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## An Interim Utilitarian ("User-friendly") Hierarchical Classification and Characterization of the Protists

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**Summary.** Continuing studies on the ultrastructure and the molecular biology of numerous species of protists are producing data of importance in better understanding the phylogenetic interrelationships of the many morphologically and genetically diverse groups involved. Such information, in turn, makes possible the production of new systems of classification, which are sorely needed as the older schemes become obsolete. Although it has been clear for several years that a Kingdom PROTISTA can no longer be justified, no one has offered a single and compact hierarchical classification and description of all high-level taxa of protists as widely scattered members of the entire eukaryotic assemblage of organisms. Such a macrosystem is proposed here, recognizing Cavalier-Smith's six kingdoms of eukaryotes, five of which contain species of protists. Some 34 phyla and 83 classes are described, with mention of included orders and with listings of many representative genera. An attempt is made, principally through use of well-known names and authorships of the described taxa, to relate this new classification to past systematic treatments of protists. At the same time, the system will provide a bridge to the more refined phylogenetically based arrangements expected by the turn of the century as future data (particularly molecular) make them possible. The present interim scheme should be useful to students and teachers, information retrieval systems, and general biologists, as well as to the many professional phycologists, mycologists, protozoologists, and cell and evolutionary biologists who are engaged in research on diverse groups of the protists, those fascinating "lower" eukaryotes that (with important exceptions) are mainly microscopic in size and unicellular in structure.

**Key words.** Protists, algae, fungi, protozoa; macrosystematics of the Eukaryota: kingdoms, phyla, classes, orders, and representative genera.

### INTRODUCTION

During the past 20 years, studies on the systematics and evolution of the protists (essentially all protozoa,

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This paper is dedicated to the memory of Zdzisław Raabe (1909-1972) who, 30 years ago, perceptively foresaw the problems involved in constructing a macrosystem for the Protozoa based on evolutionary principles (Raabe 1964a) and who, in the same year, published a comprehensive protozoological textbook (Raabe 1964b) and, in the preceding year, had founded the international journal *Acta Protozoologica*.

eukaryotic algae, and "lower" fungi) have been in a state of great activity, with an increasing number of biologists becoming interested in such research. As our knowledge has grown concerning the cytoarchitecture and the phylogenetic interrelationships of the large number of species (and their higher taxa) involved, so has our understanding with respect to the most "natural" scheme of classification to employ for these ubiquitous and cosmopolitan eukaryotic - generally microscopic and often unicellular - organisms. In recent years, with the development of molecular chronometric techniques (e.g. ribosomal RNA sequencing: see Christen 1992), com-



bined with ultrastructural investigations and the application of sophisticated cladistic analyses, the outlook is even more auspicious for our learning enough about the evolution of protistan groups to be able to propose a robust classification system that will withstand the test of such phylogenetic principles as monophyly and can thus be expected to endure for a reasonable number of years.

At the present time, however, we are taxonomically in a state of flux. We are frustratingly trapped between existing classifications of protists that are recognized to be faulty and some future scheme(s) not yet available. The latter, hopefully closer to the ideal natural system long awaited, probably will not be ready for at least several years yet, perhaps not until the turn of the century.

This paper represents an earnest attempt to fill in that long time-gap between available classifications. I believe that there is a pressing need now for a useful/usable interim system treating the protists overall in a manner understandable to the general protozoologist/phycologist/mycologist and the myriads of cell and evolutionary biologists, biochemists, and general biologists (including students and teachers as well as the many professional researchers) who use or talk about these fascinating yet often neglected eukaryotes the described species of which may have already reached the respectable number of 200,000. I am presenting a compact "user-friendly" taxonomic scheme that is built along traditional lines but also incorporates the latest ultrastructural and molecular data that are available.

A major aim here is to offer the higher protistan taxa in a standard hierarchical arrangement, even if a measure of speculation or presumption concerning relationships must sometimes be invoked to do this. The desired result should be a system conveniently understandable to more than just a few specialists. Finally, in order to link the present with both the past and the future, a deliberate effort is made to preserve groups and names of groups either familiar from past classifications or potentially familiar (or at least palatable!) in cases of certain newer groups or names that I have adopted from research papers of current workers in fields that impact on protistological systematics. An **INDEX of Taxonomic Names** is supplied to aid the reader in locating genera or higher groups of special interest to him or her. Some of my taxa may not be identical with putative evolutionary lines of the very recent literature; that is, they may not be indisputably monophyletic in nature. In fact, several are likely paraphyletic and a few perhaps polyphyletic

(Wiley 1981). But such assemblages, so identified, are sometimes used here. I am in sympathy with Raabe's (1964a) observation of 30 years ago that it is "not necessary nor possible to follow the rules of a strict purism as to the monophyletism of groups in protozoological systematics".

Scattered controversial matters (ever present in taxonomy!) are arbitrarily resolved in place, sometimes purely by intuition, but with due attention to priority, common sense, courtesy, and stability (Corliss 1972), as well as to (my interpretation of) the facts available in the case. I agree with Silva (1984) that a considerable degree of subjectivity is inevitable when anyone attempts to construct a macrosystem for a large and diverse group of organisms, many poorly known, no matter what approaches or principles are used nor how conscientiously they are followed.

In the present effort, I acknowledge my dependence on the insightful analyses of Cavalier-Smith (1981, 1986, 1989b, 1991b, 1993a-c). He has provided the evolutionary framework for much of the classification presented on the following pages. But I make no attempt to utilize most of his proposed intermediate-level groupings, his frequently interposed sub-, infra-, and supra-taxa at kingdom, phyletic, class, and ordinal levels, although I appreciate their value to him. My system also differs from his in other ways (e.g. I have fewer protozoan but more chromist phyla, and I cover the fungal and plant protists as well); and I offer more detailed comparative descriptions of groups and list many more representative genera for each major taxon covered. As a born "splitter", Cavalier-Smith may indeed have been guilty of a degree of "taxonomic inflation" in his classifications. I have tried to avoid this myself; and it may be noted that no taxa are erected as new in this paper. As our knowledge increases, however, newly discovered significant differences between organisms or groups of organisms often require their greater, even much greater, separation taxonomically than was previously given to them. In my scheme, for example, I have endorsed far more phyla and classes than appeared in the Levine Report of 14 years ago (Levine et al. 1980).

For details, I have depended heavily on the literature. Monographs (and shorter papers as well) by phycological, protozoological, and mycological specialists on different taxa have been indispensable for my understanding of the composition and taxonomic boundaries of such groups: some of the major works among these are cited in the immediately following section. The authoritative chapters in four recent treatises (Harrison



and Corliss 1991, Lee et al. 1985, Margulis et al. 1990, Parker 1982) deserve special mention; in general, however (to save space), these individual specialist-contributions - like many of the other numerous scattered taxonomic papers consulted - are not directly cited in this paper.

## FURTHER BACKGROUND INFORMATION

The protist literature has become so vast, with a continuing avalanche of papers since my reviews of 8-10 years ago (Corliss 1984, 1986a), that no attempt can be made here to cite all works of some relevance to my present broad topic. The reader is referred to the following publications (which include reviews and overviews containing bibliographic sections rich in references to hundreds of significant individual papers) that are mostly concerned with recent ultrastructural or molecular researches directly bearing on protist systematics:

Alexopoulos and Mims (1979), Andersen (1989, 1991, 1992), Andersen et al. (1993), Anderson (1983), Bardele (1987), Baroin et al. (1988), Baroin-Tourancheau et al. (1992), Barr (1992), Bold and Wynne (1985), Bowman et al. (1992), Bremer (1985), Bremer et al. (1989), Bovee (1991), Broers et al. (1990), Brugerolle (1991a,b), Canning and Lom (1986), Cavalier-Smith (1986, 1987, 1989a,b, 1991a,b, 1993a-c), Chapman and Buchheim (1991), Christensen (1980, 1989, 1990), Cole and Sheath (1990), Corliss (1979, 1984, 1986a, 1987, 1989, 1991a), Copeland (1956), Cox (1980), Davidson (1982), Dodge (1979), Douglas et al. (1991), Dragesco and Dragesco-Kernéis (1986), Farmer (1993), Felsenstein (1988), Fenchel (1987), Fenchel and Finlay (1991), Fensome et al. (1993), Fleury et al. (1992), Foissner and Foissner (1993), Foissner (1987, 1993), Foissner et al. (1988), Gajadhar et al. (1991), Grain (1986), Green et al. (1989), Grell (1991a,b), Grell et al. (1990), Hanson (1977), Hasegawa et al. (1993), Hausmann et al. (1985), Hawksworth et al. (1983), Hibberd and Norris (1984), Hori and Osawa (1987), Hülsmann (1992), Irvine and John (1984), Karpov (1990), Karpov and Mylnikov (1989), Kendrick (1985), Kivic and Walne (1984), Knoll (1992), Kreier (1977-1978), Kreier and Baker (1991), Kristiansen and Andersen (1986), Krylov (1981), Krylov and Starobogatov (1980), Kuźnicki and Walne (1993), Larsen and Patterson (1990), Larsson (1986), Lee et al. (1985), Lee and Kugrens (1992), Leedale (1974, 1980), Leipe et al.

(1993), Leipe and Hausmann (1993), Levine (1988), Lipscomb (1985, 1991), Lom (1990), Lom and Dyková (1992), Lynn (1981), Lynn and Corliss (1991), Margulis (1970, 1981, 1993), Margulis et al. (1990), Margulis et al. (1993), Margulis et al. (1984), Mattox and Stewart (1984), Melkonian (1984), Melkonian et al. (1991), Mishler and Churchill (1985), Moestrup (1982, 1991), Möhn (1984), Moss (1991), Müller (1992), Mylnikov (1991), O'Kelly (1992, 1993a,b), O'Kelly and Floyd (1984), Olive (1975), Page and Blanton (1985), Page and Siemensma (1991), Parker (1982), Patterson (1989a,b), Patterson and Fenchel (1985), Patterson and Larsen (1991), Patterson et al. (1989), Patterson and Sogin (1993), Patterson and Zölffel (1991), Perkins (1991), Powers (1993), Preisig (1989), Preisig et al. (1991), de Puytorac et al. (1974, 1987, 1993), Ragan (1988), Ragan and Chapman (1978), Raikov (1982), Rothschild (1989), Rothschild and Heywood (1987), Round (1984), Round et al. (1990), Schlegel (1991), Silva (1980), Sleigh (1989), Sluiman (1985), Small and Lynn (1985), Smith and Patterson (1986), Sogin (1991), Sogin et al. (1989), Sprague (1977), Sprague et al. (1992), Stewart and Mattox (1980), Tappan (1980), Taylor (1978, 1987), van den Hoek et al. (1993), Vickerman (1992), Vickerman et al. (1991), Vossbrinck et al. (1987), Wainright et al. (1993), Whittaker (1969, 1977), Whittaker and Margulis (1978), Woese (1987), Woese et al. (1990), Wolters (1991).

For nomenclatural help, the original literature has, once again, been indispensable. But several comprehensive works deserve special mention: Bütschli (1880-1889), Cavalier-Smith (1993c), Chrétiennot-Dinet et al. (1993), Copeland (1956), Karpov (1990), Krylov and Starobogatov (1980), Levine et al. (1980), Poche (1913), de Puytorac et al. (1987), and Silva (1980).

In "pre-protist" days and before the advent of widespread usage of electron microscopy in study of microorganisms ("Age of Ultrastructure": Corliss, 1974), biologists did not find it too difficult to recognize or classify the several major groups of algae ("mini-plants") and protozoa ("mini-animals"). Algae were predominantly photosynthetic organisms, often non-motile, mainly unicellular or filamentous in organization; protozoa were mostly phagotrophic, motile, and unicellular. The bases for separation of groups of species at higher taxonomic levels included differences in life cycles and pigmentation for algae (e.g. green, red, brown, golden-brown) and variation in kinds and numbers of locomotory structures (e.g. pseudopodia, flagella, cilia) and other specialized organelles in the case of



protozoa. Ecological characters (e.g. free-living vs parasitic, marine vs fresh-water, sessile vs free-swimming, and nutritional proclivities) were also often invoked. Botanists studied the algae; zoologists, the protozoa.

A few years after the great evolutionary discovery of (the concept of) the prokaryotes and the eukaryotes, the "protist perspective" began to be adopted when considering the "lower" eukaryotes (see historical review in Corliss 1986a). At about the same time, growing acceptance of the Serial Endosymbiosis Hypothesis explained the likely endosymbiotic origins of plastids and mitochondria, answering some previously inexplicable questions while raising some new ones concerning the evolution of organisms possessing such organelles.

Most botanists have long accepted traditional views in setting up hierarchical classifications for their divisions and classes of algae and "lower" fungi, following such great authorities of the past as the Agardhs, Blochmann, Chodat, Dangeard, de Bary, Fritsch, Kjellman, Klebs, Kützing, Lamouroux, Lemmermann, Lister, Luther, Pascher, Rabenhorst, Smith, West, Wetstein, Wille, Winter, and Zopf. See the widely accepted systems, with minor changes, adopted in many botanical and phycological (e.g. Bold and Wynne, 1985; van den Hoek et al. 1993) textbooks and in numerous monographs as well. The zoologists have acted essentially the same with respect to the protozoa, relying on the works of such leaders as Alexeieff, Balbiani, Bütschli, Calkins, Cash, Cépède, Chatton, Deflandre, Doflein, Dogiel, Dujardin, Ehrenberg, Entz (Jr. and Sr.), Grassé, Haeckel, Hartmann, Hertwig, Kahl, Kent, Kofoid, Kudo, Lankester, Laveran and Mesnil, Léger, Leuckart, O.F. and J. Müller, Penard, Prowazek, Schaudinn, Schewiakoff, Stein, and Wenyon. For example, see the highly popular and authoritative protozoological volumes by Grell (1973) and Kudo (1966).

In more recent years, the Society of Protozoologists has established a special committee to produce "updated" systems of protozoan classification: see the reports of Honigberg et al. (1964) and Levine et al. (1980). The resulting schemes have often been considered authoritative for some years following their promulgation: for example, the popular "Illustrated Guide to the Protozoa," edited by Lee et al. (1985), in large measure endorsed the Levine Report. These "consensus" classifications have indeed, in many ways, represented improvements over previous systems. The Society now has a new committee working on a fresh

revision; although the writer is a past chairman of the committee, the present paper in no way is to be considered the outcome of the committee's current deliberations, which are continuing without my participation. Also, independent of the Society, de Puytorac et al. (1987) and Sleigh (1989), in editions of their well-known textbooks on the protozoa and other protists, have used taxonomic arrangements mostly of their own making, although largely based on taxonomic works from the literature.

In addition to the classifications mentioned above that involve protists, the most outstanding recent attempt to bring these organisms together under a single taxonomic heading - viz. the Pro(toc)tista - has been that of Margulis and colleagues, commencing with such seminal papers as those by Whittaker (1969, 1977), Margulis (1974), and Whittaker and Margulis (1978) and culminating in book form in Margulis et al. (1990). Many workers, including the present author (e.g. note my enthusiasm for the idea in Corliss 1984, 1986a,b, 1991a) and numerous teachers and textbook writers around the world, have adopted this appealing way of viewing the living world as divisible taxonomically into five convenient kingdoms, among them the Protista. Some 27-45 phyla are generally assigned to the protist kingdom, in recognition of the great diversity (supported today by hundreds of ultrastructural observations) found among its numerous members (Barnes 1984; Corliss 1984; Karpov 1990; Margulis and Schwartz 1982, 1988). Other scattered proposals of multikingdom systems for the eukaryotes have not linked the various taxa composed purely of protists together in a single kingdom (see the pioneering paper by Leedale 1974; Möhn 1984; and reviews in Corliss 1986a and Lipscomb 1991).

Phylogeneticists have made invaluable contributions to our understanding of the probable origins of various major monophyletic lines of protists, but they have uniformly been reluctant - to date - to suggest definitive, hierarchical arrangements of ranked taxa of the principal assemblages of eukaryotes that involve species of protists (e.g. Lipscomb 1991; Patterson 1988; Patterson and Sogin 1993). On the other hand, cell and evolutionary biologist Cavalier-Smith has published a series of heuristic papers during the past dozen years (e.g. Cavalier-Smith 1981, 1983, 1986, 1987, 1989b, 1991b, 1993a-c) in which he has boldly presented novel schemes of eukaryotic classification, naming and ranking all implicated major groups and generally distributing the protists among all but one (the Animalia) of his several kingdoms.



So, within the past 20-30 years, we have had, first, a clinging to the conventional macrosystems of algae and protozoa originally set up essentially on the basis of morphological data obtainable by use of light microscopy. Then we have witnessed the "protist revolution," with its emphasis on removing the taxonomic barriers of old (often including rejection of formal names that had become misleading or meaningless: e.g. "Phytoflagellata" and "Zoomastigophora") on the basis of abundant and more precise ultrastructural and molecular information. This integrated protistan approach so permeated our thinking that there was an exuberant and intensive drive to lump all protists together into a single kingdom (although with many separate evolutionary lines within that great assemblage), as discussed above. Today, the prevailing view among leading protistological researchers is that these "lower" eukaryotes can no longer be properly restricted to a single taxonomic kingdom, although few investigators have stated so directly and even fewer - aside from Cavalier-Smith (1981 et seq.), the most notable exception - have relieved the problem in a constructive way, by proposing explicit hierarchical classifications to contain the multiple kingdoms and phyla assignable to the eukaryotic assemblage overall.

