838

10. Chlorarachniophyta Hibberd & Norris, 1984

Comment: The first seven phyla of this kingdom are segregated out into a separate subkingdom, the HETEROKONTA Luther, 1899, a high-level taxon and name long favored by phycologists (Moestrup, 1992). Also, each of the last three phyla has its own distinct subkingdom (not named here). One or more of these subkingdoms some workers might wish to shift (hack) to the PROTOZOA or elevate to independent full kingdom status.

Included *protistan* phyla of the Kingdom PLANTAE Linnaeus, 1753

1. Prasinophyta Christensen, 1962

2. Chlorophyta Pascher, 1914

3. Ulvophyta Stewart and Mattox, 1978

4. Charophyta Rabenhorst, 1863

5. Rhodophyta Rabenhorst, 1863

6. Glaucophyta Bohlin, 190]

Comment: Two subkingdoms are recognized here: the VIRIDIPLANTAE Cavalier-Smith, 1991, for the first four phyla listed above *plus* the *non-pro*tist plant phyla (Bryophyta, Pteridophyta, and Spermatophyta, groups beyond further consideration here); and the BILIPHYTA Cavalier-Smith, 1981, for the controversial last two protistan phyla. Some workers might wish to elevate the second subphylum to independent full kingdom status.

Included *protistan* phylum of the Kingdom FUNGI Linnaeus, 1753

Chytridiomycota Sparrow, 1959

Comment: The great majority of species of fungi belong to the three non-protist phyla (Ascomycetes, Basidiomycetes, and Zygomycetes, multicellular forms beyond further consideration here). The chytrids are unicellular protists with a naked, posteriorly directed flagellum -- otherwise, they show typical fungal characteristics.

Included *protistan* phylum of the Kingdom ANIMALIA Linnaeus, 1753

Myxozoa Grassé, 1970

Comment: Practically *all* animal species belong to (numerous) phyla characterized by being multicellular, multitissued, organ-bearing forms with complex embryological development in their ontogenies. Recent rRNA research, however, has revealed an undeniable closeness of the Myxozoa to the “Bilateria” group of the ANIMALIA (Smothers *et al.,* 1994). Therefore, I am here considering these long-curious and relatively complex protists (Kent *et al.*, 1994), formerly placed in the PROTOZOA, as very likely better placed in the present kingdom.

Concluding Remarks

In this brief essay, I have attempted to trace the history of the high-level taxonomic treatment of the essentially microbial eukaryotes, the protists *sensu lato.* The heuristic view of Ernst Haeckel, 125 years ago, was resurrected and refined some 100 years after its original promulgation, first by the ecologist Robert Whittaker and the evolutionary biologist Lynn Margulis and then by a host of others. With the accelerating accumulation of fresh information from precise ultrastructural investigations and from sophisticated molecular approaches (e.g., comparative use of ribosomal RNA sequencing), protistologists have gradually become aware, in very recent years, of the tremendous diversity of protistan assemblages. This awareness, in turn, is obliging us to take a new look at the macrosystematics of these groups, groups no longer unitable under a single kingdom heading.

With the demise of the popular kingdom PROTISTA, we need to reconsider what (other) options are available to us with respect to the classification of all protists. Along with others, notably Tom Cavalier-Smith, I have concluded that the most satisfactory solution at the present time is to recognize that (former groups of) protists are assignable to half a dozen distinct kingdoms of eukaryotes, three of which also contain multiple phyla of multicellular (and often highly complex) organisms. This number of kingdoms may be a conservative one: adherence to the principle of monophyly will very likely oblige us, in the future, to recognize a greater number.

A definitive skeletal scheme of classification (based largely on the conclusions of Cavalier-Smith, 1993, although with some significant taxonomic revisions of my own: see Corliss, 1994a) is offered on preceding pages. While all of its contained high-level units are not necessarily monophyletic in nature, it does have some advantages over strictly cladistic approaches (e.g. those of Patterson, 1994): its named ranks are presented in a conventional hierarchical arrangement; names and authorships have been chosen to provide continuity with systems of past decades; evolutionary considerations are underscored by recognition of the closeness of some protistan phyla to (and their inclusion in) the traditional "big three" multicellular kingdoms (the PLANTAE, FUNGI, and ANIMALIA); a primitive kingdom (the ARCHEZOA) has been accepted to bridge the gap between prokaryotes and the first eukaryotes; the PROTOZOA have been recognized as the pivotal kingdom, the group in which the most evolutionary "experiments" have been tried/carried out, some leading to the origin of the four subsequent eukaryotic kingdoms; and the classification is expanded at infraphyletic levels (not directly described in this brief paper: but see Cavalier-Smith, 1993 and Corliss, 1994a) to reveal more properly the morphological, physiological, ecological, and genetic diversity found among protistan groups.

The system overall is predicted to be pragmatically useful -- and easily alterable, as will likely be demanded by future pertinent data -- for biologists in all areas or fields of research, teaching, and service.

Such an interim classification (Corliss, 1994a), with occasional minor repair, should satisfy our general needs until the time arrives — predictably the year 2000? — when accumulated data and sophisticated analyses allow a significant overhauling of the macrosystematics of all of these microbial eukaryotes, the diverse and far-flung protists whose described species, fossil and contemporary, number over 200,000, with tens of thousands more still awaiting discovery.

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