Thus a single kingdom Protista as such must be laid to rest, but long live the **protists** themselves in all their awesome diversity!

## MAJOR GROUPS OF EUKARYOTES

### The kingdoms

Although all the desired information is far from being available, one may find it useful to consider what choice and what number of kingdoms may best represent the principal groups of eukaryotes as they are known to date. Certainly modern evolutionary studies have supplied sufficient data to demonstrate the tremendous phylogenetically significant diversity among the protists alone to warrant unequivocally the demise of a single kingdom Protista. Furthermore, the nature of the several high-level groups of these organisms makes clear what the writer and others have often been reluctant to admit in the past, viz., that some protists are more closely related to members of other long-accepted kingdoms or assemblages (e.g. Plantae, Fungi, Animalia) than they are to each other.

Multiple kingdoms of eukaryotes have been suggested in the past, as mentioned on a preceding page. The number has most commonly been four, of which often the protists have represented one (except in the works of Cavalier-Smith, who some years ago foresaw the necessity for the demise of Protista as such: see references to his relevant papers above and below). Unusual was Möhn's (1984) proposal of 16 kingdoms, with protists alone comprising 10 of them.

If one recognizes **kingdoms** within the great eukaryotic group, and - for that matter - among the prokaryotes as well, then a name of still higher taxonomic rank must be found for those two "super" assemblages. There is considerable controversy over the most appropriate appellation; I am going to employ the term "**empire**" without strong feelings either pro or con. Thus, the kingdoms described below comprise the empire **EUKARYOTA**.

Here, as in following sections, I am presenting a classification in the conventional manner: naming the taxon (with authorship and date) and offering a very brief diagnosis, description, or characterization, followed by mention of major embraced sub-taxa. I am essentially endorsing the six (a reasonable number) eukaryotic kingdoms of Cavalier-Smith (1989a): three are comprised solely of protist species, one includes many, another has only a few; and his sixth, Animalia, has none at all, in my view. It may be noted that the great bulk of the photosynthetic or "algal" protists, with the important exceptions of the euglenoids and the dinoflagellates, falls into two kingdoms, the Chromista and the Plantae; the largely heterotrophic or "protozoan" protists dominate two kingdoms also, the Archezoa and the Protozoa. Mixotrophic species occur mainly in the Chromista (except, again, for numerous members of the protozoan phyla Euglenozoa and Dinozoa). The single phylum of protists in the kingdom Fungi is composed solely of osmotrophic forms; and the heterotrophic, multicellular, multitissued kingdom Animalia is considered to be without species of protists.

A brief nomenclatural note regarding authorities for the names of all kingdoms but the (modern) **Chromista** is needed here. I am crediting early workers with the names **Archezoa**, **Protozoa**, **Plantae**, **Fungi**, and **Animalia**, while aware of the substantial changes over the past 100-240 years in the concepts, circumscription, and composition applied to these top-level groups of eukaryotic organisms. In the case of the **Archezoa**, I am disagreeing with both Cavalier-Smith and other workers by assigning the authorship to Haeckel who, I am con-



vinced, has been misunderstood with respect to his use and concept of the term. For the **Protozoa**, I am crediting Goldfuss with the name and the general concept, as is conventionally done. Finally, in the case of the "big three" multicellular "higher" eukaryotic assemblages, I am honoring Linnaeus with all the names (and as of the date 1753), although the plants were originally established by him as comprising a kingdom **VEGETABILIA**.

As is evident, much has happened taxonomically and nomenclaturally in the 10-year period since my last attempt to review the high-level status of the protists (Corliss 1984). Yet, as will be clear from even a cursory glance at the classification of the 34 phyla and 83 classes detailed on the following pages (and see Table 1), the majority of my formerly proposed 18 "supraphyletic assemblages" and most of the 45 phyla suggested at that time have survived in one form or at one level or another. Some significant changes/interpretations have nevertheless been made - an indication of the impact of new data on postulated phylogenetic interrelationships among the diverse groups of protists and, thus, on their macrosystematics. And far more information is made available in the present - and considerably longer - paper, including a helpful **INDEX** of taxonomic names.

Table 1

The taxonomic assignment of 34 phyla and 83 classes of protists to kingdoms of the <b>EUKARYOTA</b>	
Kingdom I. <b>ARCHAEZOA</b> Haeckel, 1894	
Phylum 1. <b>ARCHAMOEBAE</b> Cavalier-Smith, 1983	Class <b>Pelobiontea</b> Page, 1976
Phylum 2. <b>METAMONADA</b> Grassé, 1952	Class (1) <b>Trepomonadea</b> Cavalier-Smith, 1993 Class (2) <b>Retortamonadea</b> Grassé, 1952 Class (3) <b>Oxymonadea</b> Grassé, 1952
Phylum 3. <b>MICROSPORA</b> Sprague, 1977	Class (1) <b>Rudimicrosporea</b> Sprague, 1977 Class (2) <b>Microsporea</b> Delphy, 1963
Kingdom II. <b>PROTOZOA</b> Goldfuss, 1818	
Phylum 1. <b>PERCOLOZOA</b> Cavalier-Smith, 1991	Class (1) <b>Percolomonadea</b> Cavalier-Smith, 1993 Class (2) <b>Heterolobosea</b> Page & Blanton, 1985 Class (3) <b>Lyromonadea</b> Cavalier-Smith, 1993 Class (4) <b>Pseudociliata</b> Corliss & Lipscomb, 1982
Phylum 2. <b>PARABASALA</b> Honigberg, 1973	Class (1) <b>Trichomonadea</b> Kirby, 1947 Class (2) <b>Hypermastigotea</b> Grassi & Foà, 1911
Phylum 3. <b>EUGLENOZOA</b> Cavalier-Smith, 1981	Class (1) <b>Diplonematea</b> Cavalier-Smith, 1993 Class (2) <b>Euglenoidea</b> Bütschli, 1884 Class (3) <b>Kinetoplastidea</b> Honigberg, 1963
Phylum 4. <b>OPALOOZOA</b> Cavalier-Smith, 1991	Class (1) <b>Proterozoea</b> Cavalier-Smith, 1981 Class (2) <b>Opalinata</b> Wenyon, 1926 Class (3) <b>Kinetomonadea</b> Cavalier-Smith, 1993 Class (4) <b>Hemimastigophorea</b> Foissner et al., 1988
Phylum 5. <b>MYCETOZOA</b> de Bary, 1859	Class (1) <b>Protostelea</b> Olive & Stoianovitch, 1966 Class (2) <b>Myxogastrea</b> Fries, 1829 Class (3) <b>Dictyostelea</b> Lister, 1909
Phylum 6. <b>CHOANOZOA</b> Cavalier-Smith, 1989	Class <b>Choanoflagellata</b> Kent, 1980
Phylum 7. <b>DINOZOA</b> Cavalier-Smith, 1981	Class (1) <b>Protalveolata</b> Cavalier-Smith, 1991 Class (2) <b>Dinoflagellata</b> Bütschli, 1885
Phylum 8. <b>CILIOPHORA</b> Doflein, 1901	Class (1) <b>Karyorelictea</b> Corliss, 1974 Class (2) <b>Polyhymenophorea</b> Jankowski, 1967 (= <b>Heterotrichea</b> Stein, 1859 + <b>Spirotrichea</b> Bütschli, 1889) Class (3) <b>Colpodea</b> Small & Lynn, 1981 Class (4) <b>Phyllopharyngea</b> de Puytorac et al., 1974 Class (5) <b>Nassophorea</b> Small & Lynn, 1981 Class (6) <b>Oligohymenophorea</b> de Puytorac et al., 1974 Class (7) <b>Prostomatea</b> Schewiakoff, 1896 Class (8) <b>Litostomatea</b> Small & Lynn, 1981
Phylum 9. <b>APICOMPLEXA</b> Levine, 1970	Class (1) <b>Perkinsidea</b> Levine, 1978 Class (2) <b>Gregarinidea</b> Dufour, 1828 Class (3) <b>Coccidea</b> Leuckart, 1879 Class (4) <b>Haematozoa</b> Vivier, 1982
Phylum 10. <b>RHIZOPODA</b> von Siebold, 1845	Class (1) <b>Lobosea</b> Carpenter, 1861 Class (2) <b>Entamoebidea</b> Cavalier-Smith, 1991 Class (3) <b>Filosea</b> Leidy, 1879 Class (4) <b>Granuloreticulosea</b> de Saedeleer, 1934 (= mostly <b>Foraminifera</b> d'Orbigny, 1826) Class (5) <b>Xenophyphorea</b> Schulze, 1904
Phylum 11. <b>HELIOZOA</b> Haeckel, 1866	Class (1) <b>Actinophryidea</b> Hartmann, 1913 Class (2) <b>Centrophelidea</b> Kühn, 1926 Class (3) <b>Desmothoracidea</b> Hertwig & Lesser, 1874 Class (4) <b>Taxopodea</b> Fol, 1883
Phylum 12. <b>RADIOZOA</b> Cavalier-Smith, 1987	<i>Subphylum</i> -1- <b>ACANTHARIA</b> Haeckel, 1881 Class <b>Acantharea</b> Haeckel, 1881 <i>Subphylum</i> -2- <b>RADIOLARIA</b> J. Müller, 1858 Class (1) <b>Polycystinea</b> Ehrenberg, 1838 Class (2) <b>Phaeodarea</b> Haeckel, 1879
Phylum 13. <b>MYXOZOA</b> Grassé, 1970	Class <b>Myxosporea</b> Bütschli, 1881
Phylum 14. <b>ASCETOSPORA</b> Sprague, 1978	Class <b>Haplosporidea</b> Caullery & Mesnil, 1899



Kingdom III. **CHROMISTA** Cavalier-Smith, 1981

Subkingdom (I) **HETEROKONTA** Luther, 1899

Phylum 1. **BICOSOECAE** Cavalier-Smith, 1989  
 Class **Bicosoecidea** Grassé & Deflandre, 1952

Phylum 2. **LABYRINTHOMORPHA** Page in Levine et al., 1980  
 Class (1) **Labyrinthulea** Cienkowski, 1867  
 Class (2) **Thraustochytriacea** Sparrow, 1943

Phylum 3. **DICTYOCHEAE** Haeckel, 1894  
 Class (1) **Silicoflagellatae** Borgert, 1891  
 Class (2) **Pedinella** Kristiansen, 1990

Phylum 4. **RAPHIDOPHYTA** Chadeffaud, 1950  
 Class **Raphidomonadea** Chadeffaud, 1950

Phylum 5. **PHAEOPHYTA** Wettstein, 1901  
 Class (1) **Phaeophyceae** Kjellman, 1891  
 Class (2) **Chrysophyceae** Pascher, 1914  
 Class (3) **Synurophyceae** Andersen, 1987  
 Class (4) **Pelagophyceae** Andersen & Saunders, 1993  
 Class (5) **Eustigmatophyceae** Hibberd & Leedale, 1970  
 Class (6) **Xanthophyceae** Allorge in Fritsch, 1935

Phylum 6. **DIATOMAE** Agardh, 1824  
 Class (1) **Coscinodiscophyceae** Round & Crawford, 1990  
 Class (2) **Fragilariophyceae** Round, 1990  
 Class (3) **Bacillariophyceae** Haeckel, 1878

Phylum 7. **PSEUDOFUNGI** Cavalier-Smith, 1986  
 Class (1) **Oomycetes** Winter in Rabenhorst, 1879  
 Class (2) **Hypochytriomycetes** Sparrow, 1959

Subkingdom (II) **HAPTOPHYTA** Christensen, 1962

Phylum **HAPTOMONADA** Cavalier-Smith, 1989  
 Class (1) **Pavlovia** Cavalier-Smith, 1986  
 Class (2) **Patellifera** Cavalier-Smith, 1993

Subkingdom (III) **CRYPTOPHYTA** Pascher, 1914

Phylum **CRYPTOMONADA** Ehrenberg, 1838  
 Class (1) **Goniomonadea** Cavalier-Smith, 1993  
 Class (2) **Cryptomonadea** Stein, 1878

Subkingdom (IV) **CHLORARACHNIOPHYTA** Hibberd & Norris, 1984

Phylum **CHLORARACHNIOPHYTA** Hibberd & Norris, 1984  
 Class **Chlorarachniophyceae** Hibberd & Norris, 1984

Kingdom IV. **PLANTAE** Linnaeus, 1753

Subkingdom (I) **VIRIDIPLANTAE** Cavalier-Smith, 1981

Phylum 1. **PRASINOPHYTA** Christensen, 1962  
 Class (1) **Pedinophyceae** Moestrup, 1991  
 Class (2) **Prasinophyceae** Christensen, 1962

Phylum 2. **CHLOROPHYTA** Pascher, 1914  
 Class **Chlorophyceae** Wille in Warming, 1884

Phylum 3. **ULVOPHYTA** Stewart & Mattox, 1978  
 Class **Ulvophyceae** Stewart & Mattox, 1978

Phylum 4. **CHAROPHYTA** Rabenhorst, 1863

Class (1) **Charophyceae** Rabenhorst, 1863  
 Class (2) **Conjugatophyceae** Engler, 1892

Subkingdom (II) **BILIPHYTEA** Cavalier-Smith, 1981

Phylum 1. **RHODOPHYTA** Rabenhorst, 1863  
 Class (1) **Bangiophyceae** Wettstein, 1901  
 Class (2) **Florideophyceae** Warming, 1884

Phylum 2. **GLAUCOPHYTA** Bohlin, 1901  
 Class **Glaucoophyceae** Bohlin, 1901

Kingdom V. **FUNGI** Linnaeus, 1753

Phylum **CHYTRIDIOMYCOTA** Sparrow, 1959  
 Class **Chytridiomycetes** Sparrow, 1959

Kingdom VI. **ANIMALIA** Linnaeus, 1753

(no taxa of protists here)

**Empire EUKARYOTA**

**Kingdom I. ARCHEZOA Haeckel, 1894**

Unicellular protists that (allegedly) primitively lack mitochondria, plastids, typical Golgi bodies, hydrogenosomes, and peroxisomes, while manifesting various prokaryotic features in their ribosomes and their rRNAs. Energy produced by anaerobic glycolysis. Included species are amoeboid or flagellated (with low number of flagella), or have no means of independent locomotion. Some free-living, majority symbiotic in variety of hosts and of small to very small body size. Entire group is possibly polyphyletic; yet some workers would add the protozoan parabasalans to it as well.

Contains three phyla and several classes and orders.

**Kingdom II. PROTOZOA Goldfuss, 1818**

Predominantly unicellular, plasmodial, or colonial phagotrophic, colorless protists, wall-less in the trophic state. Included species that are capable of photosynthesis (some mixotrophic) typically have cytosolic chloroplasts with stacked thylakoids, lacking starch, and usually surrounded by three membranes. Nearly universally present are tubular (with a few notable exceptions) cristate mitochondria (when absent, replaced by hydrogenosomes), Golgi bodies, and peroxisomes. Flagellar mastigonemes, if present, never rigid and tubular. Numerous free-living (typically independently motile) and symbiotic species, commonly microscopic



in size. As alleged progenitors of the following four kingdoms, the protozoa - not unexpectedly - exhibit the greatest morphological, physiological, and genetic diversity of all. The assemblage, although still broad and large and very likely paraphyletic, represents a taxonomic refinement over the classically known "phylum Protozoa".

Contains numerous phyla, classes, and orders.

### **Kingdom III. CHROMISTA Cavalier-Smith, 1981**

Predominantly unicellular, filamentous, or colonial phototrophic protists. Chloroplasts, located in lumen of rough endoplasmic reticulum, lack starch and phycobilisomes and have a two-membraned envelope inside a periplastid membrane (all within the rough, occasionally smooth, ER). Mitochondria (generally with tubular cristae), Golgi bodies, and peroxisomes always present. When flagella present, at least one bears rigid, tubular, and usually tripartite flagellar hairs or mastigonemes (most notable exception, the haptophytes). The relatively few species without plastids share other features in common with majority of forms embraced here. Mostly free-living (but some groups not independently motile); many microscopic in size, with some major exceptions (e.g. brown algae).

Contains several phyla with numerous classes and orders.

### **Kingdom IV. PLANTAE Linnaeus, 1753**

Unicellular, colonial, or multicellular phototrophic protists and multicellular photosynthetic "higher" eukaryotes, all typically (but not universally) with cellulosic cell walls in trophic stages. Cytosolic plastids, enveloped by two membranes, usually contain starch or phycobilisomes. Mitochondria (with flattened cristae), Golgi bodies, and peroxisomes always present. Green species have stacked thylakoids with chlorophylls a and b; red algae, totally without flagella, have single unstacked thylakoids covered with phycobilisomes, with cytosolic starch. Predominantly free-living, and non-motile in trophic stages. The "higher" plants, commonly macroscopic in size, develop from embryos and are mostly terrestrial and vascular forms with alternation of haploid and diploid generations.

Contains several phyla with quite a number of classes and orders.

### **Kingdom V. FUNGI Linnaeus, 1753**

Eukaryotic organisms without plastids or phagotrophy (osmotrophic/absorptive nutrition instead) and possessing cell walls containing chitin and  $\beta$ -glucans. Mitochondria (with flattened cristae) and peroxisomes nearly always present; Golgi bodies or individual cisternae present. Contains one phylum of flagellated unicellular (occasionally filamentous) protists; all of the supra-protistan groups have multicellular mycelia composed of hyphae and are completely without pseudopodia, flagella, or even centrioles. Many symbiotic species but also many free-living, with the latter often macroscopic in size.

Contains four phyla, only one of which is composed of protists.

### **Kingdom VI. ANIMALIA Linnaeus, 1753**

Multicellular, non-photosynthetic, usually phagotrophic eukaryotes exhibiting a triploblastic body organization with collagenous connective tissue sandwiched between two dissimilar epithelia. Mitochondria (with flattened or rarely tubular cristae), Golgi bodies, and peroxisomes always present. Multiple tissues and organ systems, and typically with complex embryological development during ontogeny. Commonly macroscopic in size. Mostly free-living and motile but with some symbiotic groups, latter usually exhibiting osmotrophic nutrition.

Contains numerous phyla, classes, and orders, none of which includes any protists.

### **The phyla and their major lesser taxa**

In recent years, the **phylum** (or, often, in the case of algae, the **division**) has become the principal high-level taxonomic rank in considering both phylogeny and systematics of protists, a fact to which many papers in the literature attest (see reviews in Corliss 1984, 1986a, 1993). And it is widely admitted that the number of phyla of these "lower" eukaryotes must be a large one, not surprising in consideration of their great morphological and genetic diversity.

In view of relatively meager molecular data, the cladistic protistologist faces a difficult problem not only in identifying these phyla (or appreciating that such a rank is appropriate for them) but in interrelating them phylogenetically on the protistan *sensu lato* "tree". Some evolutionary biologists, on the other hand, feel a need



to assemble such groups into still higher packages (e.g. superphyla, infra- and subkingdoms, and kingdoms) and also to subdivide them unmercifully at lower ranks, interposing between phyla and classes such ranks as sub- and infraphyla and superclasses (not to mention intermediate taxa at ordinal, familial, and generic levels as well). I can understand the rationale involved in the latter practices, for they allow the user of the resulting schemes to appreciate the clustering of certain taxa that share key characters. Yet, for the general user, the teacher and the student, and the person interested in having a classification helpful in information retrieval, too much detail is not a desirable feature, in my opinion. Also, the introduction of intermediate ranks often requires new names, adding to the memory burden of the non-specialist. Therefore, in the present treatment of the protists, I am usually omitting reference to many of the "intermediate" ranks employed, for example, in the longer works of Cavalier-Smith (e.g. 1993c).

Whenever possible, I have adopted phyletic names familiar from the literature, as long as the composition and the rank of the taxon have not been too drastically changed over time (see **DISCUSSION**). With respect to the spelling of names of protist phyla, especially the prefixes and suffixes, I have - once again - tried to maintain traditional forms of the words. In particular, I have retained the phylum/division ending "-a" (exceptionally, "-ae" and one time "-i") so long used in both botanical and zoological taxonomic literature. For classes, I have used the traditional protozoological and botanical suffixes of "-ea" and "-phyceae" (occasionally, "-cetes"); and for subclasses, "-ia". My orders end in "-ida"; but, in the interest of saving space, not many orders are included on the following pages.

As an aid to readers of various backgrounds with respect to protistological high-level systematics, names of a goodly number of representative or common or familiar genera (plus some new within the past several years) are given under the lowest-ranked taxa listed within a specific phylum. The **INDEX** will serve as a convenient guide to the page-locations of these generic names.

My ordering of phyla within a kingdom is basically (meant to be) phylogenetic. An alphabetical arrangement would be of little value. On the other hand, to make up for our ignorance of "true" evolutionary interrelationships, a measure of "educated guess-work" (= healthy speculation?) is required in quite a number of instances. Quite often, brief comments are offered in place in controversial situations; otherwise, the reader is referred

to my **DISCUSSION** section for lengthier consideration of some major evolutionary or taxonomic problems.

For a convenient summary of the classification presented in this paper, the reader is referred to Table 1

### Phyla of Kingdom ARCHEZOA

In addition to the three quite disparate phyla described below, some workers have suggested the inclusion here, also, of the parabasalan flagellates (considered as the second phylum of the kingdom **PROTOZOA** in the present work) and/or of the family Entamoebidae (in a class of the protozoan phylum **Rhizopoda** here). Other taxonomists conservatively feel that this entire kingdom itself should be subsumed by the **PROTOZOA**.

#### Phylum 1. **ARCHAMOEBAE** Cavalier-Smith, 1983

Amoeboid or amoeboflagellated (generally a poorly motile single flagellum) protists with characteristics of the kingdom (q.v.), although presumed presence of 70s ribosomes not yet confirmed. Microaerobic, with symbiotic bacteria; free-living, mostly freshwater habitats.

#### Class **Pelobiontea** Page, 1976

(syn. **Karyoblastea** Margulis, 1974 *p.p.*)

Single class, thus with characters of phylum. Two orders recognized by some workers: Mastigamoebida Frenzel, 1892; and Phreatamoebida Cavalier-Smith, 1991, latter solely for the genus *Phreatamoeba*.

*Mastigamoeba*, *Mastigella*, *Mastigina*, *Pelomyxa*, *Phreatamoeba*

#### Phylum 2. **METAMONADA** Grassé, 1952

Bi-, quadri-, octo- (or occasionally more) flagellated protists, mostly symbiotic species, with characters of the kingdom (q.v.), including 70s ribosomes and (e.g. *Giardia*) 16s rRNA. Some free-living, majority intestinal symbionts of various hosts. Parabasalans (see second phylum of kingdom Protozoa) are here tentatively excluded from the present phylum.

#### Class (1) **Trepomonadea** Cavalier-Smith, 1993

One or two karyomastigonts, each with 1-4 flagella; contractile axostyle absent; cytostomal-cytopharyngeal apparatus present; few cell-surface cortical microtubules. Free-living or symbiotic.



Order 1. Diplomonadida Wenyon, 1926  
*Brugerolleia, Giardia, Hexamita, Octomitus, Spironucleus, Trepomonas, Trigonomonas*

Order 2. Enteromonadida Brugerolle, 1975  
*Caviomonas, Enteromonas, Trimitus*

Class (2) **Retortamonadea** Grassé, 1952  
Generally with characteristics given for the first class (above), but with cortical microtubules over entire body surface. Mostly intestinal symbionts (e.g. of insects and mammals). Single order.

Order Retortamonadida Grassé, 1952  
*Chilomastix, Retortamonas*

Class (3) **Oxymonadea** Grassé, 1952  
One or more karyomastigonts, each with 4 flagella; basal bodies of flagellar pairs are connected by a paracrystalline paraxostyle in which are embedded anterior ends of axostylar microtubules; axostyles typically contractile; cytopharynx absent. Intestinal symbionts of insects. Single order.

Order Oxymonadida Grassé, 1952  
*Monocercomonoides, Notila, Oxymonas, Pyrsonympha, Saccinobaculus*

Phylum 3. **MICROSPORA** Sprague, 1977

Minute, unicellular, obligate intracellular symbionts, with characteristics of the kingdom (including 70s ribosomes); sporoplasm uni- or binucleate; no flagellated stage in life cycle; underdeveloped Golgi(?) bodies; resistant spores contain complex extrusome, with polar tube and cap; one layer of thick spore wall chitinous. Commonly in variety of cells of diverse fresh-water, marine, or terrestrial hosts, mainly arthropods (especially insects) and fishes, but including even other protists. Name of the phylum is, unfortunately, identical to the generic name of a green algal protist in the kingdom Plantae.

Class (1) **Rudimicrosporea** Sprague, 1977  
Extrusion apparatus rudimentary, with thick (manubroid) non-spiraled polar tube and no polaroplast or posterior vacuole. Single order.

Order Metchnikovellida Vivier, 1975  
*Amphiacantha, Desportesia, Metchnikovella*

Class (2) **Microsporea** Delphy, 1963  
Complex extrusion apparatus, with coiled polar tube, polaroplast and posterior vacuole typically present. Many species in second order.

Order 1. Minisporida Sprague, 1972  
*Burkea, Buxtehudea, Chytridiopsis, Hessea*

Order 2. Microsporida Balbiani, 1882  
*Culicospora, Encephalitozoon, Endoreticulatus, Enterocytozoon, Glugea, Gurleya, Loma, Microfilum, Mrazekia, Nosema, Perezia, Pleistophora, Spraguea, Stempellia, Tardivesicula, Telomyxa, Thelohania, Tricornia, Tuzetia, Unikaryon, Vairimorpha*

## Phyla of Kingdom PROTOZOA

Phylum 1. **PERCOLOZOA** Cavalier-Smith, 1991

Unicellular, non-pigmented protozoa allegedly primitively lacking Golgi bodies; peroxisomes usually present; mitochondria or, more rarely, hydrogenosomes present; mitochondrial cristae flat, sometimes discoidal, atypical of kingdom. Flagella usually present, 1-4 (occasionally more), without mastigonemes; some species are amoeboid flagellates, several of which never have flagella; fresh-water and marine habitats.

Class (1) **Percolomonadea** Cavalier-Smith, 1993  
Non-amoeboid, quadriflagellated forms; striated rootlets absent. Exhibiting the most primitive characters of the phylum and comprising only a single genus, species here have been assigned by past workers to the following much larger class.  
*Percolomonas*

Class (2) **Heterolobosea** Page & Blanton, 1985  
Monopodial amoeboid trophic form; transitory flagellated stage, sometimes missing altogether; striated rootlets present; close association of rough endoplasmic reticulum with mitochondria. Fruiting bodies present in the first order, absent in the second. Is the genus *Fonticula* here or in Rhizopoda?

Order 1. Acrasida Schröter, 1886  
*Acrasis, Pocheina*

Order 2. Schizopyrenida Singh, 1952  
*Adelphamoeba, Gruberella, Heteramoeba, Naegleria, Paratetramitus, Pernina, Pseudovahlkampfia, Singhamoeba, Tetramastigamoeba, Tetramitus, Vahlkampfia*

Class (3) **Lyromonadea** Cavalier-Smith, 1993  
Anaerobic flagellates with hydrogenosomes and no peroxisomes; harp-shaped structure of microtubules; two pair anterior flagella, 1-4 nuclei. Only two genera.  
*Lyromonas, Psalteriomonas*



Class (4) **Pseudociliata** Corliss & Lipscomb, 1982  
Multiflagellated, multinucleate forms with mitochondria (with rigid discoid cristae) and peroxisomes. Single genus, with several species. Some workers have appended these protists to the phylum Euglenozoa (below).  
*Stephanopogon*

Phylum 2. **PARABASALA** Honigberg, 1973

Unicellular, almost exclusively symbiotic, flagellates with mastigont system typically with multiple flagella and one or more nuclei; 70s ribosomes; no mitochondria but hydrogenosomes in a double envelope; characteristic complex parabasal body apparatus (= Golgi body). Wide range of hosts, including humans, but many species in termites and wood-feeding roaches. Some workers place this phylum in the kingdom Archezoa.

Class (1) **Trichomonadea**

Typically 4-6 flagella; pelta and non-contractile axostyle part of each mastigont (one exception); trophic form in one genus (*Dientamoeba*) permanently amoeboid with no flagella.

Order Trichomonadida Kirby, 1947

*Bullanympha*, *Calonympha*, *Devescovina*, *Dientamoeba*, *Ditrichomonas*, *Hexamastix*, *Histomonas*, *Monocercomonas*, *Pseudotrichomonas*, *Snyderella*, *Trichomonas*

Class (2) **Hypermastigotea** Grassi & Foà, 1911

Mastigont system with numerous flagella and multiple Golgi bodies; basal bodies of flagella often arranged in closely packed longitudinal or spiral rows; single nucleus.

Order 1. Lophomonadida Light, 1927

*Joenia*, *Lophomonas*, *Mesojoenia*, *Microjoenia*

Order 2. Trichonymphida Poche, 1913

*Barbulanympha*, *Deltotrichonympha*, *Holomastigotoides*, *Hoplonympha*, *Kofoidia*, *Macrospironympha*, *Spirotrichonympha*, *Teranympha*, *Trichonympha*

Phylum 3. **EUGLENOZOA** Cavalier-Smith, 1981

Forms with 1-4 flagella, with paraxial rods and non-tubular mastigonemes; with peroxisomes and commonly discoidal mitochondrial cristae, latter atypical of kingdom; cytoskeleton of microtubules reinforcing cortex; Golgi bodies well developed; nuclear division

with persistent nucleolus; many fresh-water free-living forms, but also number of important symbiotic species (e.g. human blood parasites); some species photosynthetic, with chloroplasts in cytosol with chlorophylls a and b and enveloped in three membranes but lacking starch. Three classes; a possible fourth, Pseudociliata, now appears in phylum 1, Percolozoa (above), and a possible fifth, Hemimastigophorea, is placed tentatively in phylum 4, Opalozoa (below). The bodonids plus the trypanosomatids might deserve taxonomic separation from the euglenoids proper at the level of subphylum.

Class (1) **Diplonematea** Cavalier-Smith, 1993

Phagotrophic flagellates (two equal flagella) lacking chloroplasts, pellicular plates, kinetoplasts, paraxial rods; plate-like mitochondrial cristae; feeding apparatus with vanes and two supporting rods. Single genus.

*Diplonema* (syn. *Isonema*)

Class (2) **Euglenoidea** Bütschli, 1884

Unicellular or colonial, bi- (rarely more) flagellated forms; phagotrophic, photosynthetic (with paramylon storage product), osmotrophic, or mixotrophic; all pigmented species with stigma (eyespot) containing  $\beta$ -carotene derivatives and other carotenoid pigments. Numerous species. The exact taxonomic placement within the class of a number of species symbiotic in copepods (especially members of such genera, themselves of doubtful validity, as *Conradinema*, *Paradistigma*, *Parastasia*, and others) must await further study.

Order 1. Euglenida Bütschli, 1884

*Astasia*, *Colacium*, *Distigma*, *Euglena*, *Eutreptia*, *Khawkinia*, *Phacus*, *Trachelomonas*

Order 2. Euglenamorphida Leedale, 1967

*Euglenamorpha*, *Hegneria*

Order 3. Rhabdomonadida Leedale, 1967

*Menoidium*, *Rhabdomonas*

Order 4. Heteronematida Leedale, 1967

*Entosiphon*, *Heteronema*, *Peranema*, *Petalomonas*, *Ploeotia*, *Sphenomonas*

Class (3) **Kinetoplastidea** Honigberg, 1963

Small, colorless flagellates with 1-2 flagella (arising from pocket and possessing paraxial rod) and prominent kinetoplast (distinctive body of massed DNA) within single mitochondrion, latter typically extending length of body; numerous peroxisomes



(known as glycosomes) present; free-living or symbiotic, with latter (including blood parasites, often highly pathogenic) exhibiting elaborate life cycles frequently involving two hosts.

Order 1. Bodonida Hollande, 1952

*Bodo*, *Cephalothamnium*, *Cryptobia*, *Ichthyobodo*, *Procryptobia*, *Rhynchomonas*

Order 2. Trypanosomatida Kent, 1880

*Blastocrithidia*, *Crithidia*, *Endotrypanum*, *Herpetomonas*, *Leishmania*, *Leptomonas*, *Phytomonas*, *Trypanosoma*

Phylum 4. **OPALOOZOA** Cavalier-Smith, 1991

Predominantly small, free-living, unicellular, uninucleate, biflagellated protozoa with tubular mitochondrial cristae and totally lacking chloroplasts, cortical alveoli, and rigid tubular mastigonemes. Likely a paraphyletic assemblage, many of its species have not yet been well studied by modern techniques. Cavalier-Smith (1993b, c) assigns some 20 generally small orders here, many new, only a few are considered below. Among problematical groups possibly in this phylum, mostly in my class 1, are various proteomyxids *s.l.*, *Ebria*, *Phagodinium*, *Phagomyxa* and the fungus-like *Nephromyces*.

Class (1) **Proterozoea** Cavalier-Smith, 1981

Generally with characters of phylum; rarely, with flattened mitochondrial cristae; a few groups contain symbiotic forms. Many minute, little-studied free-living marine, fresh-water, and soil flagellates or amoeboid flagellates may belong here (some included in partially tentative lists of genera given below).

Order 1. Heteromitida Cavalier-Smith, 1993

*Amastigomonas*, *Anisomonas*, *Apusomonas*, *Cercomonas*, *Diphyllea*, *Discocelis*, *Heteromita*, *Jakoba*, *Leucodictyon*, *Massisteria*, *Proteromonas*, *Pseudospora*, *Thaumatomastix*

Order 2. Cyathobodonida Cavalier-Smith, 1993

*Cyathobodo*, *Kathablepharis*, *Leucocryptos*, *Phalansterium*, *Platychilomonas*, *Pseudodendromonas*, *Spongomonas*

Order 3. Plasmodiophorida Cook, 1928

(name better credited to Zopf, 1885?)

*Octomyxa*, *Plasmodiophora*, *Polymyxa*, *Sorodiscus*, *Spongospora*, *Tetramyxa*, *Woronina*

Class (2) **Opalinatea** Wenyon, 1926

(syns. **Protociliata** Metcalf, 1918, **Paraflagellata** Corliss, 1955, **Slopalinida** Patterson, 1986 *p.p.*)

Four (in first order) to many flagella, apical or arranged in oblique longitudinal rows; typically one (first order) or either two or many nuclei; no peroxisomes; osmotrophic nutrition; all species symbiotic, endocommensals principally in amphibian hosts. Differences between members of first and second order, all not listed here, may require greater taxonomic separation in the future. The entire class is rather atypical of the phylum *s.s.* Patterson's (1986a) recent taxon Slopalinida also embraced *Proteromonas*, which I have placed in the preceding class, **Proterozoea**.

Order 1. Karotomorphida Cavalier-Smith, 1993

*Karotomorpha*

Order 2. Opalinida Poche, 1913

*Cepedea*, *Opalina*, *Protoopalina*, *Protozelleriella*, *Zelleriella*

Class (3) **Kinetomonadea** Cavalier-Smith, 1993

Free-living uninucleate forms with 2-4 flagella, peroxisomes, usually unique extrusomes (kinetocysts); mitochondrial cristae flat or with branched tubules; some species with axopodial axonemes nucleated by axoplast associated with exceptionally long centrioles. Possibly multiple orders in this class, which includes some of the "helioflagellates" of the literature.

*Ancyromonas*, *Dimorpha*, *Heliomonas*, *Histiona*, *Reclinomonas*, *Tetradimorpha*

Class (4) **Hemimastigophorea** Foissner, Blatterer & Foissner, 1988

Small, colorless, multiflagellated, phagotrophic (but no permanent cytostome) protists with "infraciliature" reminiscent of ciliates; mitochondrial cristae saccular-tubular; no paraxial rods, no mastigonemes; two microtubule-bearing pellicular plates; complex extrusomes. Found primarily in soils. Some workers consider this class as possibly a separate phylum, and even closer to the phylum Euglenozoa (above) than indicated here. Single order, three genera.

Order Hemimastigida Foissner et al., 1988

*Hemimastix*, *Spironema*, *Stereonema*

Phylum 5. **MYCETOZOA** de Bary, 1859

(syns. ± **EUMYCETOZOA** Zopf, 1885, and **MYXOMYCETES** & **MYXOMYCOTA** auctt. *pp*)

Free-living, unicellular or syncytial plasmodial forms, non-flagellated in their uni- or multinucleate



phagotrophic stages; mitochondrial cristae tubular; uni- or multicellular aerial fruiting bodies (sporophores or sorocarps) bearing one to many spores with cellulosic or chitinous walls; spore germination produces amoeboid or uni- or biflagellated cells. Widely distributed in decaying vegetation. Perhaps the characterization of the whole phylum should be expanded to include many of the taxonomically enigmatic marine plasmodial protists with reticulopodia studied by Grell (e.g. 1985, 1991b) and placed by him in an order Promycetozoida Grell, 1985: for example, *Corallomyxa*, *Megamoebomyxa*, and *Thalassomyxa*. But relationships of such genera to the Rhizopoda (**Lobosea** or maybe the athalamid **Granuloreticulosea**), or even to certain heterokonts (in the kingdom Chromista), remain unresolved possibilities. Phylum contains both cellular and "acellular" slime molds.

Class (1) **Protostelea** Olive & Stoianovitch, 1966

Single amoeboid cells, with filose pseudopodia, give rise to simple sorocarps (= sporocarps) of one to few spores on delicate, narrow stalk. Several species (amoeboflagellates, in effect) have a flagellated stage in their life cycle.

*Cavostelium*, *Ceratiomyxa*, *Protostelium*

Class (2) **Myxogastrea** Fries, 1829

Generally with characters of phylum, as largest group of the plasmodial (or "acellular") slime molds. Multiple orders recognized.

*Badhamia*, *Comatricha*, *Cribraria*, *Didymium*, *Echinostelium*, *Fuligo*, *Licea*, *Lycogala*, *Physarum*, *Stemonitis*, *Trichia*, *Tubulina*

Class (3) **Dictyostelea** Lister, 1909

Cellular slime molds from soil with triphasic life cycle: unicellular amoeboid microphage, pseudoplasmodium (slug) formed by aligned aggregating myxamoebae, and multicellular sorocarp on branched or unbranched stalks.

*Acytostelium*, *Dictyostelium*, *Polysphondylium*

Phylum 6. **CHOANOZOA** Cavalier-Smith, 1989

Free-living, unflagellated, colorless, unicellular or colonial forms with non-diskoid flattened (atypical of kingdom) mitochondrial cristae; single flagellum surrounded by collar of microvilli (actin filaments internally) used in microphagous feeding; marine

species may have quite complex basket-like loricae of siliceous costae arranged longitudinally. These widely distributed protists (especially in marine habitats), known familiarly as the collar flagellates, have also been called choanoflagellates, choanomnads, craspedomonads, craspedophyceans and even craspedomonadophyceans. Cavalier-Smith's phyletic name, originally published as "Choanociliata", emended by him in 1989. Single class with single order: names both credited to Kent here.

Class **Choanoflagellata** Kent, 1880

(syn. **Craspedophyceae** Chadeffaud, 1960)

Order Choanoflagellida Kent, 1880

*Acanthoeca*, *Acanthoecopsis*, *Bicosta*, *Calliacantha*, *Codosiga*, *Conion*, *Diaphanoeca*, *Monosiga*, *Parvicorbicula*, *Pleurasiga*, *Proterospongia*, *Salpingoeca*, *Stephanoeca*

Phylum 7. **DINOZOA** Cavalier-Smith, 1981

Biflagellated, uninucleate protozoa with amphiesmal vesicles or cortical alveoli (containing cellulosic plates in some groups), tubular (sometimes ampulliform) mitochondrial cristae, and peroxisomes; one flagellum typically with paraxial rod; ca. 50% of extant species pigmented, with chloroplasts containing chlorophylls a and c, enveloped by three (rarely two) membranes, lacking phycobilisomes, and located in cytosol; non-pigmented and some colored species phagotrophic; nucleus haploid, typically with distinctive chromosomes consisting primarily of non-protein complexed DNA. Assemblage at one time called the "Mesokaryota" because of its alleged possession of a combination of pro- and eukaryotic characters. First of three phyla known collectively as the "Alveolata", a super-category designated a parvkingdom by Cavalier-Smith (1993c). Possibly assignable somewhere here is the puzzling "giant protist" *Hochbergia* (a cephalopod symbiont measuring 1-2 mm in length: Shinn and McLean, 1989).

Class (1) **Protalveolata** Cavalier-Smith, 1991

Atypical dinozoa; closed mitosis, but mitotic spindle intranuclear; chromatin of normal eukaryotic form; all non-photosynthetic species, mostly free-living phagotrophs but some marine forms totally symbiotic (osmotrophic); typically unicellular and uninucleate, but symbiotic forms may be branched and multi-



nucleate. Several quite distinctive orders may be justifiable here. Some of the included genera require further study to be certain of their taxonomic assignment.

*Colponema, Ellobiopsis, Oxyrrhis, Thalassomyces*

#### Class (2) **Dinoflagellata** Bütschli, 1885

With characters of phylum, as its major class; mostly unicellular species, but some form colonies (especially catenoid); often free-living, auto- or phagotrophic or both (mixotrophic), but some groups symbiotic (osmotrophic); members of a major endosymbiotic sub-taxon have no pellicular alveoli and very low number of chromosomes with histones clearly present, but dinospores prove their position here. Widely distributed forms, mostly planktonic. Multiple orders in literature, with half of contained species represented by fossil forms (but only genera with living species are listed below). Class described here is essentially the equivalent of botanists' **Pyrrophyta** Pascher, 1914, and **Dinophyceae** Fritsch, 1927.

*Alexandrium, Amoebophrya, Amphidinium, Blastodinium, Ceratium, Chytriodinium, Cryptothecodinium, Cystodinium, Dinophysis, Dubosquella, Erythrospidinium, Glenodinium, Gleodinium, Gonyaulax, Gymnodinium, Gyrodinium, Haplozoon, Kofoidinium, Noctiluca, Oodinium, Oxytoxum, Peridinium, Polykrikos, Prorocentrum, Protoperidinium, Ptychodiscus, Pyrocystis, Pyrophacus, Rhizodinium, Roscoffia, Symbiodinium, Syndinium, Thoracosphaera, Zooanthea*

#### Phylum 8. **CILIOPHORA** Doflein, 1901

Commonly with numerous longitudinal rows of cilia (single or paired), with perkinetal fission (homothetogenic, as opposed to the symmetrogenic of flagellates), and distinctive kinetidal infraciliature; many have complex oral ciliature; cortical alveoli characteristic of most groups; mitochondrial cristae tubular, often curved; in anaerobic species, mitochondria may be missing or replaced by hydrogenosomes; nuclear apparatus heterokaryotic, typically with one or more diploid micronuclei and one or more polyploid macronuclei; sexual phenomenon of conjugation; heterotrophs nutritionally, but some species have photosynthetic algal protists as endosymbionts. Widely distributed, often conspicuous forms, mostly free-living in aquatic and

terrestrial habitats, but symbiotic and symphoriontic species associated with great variety of host organisms. Sometimes known as the **INFUSORIA** auctt. (a very old and vague term) or by the more apt name of **HETEROKARYOTA** Hickson, 1903, the cilioprotists comprise one of the largest protist phyla, with 8-10 classes and many orders. Second member of "Alveolata" group.

#### Class (1) **Karyorelictea** Corliss, 1974

Flattened body, often ribbon-like and contractile; habitat commonly interstitial niches of marine sands (one major genus fresh-water); two to many non-dividing (and essentially diploid) macronuclei formed anew at organism's fission from dividing diploid micronuclei; postciliodesmata characteristically present; generally without cortical alveoli; many species without definitive mouth but phagotrophic via non-ciliated area of ventral surface. The group, considered primitive by a number of workers, is divisible into two orders. But the class itself should perhaps be reduced to a subordinate taxon of (part of) the next class, below: see comments there.

*Kentrophoros, Loxodes, Remanella, Trachelocerca, Trachelonema, Tracheloraphis*

#### Class (2) **Polyhymenophorea** Jankowski, 1967

(syns. **Heterotrichea** Stein, 1859 plus **Spirotrichea** Bütschli, 1889, in effect; and **Postciliodesmatophora** Gerassimova & Seravin, 1976 *p.p.*)

Diverse body shapes and sizes (some quite large), of both free-living (marine and fresh-water) and symbiotic species; some groups with postciliodesmata; characteristically with many conspicuous buccal membranelles, plus compound somatic ciliature (cirri) in some groups. Based on recent rRNA analyses, supported by ultrastructural observations, some workers would split this huge and probably paraphyletic assemblage into at least two classes (thus elevating **Polyhymenophorea** to some supra-level or even eliminating it), with my first class **Karyorelictea** embraced by the heterotrich moiety and the remainder of my polyhymenophoreans assigned to a spirotrich group. Here, each such major section is conservatively treated as a subclass. Each has many orders (the first one would also have two subclasses of its own, the karyorelictians and the heterotrichians *s.s.*, if it were elevated to independent class status).



Subclass 1. **Heterotrichia** Stein, 1859

The classically known heterotrichs *s.l.* plus the newer protoheterotrichs and possibly (as discussed above) the karyorelictids (see my class 1).

*Anigsteinia, Ascobius, Avelia, Blepharisma, Brachonella, Caenomorpha, Clevelandella, Climacostomum, Condylostoma, Epalxella, Fabrea, Folliculina, Geleia, Lagotia, Licnophora, Metopus, Mylestoma, Nyctotheroides, Nyctotherus, Paracichlidotherus, Peritromus, Phacodinium, Protocrusia, Reichenowella, Saprodinium, Sicutophora, Spirostomum, Stentor, Transitella*

Subclass 2. **Spirotrichia** Bütschli, 1889

The classically known oligotrichs *s.l.* (i.e. oligotrichs *s.s.* + tintinnids *s.l.* = today's choreotrichs) and the old hypotrichs *s.l.* (i.e. the pre-1980 stichotrichs and sporadotrichs).

*Amphisiella, Aspidisca, Australothrix, Bakuella, Cirrhogaster, Codonella, Cyrtostrombidium, Diophryopsis, Diophrys, Discocephalus, Euplotes, Favella, Gastrostyla, Halteria, Kahliella, Kerona, Kiitricha, Laboea, Lamtostyla, Leegaardiella, Lohmanniella, Nolaclusilis, Onychodromus, Oxytricha, Pelagohalteria, Pelagostrombidium, Plagiotoma, Strobilidium, Strombidium, Stylonychia, Territricha, Tintinnopsis, Tontonia, Tricoronella, Undella, Uronychia, Urosomoides, Urostyla, Wallackia, Xystonellopsis, Yvonniellina*

Class (3) **Colpodea** Small & Lynn, 1981

Somatic dikinetids, reticulate silverline system, and somatic stomatogenesis; posterior kinetosome has well developed transverse microtubular ribbon extending posteriorly, forming LKm fiber by paralleling and overlapping with ribbons from more anterior dikinetids; oral ciliature consists of right and left ciliary fields; mainly terrestrial or edaphic forms. Two subclasses, second one solely for five small families; great bulk of the species are in the nominate subclass, which contains half a dozen orders.

*Aristerostoma, Bresslaua, Bryometopus, Bryophrya, Bursaria, Bursaridium, Colpoda, Cosmocolpoda, Cyrtolophosis, Grandoria, Grossglockneria, Hausmanniella, Kreyella, Maryna, Mycterothrix, Platyophrya, Pseudoglaucoma, Sorogena, Thylakidium, Trihymena, Woodruffia*

Class (4) **Phyllopharyngea** de Puytorac et al., 1974

Cytopharynx lined with radially arranged leaf-like microtubular ribbons (= phyllae), themselves typical-

ly surrounded, in the old cyrtophorids, by nematodesmata (= cytopharyngeal basket or cyrtos); macronucleus characteristically heteromorous in many (but not suctorian) species; suctorians also atypical in other ways: polystomic with sucking tentacles, non-ciliated trophic stage carnivorous, commonly stalked, reproduction by budding; chonotrichs likewise specialized: heteromorous macronucleus but no nematodesmata, sessile forms (ectosymbionts on crustaceans), limited ciliation, reproduction by budding. Three subclasses with several orders.

*Acineta, Ancistrocoma, Brooklynella, Chilodochona, Chilodonella, Chlamydodon, Cyathodinium, Dendrocometes, Dendrosoma, Dysteria, Endosphaera, Ephelota, Hartmannula, Heliochona, Helio-phrya, Hypochona, Isochona, Lobochocha, Lorico-phrya, Lwoffia, Lynchella, Ophryodendron, Paracineteta, Phalacrocleptes, Phascolodon, Podophrya, Raabella, Rhabdophrya, Sphenophrya, Spirochona, Stylochona, Tachyblaston, Thecacineteta, Tokophrya, Trichochona, Trichophrya, Trochilia, Vasichona*

Class (5) **Nassophorea** Small & Lynn, 1981

Characterized by common possession of highly distinctive "nasse" or cyrtos in cytopharyngeal area; hypostomial fringe prominent or reduced to few pseudomembranelles; fibrous trichocysts; mostly free-living, fresh-water forms. Several orders, but peniculines (e.g. *Paramecium*) are excluded (see 6th subclass of next class, below), leaving only (some of) the old cyrtophorids here.

*Furgasonia, Leptothorax, Microthorax, Nassula, Nassulopsis, Pseudomicrothorax, Scaphidiodon, Zosterodasys*

Class (6) **Oligohymenophorea** de Puytorac et al., 1974

Somatic kineties, unless entirely absent, often composed of monokinetids; buccal apparatus, when present, consists basically of paroral (formerly undulating membrane, UM) dikinetid on right and several membranelles or polykinetids (AZM) on left; distinct, overlapping kinetodesmata; mucocysts common, with explosive trichocysts in some species. Six quite diverse subclasses warrant separate descriptions here.

Subclass 1. **Hymenostomatia** Delage & Hérouard, 1896

Somatic monokinetids; right-most postoral kinety stomatogenic; buccal ciliature tetrahymenal (UM + AZM). Two orders, second - the ophryoglenids - with



a unique watchglass organelle and a complex life cycle as obligate histophagous symbionts.

*Bursostoma*, *Colpidium*, *Curimostoma*, *Espejoia*, *Glaucoma*, *Ichthyophthirius*, *Jaocorlissia*, *Lambornella*, *Monochilum*, *Ophryoglena*, *Tetrahymena*, *Turaniella*

Subclass 2. **Scuticociliatia** Small, 1967

Paroral dikinetid in three distinct segments, with stomatogenesis via third and/or scutico-vestige; ciliation usually sparse, with thigmotactic area anteriorly, caudal cilium posteriorly; mitochondria long and sometimes fused into huge chondriome. Conventionally, three orders: the philasterids, the pleuronematids, and the totally symbiotic thigmotrichs.

*Ancistrum*, *Ancistrumina*, *Boveria*, *Cinetochilum*, *Cohnilembus*, *Conchophthirus*, *Cyclidium*, *Dexiotricha*, *Dragescoa*, *Entodiscus*, *Fenchelia*, *Hemipeira*, *Histiobalantium*, *Hysterocineta*, *Loxocephalus*, *Miamiensis*, *Myxophthirus*, *Paraauronema*, *Paurotricha*, *Peniculistoma*, *Philaster*, *Pleurocoptes*, *Pleuronema*, *Proboveria*, *Ptychostomum*, *Schizocalyptra*, *Thigmocoma*, *Thigmophrya*, *Uronema*, *Urozona*

Subclass 3. **Astomatia** Schewiakoff, 1896

Mouthless forms, endosymbionts mostly in annelids (usually, but not exclusively, terrestrial oligochaetes) but one group in amphibians and turbellarians; frequently with well developed cortical endoskeleton, often with elaboration of some kind of holdfast organelle at anterior end of body. Two or three orders. *Anoplophrya*, *Buetschliella*, *Cepedietta*, *Clausilocola*, *Contophrya*, *Durchoniella*, *Haptophrya*, *Hopliophrya*, *Intoshellina*, *Lomiella*, *Maupasella*, *Radio-phrya*, *Steinella*

Subclass 4. **Peritrichia** Stein, 1859

Prominent oral ciliary field; somatic ciliature reduced to telotrochal band; widely distributed forms, many stalked and sedentary (though others mobile), some colonial, some loricate, all with aboral scopula; dispersal typically by migratory larval form (= telotroch); often with strongly contractile myonemes, body and/or stalk; fusion of micro- and macroconjugants. Symbiotic mobiline species have distinctive denticulate ring on aboral surface of the body. Two orders.

*Apiosoma*, *Astylozoon*, *Carchesium*, *Cothurnia*, *Ellobiophrya*, *Epistylis*, *Haplocaulus*, *Lagenophrys*,

*Opercularia*, *Ophrydium*, *Opisthonecta*, *Orbopercularia*, *Pallitrichodina*, *Platycola*, *Polycycla*, *Propygidium*, *Rhabdostyla*, *Scyphidia*, *Semitrichodina*, *Trichodina*, *Trichodinopsis*, *Urceolaria*, *Vaginicola*, *Vorticella*, *Zoothamnium*

Subclass 5. **Apostomatia** Chatton & Lwoff, 1928

Ciliary rows typically spiraled, widely spaced or sometimes entirely missing; cytostome inconspicuous (or absent), usually associated with unique rosette; well-developed kinetodesmata; often polymorphic life cycle, with most species ectosymbionts (phoronts) on marine crustaceans. Three orders.

*Ascophrys*, *Askoella*, *Chromidina*, *Collinia*, *Conidiophrys*, *Cyrtocaryum*, *Foettingeria*, *Gymnodinioides*, *Hyalophysa*, *Opalinopsis* *Ophiurae-spira*, *Phthorophrya*, *Vampyrophrya*

Subclass 6. **Peniculinia** Fauré-Fremiet in Corliss, 1956

Buccal cavity contains paroral membrane, peniculi, and quadrulus; oral nematodesmata also present; somatic dikinetids; cortical alveoli distinct; explosive trichocysts; predominantly monomorphic, free-living, fresh-water microphagous forms. Assigned to the class Nassophorea (above) by some taxonomic ciliatologists.

*Clathrostoma*, *Disematostoma*, *Frontonia*, *Lembadion*, *Marituja*, *Neobursaridium*, *Paramecium*, *Stokesia*, *Urocentrum*, *Wenrichia*

Class (7) **Prostomatea** Schewiakoff, 1896

Mouth at or near anterior end of body, with relatively simple oral ciliature; usually somatic monokinetids; nematodesmata form rhabdos; toxicysts common; a brosse characteristic of most species. Two orders, Prostomatida Schewiakoff, 1896, and the much larger Prorodontida Corliss, 1974. Many of the old rhabdophorids are here, but some are in the following class as well. The taxonomic place of a few genera is controversial.

*Bursellopsis*, *Coleps*, *Helicoprorodon*, *Holophrya*, *Metacystis*, *Nolandia*, *Placus*, *Plagiocampa*, *Planicoleps*, *Prorodon*, *Pseudobalanion*, *Pseudoprorodon*, *Spathidiopsis*, *Tiarina*, *Urotricha*, *Vasicola*

Class (8) **Litostomatea** Small & Lynn, 1981

Relatively inconspicuous or non-specialized oral ciliature; somatic monokinetids with two transverse



microtubular ribbons; kinetodesmata short, non-overlapping; oral ciliature derived from adjacent somatic kinetids with transverse microtubular ribbons supporting cytopharynx, latter (in many species) surrounded by nematodesmata (= rhabdos). Some species with toxicysts. Three or four subclasses with number of orders, including groups classically known as haptorids, vestibuliferans/trichostomes, pleurostomes, and entodiniomorphids. *Balantidium* is the only ciliate parasitic in humans. See also the comments under **Prostomatea**, above.

*Actinobolina, Alloiozona, Amphileptus, Arachnodinium, Askenasia, Balantidium, Blepharocorys, Bryophyllum, Chaenea, Cycloposthium, Cyclotrichium, Didesmis, Didinium, Dileptus, Enchelys, Entodinium, Gorillophilus, Isotricha, Lacrymaria, Lagynophrya, Lepidotrachelophyllum, Litonotus, Loxophyllum, Mesodinium, Ophryoscolex, Parabundleia, Paraisotricha, Phialinides, Plagiopyla, Pseudotrachelocerca, Pycnothrix, Quasillagilis, Rhabdoaskenasia, Rhinozeta, Sonderia, Spathidium, Triadinium, Trichospira, Troglodytella, Vestibulogum*

Phylum 9. **APICOMPLEXA** Levine, 1970

Unicellular endosymbionts or predators characterized by having, at some stage in life cycle, an apical complex typically composed of polar rings, rhoptries, micronemes, and usually a conoid; highly compressed smooth-membraned cisternae (= alveoli) usually present in cell cortex of infective stage; subpellicular microtubules and micropores common; flagella restricted (except in first class) to microgametes or missing entirely; mitochondrial cristae tubular, much reduced, or even absent. Except for recent (and still bit disputed) addition of *Perkinsus* to phylum, the whole assemblage remains essentially identical to **SPOROZOA** Leuckart, 1879, the name now treated by many workers as a synonym of **APICOMPLEXA**. Four classes, somewhat controversial, recognized here. Two classes proposed by parasitologists (see Levine 1988) were subsequently used by Corliss (1991c) as "group" names: Conoidea for classes 2 and 3 (below), and Aconoidea for 4; to which he added Zoosporea for class 1. This is the third (and last: but see **GLAUCOPHYTA**?) phylum of the "Alveolata" assemblage (others are the dinoflagellates and the ciliates: see above).

Class (1) **Perkinsidea** Levine, 1978

Flagellated forms, typically with two unequal flagella, but with most of apical complex organelles and with cortical alveoli; large posterior vacuole with diverse inclusions; some species with dinoflagellate-like trichocysts, some with contractile vacuoles; parasites of oysters or predators on various other protists. Two orders, one for each included genus. *Colpodella* (syn. *Spiromonas*), *Perkinsus*

Class (2) **Gregarinidea** Dufour, 1828

Mature gamonts large, extracellular, exhibiting syzygy, with production of essentially isogamous gametes, but male gametes may be flagellated (with basal body of nine singlet instead of usual eukaryotic triplet microtubules); zygotes undergo meiosis and sporogony within gametocystic membrane; trophonts with mucron or epimerite; all species in digestive tract or body cavity of invertebrates or lower chordates. Three or four orders recognized.

*Actinocephalus, Ancora, Caulleryella, Cosmetophilus, Diplocystis, Doliospora, Gonospora, Gregarina, Lankesteria, Lecudina, Monocystis, Ophryocystis, Porospora, Rhynchocystis, Schizocystis, Selenidioides, Selenidium, Siedleckia, Stephanospora, Stylocephalus, Uradiophora, Zygcystis*

Class (3) **Coccidea** Leuckart, 1879

Gamonts typically intracellular; female gamont becomes macrogamete without division, syzygy generally absent, microgametes many and with two or three flagella having basal bodies ultimately with typical nine triplet microtubules; within oocystic membrane, zygote produces sporoblasts which, in own membranes, produce two or more sporozoites; infective sporozoite invades host cell and, characteristically, grows and divides to form multiple merozoites capable of invading other host cells; eventually, some merozoites develop into gamonts, repeating cycle; highly resistant oocyst can survive outside host body (e.g. in soil) for long time before ingestion and continued development and invasion, typically, of host's gut epithelial cells. Most species monoxenous. Three orders (Eimeriida Léger, 1911 by far the largest) commonly recognized.

*Adelea, Aggregata, Besnoitia, Caryospora, Coelotropha, Cryptosporidium, Cyclospora, Diplospora, Dobellia, Dorisiella, Eimeria, Frenkelia, Goussia, Grellia, Haemogregarina, Hepatozoon, Isospora, Karyolysus, Klossia, Klossiella,*



*Lankesterella*, *Legerella*, *Sarcocystis*, *Schellackia*, *Selysina*, *Toxoplasma*, *Tyzzeria*, *Wenyonella*

Class (4) **Haematozoa** Vivier, 1982

Apical complex without conoid or conoidal rings and rudimentary in other features; mitochondria simple or absent entirely; motile zygote (= ookinete) penetrates vector-host's gut wall, producing numerous "naked" sporozoites which migrate to lumen of salivary glands, ready for transmission to next definitive host; in formation of gametes, basal bodies contain nine singlet microtubules but single flagellum produced exhibits typical 9 + 2 pattern. All species heteroxenous: merogony and formation of gamonts in blood cells of vertebrates; maturation of gametes, fertilization, and sporogony in gut of blood-sucking arthropods.

Order 1. Haemosporida Danilewsky, 1885

*Haemoproteus*, *Hepatocystis*, *Leucocytozoon*, *Plasmodium*, *Saurocytozoon*

Order 2. Piroplasmida Wenyon, 1926

*Anthemosoma*, *Babesia*, *Dactylosoma*, *Echinozoon*, *Theileria*

Phylum 10. **RHIZOPODA** von Siebold, 1845

Non-flagellated (except for gametes of class 4), unicellular or plasmodial phagotrophs lacking aerial sporangia; typically, pseudopodia serve in both locomotion and feeding; all non-photosynthetic forms, except for groups with endosymbiotic algae; Golgi bodies and mitochondria (generally with tubular cristae) always present except in class 2 where mitochondrial absence considered secondary; species typically uninucleate (some exceptions) and free-living (except for totally endosymbiotic forms of small class 2 and very few scattered other species). Classically, phyla 10-12 *sensu lato* were combined under a super-taxon called the "Sarcodina".

Class (1) **Lobosea** Carpenter, 1861

Pseudopodia lobose or somewhat filiform; body often naked, but also groups with tests (composed of organic and/or inorganic materials, with single aperture). Predominantly free-living forms in soil, freshwater, or marine habitats, widely distributed. Two subclasses and number of orders; but the class may be a polyphyletic assemblage. The genera *Copromyxa* and *Guttulinopsis* (and some other former mycetozoa proving difficult to assign) might also

belong here, as well as the baffling symbiotic *Blas-tocystis* (see comments on this genus under **FUNGI**), and the curious apseudopodial *Luffisphaera*.

*Acanthamoeba*, *Amoeba*, *Arcella*, *Balamuthia*, *Cashia*, *Centropyxis*, *Chaos*, *Cochliopodium*, *Cucur-bitella*, *Diffflugia*, *Flabellula*, *Hartmannella*, *Hydra-moeba*, *Leptomyxa*, *Lesquereusia*, *Mayorella*, *Nebela*, *Netzelia*, *Paramoeba*, *Platyamoeba*, *Ros-culus*, *Saccamoeba*, *Stereomyxa*, *Thecamoeba*, *Trichamoeba*, *Trichosphaerium*, *Vannella*, *Vexillifera*

Class (2) **Entamoebidea** Cavalier-Smith, 1991

With lobose pseudopodia, single nucleus, etc., but totally lacking mitochondria, peroxisomes, and hydrogenosomes; small, if any, Golgi bodies; no flagella; intranuclear centrosome present only during mitotic prophase. Some workers have suggested that this seemingly primitive group of symbiotic amoebae may (better) belong in the kingdom Archezoa. It is not clear whether genera allegedly related to *Entamoeba* (e.g. *Endamoeba*, *Endolimax*, *Iodamoeba*) should be assigned here or in subclass 1, above. *Dientamoeba* - long placed in the family Entamoebidae - is now known, of course, to be a flagella-less member of the flagellate phylum **PARABASALA** (above).

*Entamoeba* (plus any other genera?)

Class (3) **Filosea** Leidy, 1879

Hyaline, filiform pseudopodia, sometimes branched and occasionally anastomosing; some species naked, many with bottle-shaped tests. Several orders.

*Amphorellopsis*, *Centropyxiella*, *Chardezia*, *Chlamy-dophrys*, *Cyphoderia*, *Euglypha*, *Gromia*, *Latero-myxa*, *Nuclearia*, *Ogdeniella*, *Paulinella*, *Penardia*, *Pseudodiffflugia*, *Sphenoderia*, *Trinema*, *Vampyrella*

Class (4) **Granuloreticulosea** de Saedeleer, 1934

Granular, delicate, reticulate pseudopodia forming anastomosing networks; few species naked, others in single-chambered organic or calcareous test with no alternation of generations, but great majority in tests (organic, agglutinated, or calcareous) of one to many chambers with reticulopodia protruding from apertures and/or test wall perforations and with alternation of haploid sexual and diploid asexual generations; known gametes uni- or biflagellated or amoeboid; uni- or multinucleate forms, with asexual generation of some groups possessing dimorphic nuclei - one or more larger somatic nuclei and usually numerous



small generative nuclei, a heterokaryotic condition reminiscent of that of ciliates; species phagotrophic (although some with endosymbiotic algae) and practically all marine, benthic forms; many more fossil than contemporary genera described; class essentially composed of the foraminifers (**Foraminifera** d'Orbigny, 1826: see genera below), with additionally included separate, but dubiously distinct, orders Athalamida Haeckel, 1862 (e.g. *Arachnula* and *Biomyxa*) and Monothalamida Haeckel, 1862 (e.g. *Amphitrema*, *Lieberkuehnia*, *Microgromia*). Several orders, numerous families, and many hundreds of genera (a few with living species listed below) of forams. Does *Komokia* (still) belong here?

*Allogromia*, *Ammodiscus*, *Ammonia*, *Boderia*, *Bolivina*, *Carterina*, *Discorbis*, *Elphidium*, *Glabratella*, *Globigerinella*, *Guttulina*, *Hastigerina*, *Heterotheca*, *Iridia*, *Metarotaliella*, *Microglabratella*, *Myxotheca*, *Nonion*, *Ovamina*, *Patellinella*, *Planorbulina*, *Polystomella*, *Quinqueloculina*, *Rhizammina*, *Rosalina*, *Rotaliella*, *Saccamina*, *Schizammina*, *Schwagerina*, *Selenita*, *Sorites*, *Spirulina*, *Spiroloculina*, *Textularia*, *Triloculina*, *Uvigerina*

Class (5) **Xenophyophorea** Schulze, 1904

Relatively huge (up to 25 cm in diameter, although only ca. one mm in thickness) but little studied marine benthic protists with multinucleate plasmodial stage enclosed in branched-tube system which, in turn, is within agglutinated test; presumably with filose or reticulose pseudopodia and biflagellated gametes. Some 36 species described from dozen genera; exact rank of taxon and its placement among other protists remains uncertain.

*Galatheamina*, *Psammitta*, *Stannophyllum*

Phylum 11. **HELIOZOA** Haeckel, 1866

Unicellular phagotrophs with axopodia containing rigid microtubular axonemes; microtubules typically arrayed hexagonally, often nucleating on envelope of nucleus; kinetocysts common; mitochondrial cristae typically tubular; trophic stage usually without flagella; short filopodia in some species; several groups with stalks, one with perforated shell or test; mostly fresh-water, some marine. Controversial whether four classes named below are closely enough interrelated to warrant being clustered into one phylum; two other taxa (of once-called "helioflagellates"), convention-

ally placed here, have been removed: the dimorphids to the Opalozoa (see above) and the ciliophryids to the Dictyochae (in kingdom Chromista, below). Class 4 contains but one genus of unusual, small, biflagellated marine forms possibly more closely related to certain members of the next phylum, **RADIOZOA**. Familiar name and conventional understanding of "the Heliozoa" maintained, although considerably refined over classical usage; still, some workers might prefer to elevate all or some of my classes to independent phyletic status. Classically, the heliozoa *s.l.* and the radiozoa were combined under a super-taxon called the "Actinopoda", based on their common possession of axopodial pseudopodia.

Class (1) **Actinophryidea** Hartmann, 1913

*Actinophrys*, *Actinosphaerium*, *Camptonema*

Class (2) **Centrohelidea** Kühn, 1926

*Acanthocystis*, *Actinocoryne*, *Cienkowskya*, *Gymnosphaera*, *Hedraiphrys*, *Heterophrys*, *Raphidiophrys*

Class (3) **Desmothoracidea** Hertwig & Lesser, 1874

*Clathrulina*, *Hedriocystis*, *Orbulinella*

Class (4) **Taxopodea** Fol, 1883

*Sticholonche*

Phylum 12. **RADIOZOA** Cavalier-Smith, 1987

Typically spherical marine planktonic organisms, often of large body size, characteristically having central capsule with pores; stiff axopodial microtubules never in spiral pattern; endoskeleton either siliceous or of strontium sulfate, in latter case with radially arranged spicules; unicellular, occasionally colonial; single nucleus in early vegetative stage, organisms often becoming multinucleate subsequently; some species produce biflagellated swarmer cells, not to be confused with symbiotic dinoflagellates often present. Based on numerous differences within the assemblage, phylum probably best divided into two subphyla, with two classes in the second much larger and more familiar group.

Subphylum 1. **Acantharia** Haeckel, 1881

Class **Acantharea** Haeckel, 1881

*Acanthochiasma*, *Acantholithium*, *Acanthometra*, *Amphilonche*, *Astrolonche*, *Astrolophus*, *Haliomatidium*, *Lithoptera*, *Pleuraspis*, *Pseudolithium*, *Xiphacantha*



Subphylum 2. **Radiolaria** J. Müller, 1858

Class (1) **Polycystinea** Ehrenberg, 1838

*Cenosphaera, Coccodiscus, Collosphaera, Collozoum, Halosphaera, Octodendron, Plagiacantha, Rhizosphaera, Spongodymus, Thalassicolla, Thalassophysa*

Class (2) **Phaeodarea** Haeckel, 1879

*Atlanticella, Aulacantha, Aulosphaera, Aulotractus, Castanella, Challengeria, Challengeron, Coelodendrum, Conchopsis, Halocella, Medusetta, Phaeodina*

Phylum 13. **MYXOZOA** Grassé, 1970

Symbiotic forms with valved multicellular spores having polar capsules with extrusible filaments; trophic stages amoeboid (binucleate sporoplasm) or plasmodial (multinucleate); no flagellated stage; mitochondria with tubular to irregular-shaped cristae; somatic and generative nuclei somewhat reminiscent of condition in ciliates, some foraminifereans, and some radiolarians; commonly coelozoic or histozoic in marine and fresh-water fishes, but a number of fresh-water species are found in body cavity or intestinal epithelium of aquatic oligochaetes, probably undergoing an alternate stage in full life cycle of fresh-water fish symbionts. Assemblage contains a number of orders; but conventional breakdown into two major groups, **Myxosporidia** Bütschli, 1881 and **Actinomyxidia** Štolc, 1899, has recently become highly suspect because of findings, confirmed experimentally, that some forms formerly assigned to each are only stages in the life cycle of **single** myxosporidian species that seem to require two hosts. *Tetractinomyxon* sipunculid symbiont, may survive by transfer to a myxosporidian order. No actinomyxidian generic names are listed below since, often being of more recent date than myxosporidian ones and/or legally possibly only "collective" names, they may well be suppressed in future taxonomic works (Kent et al. 1994). Phylum contains several orders; but I consider the enigmatic *Helicosporidium* of the literature, sometimes placed here, to be a member of the kingdom Fungi. Classically, the myxosporidians *s.l.* and the microsporidians (see kingdom Archezoa) were lumped together under the name "Cnidosporidia", based on their common pos-

session of "spores" with polar filaments inside. Because of their pluricellular stages, and the similarity (in development) of their polar capsules with cnidarian nematocysts, the **MYXOZOA** are placed in the Animalia by some taxonomists. Single class.

Class **Myxosporea** Bütschli, 1881

*Ceratomyxa, Chloromyxum, Fabespora, Globospora, Henneguya, Hoferellus, Kudoa, Lomosporus, Myxidium, Myxobolus, Myxoproteus, Ortholinea, Parvicapsula, Sinuolinea, Sphaeromyxa, Sphaerospora, Trilospora, Unicapsula, Unicauda, Wardia, Zschokkella*

Phylum 14. **ASCETOSPORA** Sprague, 1978

Endosymbionts of (mainly) marine invertebrates, spores unicellular or with production of cells (sporoplasms) within cells; no polar capsules or filaments; no flagellated stage in life cycle; mitochondrial cristae tubulo-vesicular; unique haplosporosomes characteristic of most included species. Small but perhaps polyphyletic assemblage requiring more study; here it is tentatively considered to embrace one or both of the groups **Paramyxidea** Chatton, 1911 and **Marteliidea** Desportes & Ginsburger-Vogel, 1977 (as well as the haplosporidians proper), without giving them specific ranks. *Nephridiophaga* no longer here (Lange 1993)?

Class **Haplosporidea** Caullery & Mesnil, 1899

*Haplosporidium, Martelia, Minchinia, Paramartelia, Paramyxa, Urosporidium*

**Phyla of Kingdom CHROMISTA**

Four subkingdoms are recognized here in appreciation of significant differences among members of their included taxa. Some workers may prefer completely independent status for these four groupings, but the last three are relatively very small and are probably best treated as I have done below; at least, they ought to be appended in some way to the Chromista until/unless further comparative data clearly indicate otherwise. The general relationship of the informal group of "stramenopiles" (Patterson 1989a) to this kingdom is considered in my **DISCUSSION** section.



Subkingdom (I) **HETEROKONTA** Luther, 1899

Essentially with characters of the kingdom *sensu stricto*: organisms with chloroplasts (unless secondarily lost) located within rough endoplasmic reticulum instead of free in cytosol, and with mastigonemes (unless flagella lost) as rigid, tripartite, tubular hairs, on one or both flagella, functioning in thrust reversal. Bulk of the chromist species belong to phyla of this well-established and nearly universally accepted major taxonomic assemblage of "the heterokonts": the name - in one form or another (e.g. some workers call it the **HETEROKONTOPHYTA**) - and the concept are both deserving of preservation.

Phylum 1. **BICOSOECAE** Cavalier-Smith, 1989

Small, free-living, fresh-water or (few) marine, planktonic biflagellated (one flagellum with mastigonemes), heterotrophic non-pigmented forms typically living in loricae (attached by the second, smooth flagellum), and feeding on bacteria; some stalked, some form colonies.

Class **Bicosoecidea** Grassé & Deflandre, 1952

*Bicosoeca*, *Cafeteria*, *Pseudobodo*

Phylum 2. **LABYRINTHOMORPHA**

Page in Levine et al., 1980

Non-pigmented protists, trophic stage with ectoplasmic network of spindle-shaped or spherical non-amoeboid cells that move by gliding within network; unique cytoplasmic organelles, bothrosomes (first described as sagenetosomes); tubular mitochondrial cristae; known zoospores biflagellated, one bearing mastigonemes, other naked; in marine, generally coastal, waters, often associated with, or ectosymbionts of, aquatic angiosperms and certain algal protists.

Class (1) **Labyrinthulea** Cienkowski, 1867

*Labyrinthula*

Class (2) **Thraustochytriacea** Sparrow, 1943

*Aplanochytrium*, *Labyrinthuloides*, *Thraustochytrium*

Phylum 3. **DICTYOCHAE** Haeckel, 1894

Mixture of pigmented and non-pigmented heterokonts, free-swimming or stalked, marine and fresh-water habitats; often with anteriorly directed tentacles; one apically inserted flagellum typically with two rows of tripartite mastigonemes and sometimes small scales; second flagellum often reduced to basal body; some species (silicoflagellates, mostly marine fossil forms) with complex basket-shaped external siliceous skeleton. Two classes. The second, whose members have long been studied by phycologists, is here credited to Kristiansen (1990), although Cavalier-Smith (1986) had also established it as a class some four years earlier and Möhn (1984) and Karpov (1990) have both independently considered it as a new class (and a new phylum as well!). The pedinellids *s.l.*, which include some of the "helioflagellates" (see Davidson 1982) of the literature, may be polyphyletic; Cavalier-Smith (1993c) has at least partially relieved that condition by removing *Oikomonas* to a separate class of its own, although I have not done so here. Some workers vernacularly refer to (some or all of) the pedinelleans (or pedinellophyceans) as actinomonads.

Class (1) **Silicoflagellatea** Borgert, 1891

*Dictyocha* (only genus with living species)

Class (2) **Pedinellea** Kristiansen, 1990

*Actinomonas*, *Ciliophrys*, *Oikomonas*, *Parapedinella*, *Pedinella*, *Pseudopedinella*, *Pteridomonas*

Phylum 4. **RAPHIDOPHYTA** Chadeffaud, 1950

Biflagellated forms with or occasionally without plastids, fresh-water and marine; motile or palmelloid unicells; Golgi bodies in ring, over anterior surface of nucleus; unique extrusome in many species. Phylum is also known as "the chloromonads"; but this is inappropriate, because *Chloromonas* is a genus of green algal protists in the kingdom Plantae.

Class **Raphidomonadea** Chadeffaud, 1950

*Chattonella*, *Gonyostomum*, *Heterosigma*, *Mero-tricha*, *Olisthodiscus*, *Vacuolaria*

Phylum 5. **PHAEOPHYTA** Wettstein, 1901

Photosynthetic heterokonts predominantly with chlorophylls a plus c and leucosin and fat (or para-



mylon, glucose, or laminarin) as storage products; often siliceous scales covering body; characteristically, a pair of flagella with anteriorly projecting one bearing rigid tubular mastigonemes; some loricate species; many fresh-water forms with distinctive statospore; other groups almost entirely marine (e.g. brown algae); diverse morphological types: unicellular (some amoeboid), colonial, filamentous or thalloid (multicellular); sizes small to very large (brown seaweeds, kelp, up to 60 meters in length). Entire assemblage is essentially the golden-brown (plus some yellow-green) algae of the literature minus diatoms, silicoflagellates, and haptophytes but including the browns and eustigmatophytes (although latter without chlorophyll *c*, usually possess but single flagellum, and eyespot independent of chloroplast). Conservatively, I include six major classes, which contain a number of orders and numerous genera and species; but additional classes may be justified (e.g. for *Reticulosphaera* and *Vaucheria*, in class 6 below). Zoologists have traditionally claimed a number of motile chryomonads *s.l.* as members of the "old" Protozoa, assigning them mostly to a single order (Chryomonadida Engler, 1898).

Class (1) **Phaeophyceae** Kjellman, 1891

(syns. **Melanophyceae** Rabenhorst, 1863, **Fucophyceae** Warming, 1884)

*Alaria*, *Arthrocladia*, *Chordaria*, *Costaria*, *Cystoseira*, *Dictyota*, *Ectocarpus*, *Fucus*, *Giffordia*, *Homosira*, *Laminaria*, *Litosiphon*, *Macrocystis*, *Myrionema*, *Sargassum*, *Scytosiphon*, *Sorocarpus*, *Sporochnus*, *Stilopsis*, *Streptophyllum*, *Utriculidium*, *Xiphophora*, *Zonaria*

Class (2) **Chrysophyceae** Pascher, 1914

*Anthophysa*, *Chromulina*, *Chrysamoeba*, *Chryso-capsa*, *Chrysococcus*, *Chrysodendron*, *Dermatochrysis*, *Dinobryon*, *Epipyxis*, *Hibberdia*, *Microglena*, *Monochrysis*, *Ochromonas*, *Poteriochromonas*, *Rhizochromulina* (maybe better in class 4?), *Sarcinochrysis*, *Spumella*, *Triparma*, *Uroglena*

Class (3) **Synurophyceae** Andersen, 1987

*Mallomonas*, *Mallomonopsis*, *Synura*, *Tesselaria*

Class (4) **Pelagophyceae** Andersen & Saunders, 1993

*Pelagococcus*, *Pelagomonas*

Class (5) **Eustigmatophyceae** Hibberd & Leedale, 1970

*Chlorobotrys*, *Eustigmatos*, *Monodopsis*, *Nanochloropsis*, *Pseudocharaciopsis*, *Vischeria*

Class (6) **Xanthophyceae** Allorge in Fritsch, 1935

(syns. **Heterochloridea** Pascher, 1912 *p.p.*, **Tribophyceae** Hibberd, 1981)

*Botrydiopsis*, *Brachynema*, *Bumilleriopsis*, *Gloeobotrys*, *Gloeopodium*, *Heterogloea*, *Mal-lodendron*, *Ophiocytium*, *Pleurochloris*, *Reticulosphaera*, *Tribonema*, *Vaucheria*

Phylum 6. **DIATOMAE** Agardh, 1824

Pigmented unicells (occasionally colonial) with secreted silica frustule consisting of two valves and one or two girdle bands; non-flagellated except for single posterior flagellum on microgametes of one group (gametes of other groups amoeboid); yellow-brown plastids; mainly planktonic forms widespread in fresh-water and especially marine habitats, with numerous fossils; some species in moist soils. Many thousands of diatoms have been described, usually as belonging to the botanical division conventionally known as **BACILLARIOPHYTA** Engler & Gild, 1924, and assigned to two major distinct groups (centric and pennate); but at least three classes (**Coscinodiscophyceae** Round & Crawford, 1990; **Fragilariophyceae** Round, 1990; **Bacillariophyceae** Haeckel, 1878) are now recognized, with numerous subclasses and orders plus several hundred genera (Round et al. 1990).

*Achnanthes*, *Amphipleura*, *Amphora*, *Auricula*, *Bacillaria*, *Bacteriastrum*, *Biddulphia*, *Coscinodiscus*, *Cyclophora*, *Cyclotella*, *Cylindrotheca*, *Cymatopleura*, *Cymbella*, *Diadesmis*, *Diatoma*, *Fragilaria*, *Frustulia*, *Grammatophora*, *Gyrosigma*, *Hantzschia*, *Hemidiscus*, *Hydrosilicon*, *Lennoxia*, *Licmophora*, *Lithodesmium*, *Lyrella*, *Melosira*, *Minutocellus*, *Navicula*, *Nitzschia*, *Odontella*, *Pleurosigma*, *Podosira*, *Rhizosolenia*, *Stephanodiscus*, *Stichochrysis*, *Thalassionema*, *Thalassiosira*, *Toxarium*, *Triceratium*

Phylum 7. **PSEUDOFUNGI** Cavalier-Smith, 1986

Osmotrophic, minute symbionts on other protists and aquatic plants or in hosts ranging from grapes and potatoes to fishes; in fresh-water (mostly) or marine habitats or in soil; bi- or unflagellated zoospore stage; uninucleate or coenocytic walled protoplast in vegetative stage. Long conventionally considered as



a class in the kingdom **FUNGI** along with the chytrid protists, which do belong there. Synonymous names for the group include **OOMYCOTA** Dick, 1990 and **PSEUDOMYCOTA** Barr, 1992. The latter name, like **PSEUDOFUNGI**, is also attractive in emphasizing the pseudo-fungal characters of these heterokont protists, which are quite unlike the so-called "Eumycota" or true fungi. Two classes are recognized.

Class (1) **Oomycetes** Winter in Rabenhorst, 1879

Zoospores typically with two flagella, anterior one with two rows of rigid mastigonemes, posterior smooth or with only fine flexuous hairs; cytoplasmic and nucleus-associated microtubules.

*Achlya*, *Albugo*, *Brevilegnia*, *Lagenidium*, *Leptomitus*, *Myzocytiium*, *Olpidiopsis*, *Peronosclerospora*, *Peronospora*, *Phytophthora*, *Pythium*, *Rhipidium*, *Saprolegnia*, *Sclerospora*, *Verrucalvus*, *Zoophagus*

Class (2) **Hyphochytriomycetes** Sparrow, 1959

Zoospores with single, anterior flagellum (with mastigonemes); cytoplasmic and nucleus-associated microtubules absent. Following recent convention, I have dropped the "id" originally in the class name between the "tr" and the "io".

*Anisolidium*, *Hyphochytrium*, *Rhizidiomyces*

Subkingdom (II) **HAPTOPHYTA** Christensen, 1962

Typically photosynthetic unicellular biflagellated protists characterized principally by possession of a haptonema, unique filiform appendage located between anteriorly arising flagella, often very long (sometimes coiled) and containing 6-8 singlet microtubules; atypical of kingdom, neither flagellum bears tubular mastigonemes; commonly two parietal plastids, each with single pyrenoid; chloroplast endoplasmic reticulum present; with rare exception, body covered by layers of small organic scales in turn often covered by large unmineralized scales (coccoliths) on which calcium carbonate crystallized as calcite or aragonite; single Golgi body, fan-shaped near anterior end of cell; mitochondrial cristae tubular; mostly marine, few fresh-water; a few species form colonies, and a few exhibit phagotrophy; many fossil forms.

Phylum **HAPTOMONADA** Cavalier-Smith, 1989

With characters of subkingdom. Essentially synonyms for the name of (most of) the assemblage are **COCCOLITHOPHORA** Lemmermann, 1903, and **PRYMNESIOPHYTA** Casper, 1972 (latter name generally credited to "Hibberd, 1976", where first Latin diagnosis is to be found). Contains two classes: first (**Pavlovea** Cavalier-Smith, 1986) for the allegedly primitive genus *Pavlova*; second (**Patelliferea** Cavalier-Smith, 1993) for all other genera (a few of which are given below). If future ultrastructural and molecular studies show still greater differences compared with the Chromista proper, assemblage can be redefined and elevated to separate kingdom or assigned elsewhere (e.g. to the Protozoa, where it was at one time included in an order Coccolithophorida).

*Calciosolenia*, *Canistrolithus*, *Chrysidalis*, *Chrysochromulina*, *Coccolithus*, *Emiliania*, *Isochrysis*, *Ophiaster*, *Phaeocystis*, *Pleurochrysis*, *Prymnesium*, *Umbilicosphaera*

Subkingdom (III) **CRYPTOPHYTA** Pascher, 1914

Group of protists mostly photosynthetic, unicellular, and motile (biflagellated, with bipartite mastigonemes generally on both); usually paired thylakoids, chlorophylls a and c, and two phycobilins; unique features: nucleomorph, ejectosome, and periplast; mitochondrial cristae flattened; distinct gullet; chloroplast endoplasmic reticulum typically present; fresh-water and marine habitats. By zoologists at one time considered an order, Cryptomonadida Senn, 1900, of the "old" Protozoa.

Phylum **CRYPTOMONADA** Ehrenberg, 1838

With characters of subkingdom. Contains two classes: first (**Goniomonadea** Cavalier-Smith, 1993) for allegedly primitive forms (e.g. phagotrophic goniomonads); second (**Cryptomonadea** Stein, 1878) for all others. As in the cases of subkingdoms II (above) and IV (below), future molecular data may indicate a different phylogenetic/taxonomic placement for this assemblage.

*Chilomonas*, *Chroomonas*, *Cryptomonas*, *Goniomonas*, *Hemiselmis*, *Pyrenomonas*, *Rhinomonas*, *Rhodomonas*



Subkingdom (IV) **CHLORARACHNIOPHYTA**

Hibberd &amp; Norris, 1984

Marine photosynthetic protists with amoeboid plasmodial vegetative stage, with individual cells linked by fine filopodia; uniflagellated zoospore (thus = an amoeboflagellate?) with its flagellum, coiled helically around cell body, bearing delicate mastigonemes; mitochondrial cristae tubular; chlorophyll *a* and *b* but no *c* nor phycobilins; outermost membrane around chloroplast lacking ribosomes on cytosolic face; complex extrusomes.

Phylum **CHLORARACHNIOPHYTA**

Hibberd &amp; Norris, 1984

With characters of subkingdom. Contains single class, **Chlorarachniophyceae** Hibberd & Norris, 1984. Taxonomic position of the organism remains somewhat controversial, as well as the most appropriate name, authorship, and date for it at the various supraordinal levels. Tentatively, I am using the identical name for the subkingdom and phylum here. Single species? And no closely related (other) genera?

*Chlorarachnion*Phyla of Kingdom **PLANTAE**

The non-protist plant phyla (viz. **BRYOPHYTA**, **PTERIDOPHYTA**, **SPERMATOPHYTA**) are beyond the scope of this paper, so they are not further considered here. The protists of the kingdom are divided into two groups at the high level of subkingdom, the first - and much larger - assemblage containing the green algae of the literature (along with the "higher" plants proper, which clearly evolved from them) and the second the taxonomically enigmatic red algae plus, possibly, the even more refractive glaucophytes. Further research may yield additional data that will make untenable these proposed "taxonomic marriages"; in which case, appropriate classificational alterations can easily be made.

Subkingdom (I) **VIRIDIPLANTAE**

Cavalier-Smith, 1981

Typically photosynthetic organisms with chlorophylls *a* and *b* and flattened mitochondrial cristae; cellulosic cell walls common. Species of included

taxa of protists, the **green algae** *s.l.* (but excluding entirely the unrelated euglenoids of the kingdom Protozoa), are unicellular (generally biflagellated, without tubular mastigonemes), colonial, or filamentous (multicellular), many without motile vegetative stages; all with starch-containing plastids bounded by an envelope of two membranes; unmineralized scales on bodies or flagella of many species; found predominantly in fresh-water habitats, but some entire groups marine. Modern phycologists are of diverse opinions concerning the exact numbers/names of high-level taxa (phyla/divisions, classes/subclasses) to be included here: four phyla are endorsed below. As mentioned above, the non-protist phyla of the **VIRIDIPLANTAE** (i.e. the "higher" or "land" plants, bryophytes and tracheophytes) are beyond consideration in this paper.

Phylum 1. **PRASINOPHYTA** Christensen, 1962

The "grass-green scaly algae" (and close relatives), typically small biflagellated unicells, presumably most primitive group among plant protists; organic scales, with rare exceptions, on body and/or flagella; generally no cell walls; often unique extrusomes.

Class (1) **Pedinophyceae** Moestrup, 1991

No scales; second flagellum represented by only its basal body. Two genera.

*Pedinomonas*, *Resultor*Class (2) **Prasinophyceae** Christensen, 1962

(syn. **Micromonadophyceae** Mattox & Stewart, 1984)

Essentially with general characters of phylum *s.s.* Three orders recognized. In the past, some species have been considered members of the "old" Protozoa by zoologists.

*Bathycoccus*, *Dolichomastix*, *Mamiella*, *Mantoniella*, *Mesostigma*, *Micromonas*, *Nephroselmis*, *Pseudoscourfieldia*, *Pterosperma*, *Pyramimonas*, *Scourfieldia*, *Tetraselmis*

Phylum 2. **CHLOROPHYTA** Pascher, 1914

The "green algae" *s.s.* of the literature; many non-motile species; motile ones usually bi- or quadriflagellated, walled or naked; morphological types include unicellular or colonial, tetrasporal, coccal, sarcinoid, filamentous, and parenchymatous. Single class



(**Chlorophyceae** Wille in Warming, 1884) with perhaps a dozen separate orders. Traditionally, zoologists have claimed a number of motile species (outstanding examples, *Volvox* and *Chlamydomonas*) as protozoa, assigning them to the order Volvocida Francé, 1894 (replacing the highly inappropriate name Phytomonadida Blochmann, 1895, since *Phytomonas* is in the protozoan class Kinetoplastidea).

*Aphanochaete*, *Botryococcus*, *Carteria*, *Chaetochloris*, *Chlamydomonas*, *Chlorella*, *Chlorococcum*, *Chlorogonium*, *Chloromonas*, *Coccomyxa*, *Coelastrum*, *Dunaliella*, *Eudorina*, *Fritschiella*, *Gloeocystis*, *Gonium*, *Haematococcus*, *Hydrodictyon*, *Microspora*, *Nanochlorum*, *Nautococcus*, *Palmodictyon*, *Pascherina*, *Pediastrum*, *Phacotus*, *Pleodorina*, *Pleurastrum*, *Polytomella*, *Prasiola*, *Protosiphon*, *Scenedesmus*, *Schizomerus*, *Selenastrum*, *Sphaeroplea*, *Stephanosphaera*, *Tetraspora*, *Tetrasporidium*, *Trebouxia*, *Trentepohlia*, *Treubaria*, *Trichophilus*, *Volvox*, *Yamagishiella*

Phylum 3. **ULVOPHYTA** Stewart & Mattox, 1978

Most species macroscopic seaweeds (including "sea lettuce") from tropical marine waters; sessile with walled vegetative cells, thalli typically coenocytic or multicellular; bi- or quadriflagellated reproductive cells common; morphology ranges from sarcinoid and blade-like to siphonous. Single class (**Ulvoephyceae** Stewart & Mattox, 1978) and five orders recognized.

*Acetabularia*, *Acrosiphonia*, *Blidingia*, *Bryopsis*, *Chaetosiphon*, *Cladophora*, *Codium*, *Cymopohlia*, *Dasycladus*, *Eugomontia*, *Halimeda*, *Phaeophila*, *Rhizoclonium*, *Siphonocladus*, *Trichosarcina*, *Ulothrix*, *Ulva*, *Valonia*

Phylum 4. **CHAROPHYTA** Rabenhorst, 1863

Some species multicellular, macroscopic, and found submerged in shallow fresh-water habitats, a few terrestrial, but majority (including the ubiquitous desmids) unicellular or filamentous in fresh waters everywhere; the larger species, some commonly known as stoneworts, have macroscopic thalli with main axis erect plus regular whorls of lateral branches, and with male and female sex organs reminiscent of those of land plants: these charophytes have motile (flagellated) swimmers, never with eyespot, typically covered with scales; many mem-

bers of this first class possess phragmoplast similar to that of "higher" plants, and their cellulosic cell walls sometimes heavily calcified. Species of second class, with no flagellated stages in life cycle, show unique conjugation between cells (alone or of closely appressed filaments), with fusion of amoeboid gametes; in the essentially mirror-image unicellular desmids, a pair of large, complex plastids are joined at an isthmus that contains a single shared nucleus; cellulosic cell walls often slimy, organisms gliding on the secreted mucilage. Evolutionarily, members of the first class are considered directly ancestral to "higher" plants. Some taxonomic phycologists have separated the two groups named below at phylum (division) rather than class level.

Class (1) **Charophyceae** Rabenhorst, 1863

With characters given above for the first class. *Chaetosphaeridium*, *Chara*, *Chlorokybus*, *Coleochaete*, *Klebsormidium*, *Nitella*, *Nitellopsis*, *Raphidoneima*, *Stichococcus*, *Tolypella*

Class (2) **Conjugatophyceae** Engler, 1892

With characters given above for the second class. The larger group, mostly because of huge number of described desmids. Essentially synonymous names include "**Conjugaphyceae**", **Gamophyceae**, **Zygnematophyceae**, and **Zygophyceae**. *Ancylonema*, *Arthrodesmus*, *Closterium*, *Cosmarium*, *Cylindrocystis*, *Desmidium*, *Micrasterias*, *Oocardium*, *Sirogonium*, *Spirogyra*, *Staurastrum*, *Xanthidium*, *Zygnema*

Subkingdom (II) **BILIPHYTAC** Cavalier-Smith, 1981

Essentially the "red algae" of the literature. Unlike other members of the kingdom **PLANTAE** in many respects, their species also show little similarity to other taxa of *protists*. Whether they are "algal plants", as considered here, or better treated as an independent kingdom is a matter for the future when additional relevant data become available. Mostly marine protists, some unicellular, others of macroscopic size (length) - latter, like many brown (and a few green) algae, called seaweeds; particularly distinguished by total absence of centrioles and flagella and by presence of single thylakoids in their chlorophyll a containing plastids with phycobilins as accessory photosynthetic pigments; mitochondria with flattened cristae; starch stored in cytosol; often complex life



histories. Some workers accept - as a second phylum of the **BILIPHYTA**, in addition to the **RHODOPHYTA** - the enigmatic and possibly non-monophyletic **GLAUCOPHYTA** Bohlin, 1901 (single class, **Glaucophyceae** Bohlin, 1901, with genera *Cyanophora*, *Glaucocystis*, *Glaucosphaera*, *Gloeochaete*). Glaucophytes are small, fresh-water, cyanelle-containing protists commonly with a pair of flagella in their life cycle, cortical alveoli (curiously!), etc., sharing some characters with red algae (e.g. possession of phycobiliproteins). The cyanelles are presumably evolutionarily derived from blue-green algae (i.e. endosymbiotic cyanobacterial prokaryotes) on their way to becoming genuine plastids in glaucophytes and probably in several other taxa of protists as well).

#### Phylum **RHODOPHYTA** Rabenhorst, 1863

Essentially with characters of subkingdom, as given above. Some workers recognize two principal classes: the more primitive and much smaller group, the **Bangiophyceae** Wettstein, 1901; and the widespread, multicellular, much larger group, the **Florideophyceae** Warming, 1884. Numerous orders have been described.

*Audouinella*, *Bangia*, *Bangiopsis*, *Batrachospermum*, *Boldia*, *Callocolax*, *Capreolia*, *Chondrus*, *Compsopogon*, *Cyanidium*, *Dilsea*, *Endocladia*, *Erythrotrichia*, *Gigartina*, *Goniotrichum*, *Gracilaria*, *Halymenia*, *Heteroderma*, *Hildenbrandia*, *Iridaea*, *Lithophyllum*, *Mesophyllum*, *Minium*, *Naccaria*, *Palmaria*, *Phragmonema*, *Phyllophora*, *Porolithon*, *Porphyridium*, *Rhodella*, *Rhodochaete*, *Rhodophyllis*, *Rhodospora*, *Sporolithon*, *Thorea*, *Zymurgia*

#### Phyla of Kingdom **FUNGI**

The non-protist fungal phyla (viz. **ASCOMYCOTA**, **BASIDIOMYCOTA**, **ZYGOMYCOTA**) are beyond scope of this paper, so are not treated here. They embrace "typical" fungal forms, the Fungi Imperfecti, unicellular yeasts, and probably also the enigmatic "protozoon" *Helicosporidium* and the taxonomically notorious *Pneumocystis* (but see note of caution by Frenkel et al. 1990). *Blastocystis*, a common intestinal symbiont of many vertebrates including humans, was first discovered and described more than 75 years ago as a "vegetable organism" (= fungus), a taxonomic conclusion accepted by

parasitologists and medical clinicians without question for over half a century. Recently, it has been (re)classified as a sporozoon (Apicomplexa), a lobosean amoeba (Rhizopoda), an "uncertain protist", and a unique organism requiring a new phylum (named as a "protozoan subphylum": **Blastocysta** Jiang & He, 1993) of its own, but with some workers still considering it a fungus. See Belova (1992), Boreham and Stenzel (1993), Garavelli and Libanore (1993), Jiang and He (1993), Johnson et al. (1989), Zierdt (1988, 1993), and references within those papers. I favor assignment to, or near, the rhizopod class **Lobosea** (q.v.), at an undetermined rank, until more comparative data of phylogenetic significance are available on this taxonomically defiant organism.

#### Phylum **CHYTRIDIOMYCOTA** Sparrow, 1959

Protists with definite fungal affinities: non-pigmented forms (some filamentous) with chitinous cell walls in hyphal stage, flat mitochondrial cristae, absorptive mode of nutrition, symbionts or saprobes in soil or fresh-water habitats; atypical of (the majority of) the kingdom, however, are such characteristics as their motile stages in life cycle (most gametes and some asexual zoospores) with posteriorly directed single (rarely multiple) flagellum (without mastigonemes or scales), frequent unicellularity, and possession of unusual cytoplasmic structures in many species (e.g. distinctive flagellar root system and the curious rumposome in members of two orders). The chytrids *s.l.* differ significantly from members of the phylum **PSEUDOFUNGI** (q.v.), heterokonts of the kingdom Chromista.

#### Class **Chytridiomycetes** Sparrow, 1959

With characters of phylum. Four orders recognized. *Allomyces*, *Blastocладиella*, *Callimastix*, *Catenaria*, *Chytridium*, *Chytriomycetes*, *Coelomomyces*, *Karlingia*, *Monoblepharella*, *Neocallimastix*, *Olpidium*, *Physoderma*, *Rhizophyidium*, *Spizellomyces*, *Synchytrium*

#### Phyla of Kingdom **ANIMALIA**

Since none of the many phyla of animals - in my opinion - contains any protist species, they are beyond our consideration here. But, from time to time, sponges (if one classifies the choanozoa there) have represented a possible exception. And, very recently,



Cavalier-Smith (e.g. 1993c) has suggested that the multicellular, ciliated **MESOZOA**, with (usually) tubular mitochondrial cristae and lack of collagenous connective tissue, should be removed from the Animalia to the protistan kingdom Protozoa. This taxonomic shift has not been endorsed, however, in the present paper. Some place the myxozoa here.

## DISCUSSION

As inferred in the **INTRODUCTION** and manifest throughout the preceding pages of classification, biologists can no longer think of protozoa or protists as conveniently divisible into separate taxa based on general characteristics such as modes of locomotion or types of nutrition. In other words, no longer can there be named high-level taxonomic groups containing, for example, only forms with pseudopodia or with flagella or with chloroplasts or with a totally symbiotic style of life. Our attempts to erect "natural" systems of classification have now moved far beyond that stage, thanks primarily to the availability of more sophisticated ways of studying the properties/characteristics of these generally unicellular and microscopic "lower" eukaryotes.

There is no need (nor space!) to discuss all parts of the preceding classification scheme in any detail here. It is clear that the general basis or rationale for arranging the taxa as I have done is the degree to which various groups do, or do not, share key characters in common, reflecting their phylogenetic affinities. Different approaches or schools of thought have been mentioned in the **INTRODUCTION**; I consider myself an evolutionary biologist *sensu* Mayr (1990). Comments regarding various controversial taxonomic decisions have been made in place on preceding pages. Here, I wish to focus attention on four matters that deserve additional explanation or discussion: my choice of the names and concepts for the kingdoms **PROTOZOA** and **CHROMISTA**; consideration of phylum and class names in general (including authorships and dates); the taxonomic category of "incertae sedis"; and my reasons for supplying so many examples (so evident in the **INDEX** as well as in the text) of included genera.

### The Kingdom PROTOZOA

The Protozoa, united into a formal group of generally microscopic, unicellular, phagotrophic forms, have been around for 175 years. The rank accorded them has been

considerably elevated over the years (especially in recent decades), the numbers of their species have increased dramatically over time with advances in microscopy, and the contents and boundaries of the assemblage have often changed with our increased understanding of them.

Some 15-20 years ago (see historical account in Corliss 1986a), the "protist revolution" began to permeate the thinking of the biological scientific community. In due time, it became unfashionable to retain a phylum or subkingdom (of "animals") called the Protozoa in light of our new appreciation of interrelationships among (former) algal and protozoan groups, an intermingling that finally forced the breakdown of the old plant/animal barriers in taxonomy. A neoHaeckelian kingdom Protista holds way, as it does still today in many circles. Round (1980) perceptively realized that we were going too far in discarding genuine differences between many algal and protozoan taxa, but his warning was not heeded at the time.

With the emphasis on broad phylogenetic lines and the desire to break completely with the past, most protistologists failed to realize what we know today (but some still find difficult to accept), that the Protista are too diverse to remain as a single taxonomic entity and that some older concepts, properly refined, need not remain discarded. The Protozoa represent an outstanding example of this. As Cavalier-Smith (1993c, in particular) has resurrected the group - as a kingdom **PROTOZOA** - it deserves (re)acceptance, in my opinion (although a year ago I myself raised some objection to his choice of name for the new kingdom, while tacitly admitting that no better one came to mind: Corliss 1993). Its boundaries have been sharpened by removal of several taxa formerly inappropriately assigned to it: for example, groups that now reside, quite properly, in other kingdoms. The **ARCHEZOA** represent a perfect haven for the primitive amitochondrial groups of certain amoebae, symbiotic flagellates, and the unique microsporidians. The **CHROMISTA** embrace certain algal protists (e.g. chrysophyceans *s.l.* and haptophytes) totally different from the (former) algal groups of euglenoids and dinoflagellates (sensibly treated as protozoa now) but many of which were (also) once classified as protozoa. And the **PLANTAE** are the proper place for the green algae, which harbor the ancestors of the "higher" plants but some of which were traditionally labeled, simultaneously, as protozoa (e.g. *Chlamydomonas*, *Volvox*, and their close relatives: the "phytomonads" or, better, the volvocids).



Thus cleansed or purged, the Protozoa have become a much more homogeneous, if, admittedly, still possibly paraphyletic, assemblage. They certainly resemble the old "phylum Protozoa" sufficiently enough to be recognizable as the protozoa; in fact, many of the included taxa of old remain intact in the new kingdom Protozoa, which is clearly separated from the other five eukaryotic kingdoms. That the group is a large and genetically diverse one is no reason in itself to require that it must be broken up. As the evolutionary proving ground from which emerged the other eukaryotic kingdoms (except for the primitive Archezoa), the Protozoa might be expected to show greater variety and even to be taxonomically unwieldy in some respects. Not surprisingly, new data may in time oblige us to make substantial revisions among a number of its numerous subtaxa, outstanding examples - in my view - being several of the classes and orders of two of Cavalier-Smith's (1993a-c) newest phyla, viz. Percolozoa and Opalozoa.

A final argument in favor of (re)recognizing the Protozoa as a major high-level taxonomic unit among the eukaryotes is the fact that the concept underlying it continues to satisfy the needs of field and bench ecologists, who have long defined the Protozoa as basically comprised of primarily heterotrophic and colorless (with a few exceptions), motile, unicellular, mostly free-living, microscopic protists widespread in a variety of habitats. This is essentially the same general - and useful - definition found for the old phylum Protozoa in many textbooks. And, as Cavalier-Smith (1993c) has pointed out, protozoologists need not restrict their studies, or even their textbooks, to members of this kingdom alone. In fact, our knowledge concerning the archezoan groups, and other more widely dispersed protists classically thought of as "protozoa" and sometimes - at the same time - "algae", will benefit from attention by students and researchers working in any field of the biological sciences.

Unresolved taxonomic problems within the Protozoa exist mostly in areas involving groups of small-sized free-living and symbiotic heterotrophic flagellates, which abound in a great diversity of habitats (Patterson and Larsen 1991), and various amoeboid and plasmodial protists, especially taxa of mycetozoa *s.l.* and amoeboflagellates *s.l.*

### The Kingdom CHROMISTA

In a number of important characteristics, the protists assignable to my kingdom Chromista are similar or even

identical to most members of large assemblages given different names (and slightly different boundaries) in the literature. The classically known heterokonts (Pascher 1937-1939) represent one such group, and this name has been used by me for the major subkingdom of the Chromista. The Chromophyta of Bourrelly (1957), perhaps the basis for the recently appearing names Chromobionta and Chromobiota, also includes many of the same groups and has been popular as a contrast to the Chlorobionta (see Christensen 1966), a name applied essentially to the green algae.

Recently, the "stramenopiles" (more properly spelled "straminopiles"? See Vørs 1993) of Patterson (1989a) have become, in effect, a rival nomenclatural candidate for the chromists of Cavalier-Smith (1986, 1989b). In both men's cases, the same strong synapomorphic character has been used: the tripartite rigid tubular hairs or mastigonemes found on (or postulated to have been lost from) the flagella of allegedly all species assignable to the overall group. This phylogenetically important feature, however, is missing from species comprising several (but different) taxa in both Cavalier-Smith's and Patterson's suggested classifications. I accept Cavalier-Smith's arguments - explaining the absences from his several included taxa that are without them - as the more cogent ones. Thus, in brief, I agree with the latter worker in excluding Patterson's proteromonads + opalinids (= the "slopalinids") and the heliozoan actinophryids from the (mostly phototrophic, with plastids inside the rough endoplasmic reticulum) chromistic assemblage, while including the haptophytes, cryptophytes, and several other chromist taxa left out of the "stramenopiles" in Patterson's circumscription of his informal group.

The **CHROMISTA** is an important non-protzoan, non-plant kingdom of algal protists. In contrast to the bulk of the **PROTOZOA**, its members are mostly autotrophic (although many are capable of mixotrophy), unicellular forms with unique mastigonemes and a unique placement of their chloroplasts. The chromists represent a major group of "the algae" of old; and their heterokontic moiety looms large among the seven distinct phylogenetic algal lineages described by Andersen (1992) as having arisen independently during geological time.

### Names and Authorships of Higher Taxa

In general, the various codes of biological nomenclature do not have much control over the choice of names for suprafamilial taxa (Corliss 1984, 1993; Jeffrey 1990; Ride and Younès 1986). This may be considered both



"good" and "bad", but the unchecked promulgation of new ranks and names in recent years has led us nearly to the brink of chaos in protistology, nomenclaturally speaking (see extended discussions in Corliss 1984, 1990, 1991b, 1993; Patterson and Larsen 1992). Some time ago, I stressed the need for "common sense and courtesy" in the area (Corliss 1972), and Silva (1980) has urged that an overriding consideration should be "effectiveness of communication". A reasonable degree of stability is another (overlapping) goal certainly worthy of achievement in these times of perhaps too much emphasis on constant change.

In the classification of the 34 phyla formally offered in this paper, I have been confronted by the same dilemmas described in my earlier overview work (Corliss 1984), and have thus been obliged to make a number of quite subjective decisions in choice of both names and authorities for the higher taxa included. Space does not permit a detailed discussion here. Suffice it to say, in keeping with my objectives to present a "user-friendly" scheme of classification including all groups of protists, I have adopted the guidelines given below, keeping in mind the practical observation made by Raabe (1964a) some 30 years ago: "I am not an adherer of introducing new names for old taxa, although they might stress better their properties. It introduces confusion..." And Silva (1980) has sensibly suggested that a classification should be one that is "familiar and acceptable to the largest number of users".

1. When possible/defensible, I have employed the oldest and/or most familiar name for a more or less conventional group of protists. Although the concept, boundaries, composition, and even the rank-level may have changed somewhat over time, the name used may be credited to the original author, using date of his creation of the name. As might be expected, sometimes exceptions to this principle are advisable. Incidentally, to save space, I have not regularly listed all synonyms of the names selected for the various high-level taxa endorsed on preceding pages. In a number of cases, however, I have included a few for the benefit of readers who may have become more familiar with a name different from the one chosen here for a particular (generally well-known) group, keeping in mind that persons coming from a botanical background, for example, will have had a nomenclatural exposure likely differing from that of students trained in zoological taxonomy.

2. When both an original group and its later recognition as a unique higher-level taxon involve a very small

number of quite unusual organisms (e.g. a single family or even a single genus or species), then I especially have tended to use the original name and authority for the group even if the rank (usually upward) may have changed drastically. The description, while refined in light of new knowledge, is basically concerned with the same organism(s). However, there are a few defensible exceptions to this.

3. In the preceding and still other situations, I have taken the liberty of altering prefixes and/or suffixes without necessarily changing the authorship/date information. In the case of a number of former botanical classes, I have - along with other workers - felt free to elevate the group to phylum (= division) status, altering the suffix appropriately. Also, I have not been constrained by the lack of a Latin diagnosis in the first (or subsequent) description to withhold credit from the original creator/proposer of a group or of its name. This latter decision has affected the date of authorship and occasionally the authorities themselves in the case of some botanically derived names, as will be apparent in the text and in Table 1.

4. According to conventional practices, a number of group-names might well have been marked "emend", "sensu", "ex", "nom. nov.", or "stat. nov." (with or without additional author/date data), but, for the sake of consistency and simplicity, I have not done this. I offer apologies to nomenclatural purists and any offended taxonomic specialists. Today, it is generally assumed by taxonomists that for descriptions of organisms or groups of organisms one must go to the more recent rather than the older literature; in some ways, however, their nomenclature may be considered to be a separate matter - primarily one more of historical interest.

5. I am not automatically opposed to all "new" names! For instance, I have endorsed/accepted some 20 of Cavalier - Smith's numerous high-level taxonomic / nomenclatural creations of the past dozen years. For a few examples of these neologisms (some of them altered slightly in this paper in rank or in spelling of the name): his kingdom Chromista and subkingdoms Viridiplantae and Biliphyta; his phyla Archamoebae, Dinzoa, Euglenozoa, Opalozoa, Percolozoa, and Radiozoa; his classes Diplonematea, Entamoebidea, Protalveolata, and Proterozoea. I am not necessarily rejecting his large number of new names for intermediate ranks. As stated in my **INTRODUCTION**, most of these have been omitted primarily to reduce the size of my own classificatory framework, making it more easily usable for the many readers who are not taxonomic specialists and



neither want nor need such details. But I am also not always convinced that our evidence to date requires the separation of so many genera at levels so far above that of the family.

### The Category "Incertae Sedis"

I have not placed any major (or minor) taxa in the convenient category of "uncertain status" for several reasons. It is obvious that, as our knowledge continues to grow, various species and higher groups as well will need to be shifted about taxonomically. Systematics is not a static science. Furthermore, from a puristic point of view, we are really uncertain about a great many of our ranks and group-interrelationships, frustrating though this may be. It seems to me superfluous to mark nearly everything as "*incertae sedis*" when we anticipate changes based on fresh data of high phylogenetic/evolutionary (and thus taxonomic) value every year or so. It is to be expected that, at any given time, some groups are better known than others; but all deserve some place - even if it must be tenuous or tentative - in an overall hierarchical classification, as I see it.

Patterson and colleagues (e.g. Brugerolle and Patterson 1990; Larsen and Patterson 1990; Patterson 1986a, 1990; Patterson and Brugerolle 1988; Patterson and Zölffel 1991; Vørs 1988, 1993) favor labeling many unique species as "incert. sed. protists," seemingly without much desire to give them a (or place them in any preexisting) taxonomic rank above genus or family (with rare exception). Scores of exciting new protists are thus being more or less assigned to a vague "Anhangen" position. By the same token, the Patterson school (e.g. see Patterson and Sogin 1993, and references therein), and some other laboratories as well, determine monophyletic lineages of protists, excellent research to carry out, while/but making no overt effort to interrelate these lines in a manner involving ranking and production of some kind of hierarchical system useful to the many people wanting and needing the overall classification that would result.

Cavalier-Smith (e.g. 1993c, and references therein), among others of us, has attempted to find at least temporary or tentative homes for many "uncertain" protist genera (e.g. a number of those listed by Patterson and Zölffel 1991), thus stimulating future workers to confirm or disprove such allocations. Nevertheless, it is true that often protists poorly described in the older literature require rediscovery and restudy before they can be given

proper taxonomic homes. With respect to high-level lineages widely recognized as truly monophyletic, I have tried (on preceding pages) to show possible interrelatedness at phyletic (and lower) ranks, even if this process has made demands on insight and intuition and involved some healthy speculation. On more than one occasion, I have deliberately (though often in a tentative way) united paraphyletic groups under a single higher-level rank (as generally explained in the text in place).

### Listing of Multiple Genera within Classes and Phyla

I have offered far more than the usual number one sees of "representative genera" for each of the high-level taxa named on preceding pages (notable also in the **INDEX**) because I should like to enable the readers - no matter what their field of specialty - to find their "favorites" and thus be able to relate them to the ranks above and to neighboring groups. All too often, it seems to me, papers that are concerned with phyla and classes fail to supply the reader with any clues as to the location of familiar genera within a newly proposed or newly rearranged protist macrosystem (or portion thereof).

Naturally, space restrictions preclude mention of all genera, which number in the thousands. But, among the 1100 that are included in this paper, I hope that I have managed to select many of the better-known (as well as "representative") names of protists from the modern as well as the classical literature. Perceptive phycologists/protozoologists will note that certain genera are no longer where they used to be in older, conventional classifications. Ultrastructural studies, perhaps even more so than molecular biological data, have necessitated such reassignments of sometimes familiar taxa. Consider cases of formerly (thought to be) "closely related" genera or groups the members of which are now so widely separated taxonomically from each other, such as the following: *Amoeba*, *Dientamoeba*, *Entamoeba*, and *Pelomyxa*; *Proteromonas* and *Trypanosoma*; *Giardia* and *Trichomonas*; *Acrasis* and *Dictyostelium*; *Ciliophrys* and *Dimorpha*; *Stephanopogon* or *Opalina* and the ciliates; microsporidians and myxosporidians; dinoflagellates, chrysophyceans, and volvocines (a trio of taxa rather close in older zoological classifications); and oomycetes plus hyphochytriomycetes and the chytridiomycetes. More examples could be cited.

It has not been appropriate, here, to become involved in discussion/treatment of generic synonyms,



homonyms, etc. But, in choosing representative genera, I have sometimes run across dual usage of the same name, generally in cases of "botanical" versus "zoological" taxa of protists. Resolution of such duplication, somewhat like that of the particularly troublesome problems arising from having two groups of protists (e.g. dinoflagellates and euglenoids) simultaneously under jurisdiction of two different codes of nomenclature, is beyond consideration here. For the protists, cases of both an identical name for two taxonomically rather different organisms and different names for the same organism all fall under Patterson's (1986b) broad nomenclatural concept of "ambiregnal" species (see discussion and additional relevant references in Corliss, 1993). I should like to mention one outstanding example of the former situation. *Urospora*, a well-known genus and type of a family in the class Gregarinidea of the protozoan phylum Apicomplexa, is also a familiar taxon in the class Ulvophyceae of the phylum Ulvophyta (kingdom Plantae, subkingdom Viridiplantae)! Deliberately, I have not listed the name in either place, since/although it would be an excellent choice as a "representative" genus in both instances.

Species, the taxonomic level most affected by the codes of nomenclature (Corliss 1993), have received no mention in the present classification of the protists. A general idea of the numbers of them per phylum or class, however, may be gained from information included in Corliss (1984): see also Andersen (1992), Sleight et al. (1984), and Vickerman (1992). Annually, hundreds of protistan species have been described as new, even in most recent years. This fact alone stands as eloquent evidence that alpha taxonomy thrives still today.

**Acknowledgments.** Many colleagues have generously given me advice concerning possible ways to resolve at least some of the problems of classifying the protists in a way reflecting the latest information available. Among the numerous persons with whom I have worked over the years, I want to mention here, with deep feelings of gratitude, especially three: Robert A. Andersen, Thomas Cavalier-Smith, and David J. ("Paddy") Patterson. I should hasten to point out, however, that counsel received has not always been followed. Thus, no one but the author should be held responsible for the phylogenetic and taxonomic conclusions drawn and offered in the present paper.

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## INDEX of Taxonomic Names

Names of top-level taxa (empire, kingdoms, phyla) are printed in **boldface** CAPS; those of classes and subclasses, in **boldface** upper- and lowercase. Ordinal (always ending in "-ida") and informal or vernacular names and generally unused or discardable names (often in quotation marks) appear in roman type. Representative genera are shown in *italics*. Taxa that appear in Table 1. are so indicated by reference to that table following page number citations.

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## Gravity-dependent Modulation of Swimming Rate in Ciliates

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Eukaryotes including protists use gravity as a cue to know "up" and "down". Research in *Paramecium* has established that, for the induction of an orientational response to gravity, sensory transduction is not necessarily involved (see Machemer and Bräucker 1992). For instance, buoyancy of the cell body may produce negative gravitaxis. A guiding principle of our research is to search in the ciliates for evidence of a gravisensory pathway, and if such pathway exists to elucidate its mechanisms.

An implication of gravisensation is that extrinsic energy is transduced to generate a cellular signal. For a single cell, the most obvious way of transduction of the gravity vector is pressure arising from local differences in density. Independent measurements have shown that the density of the *Paramecium* cytoplasm exceeds the density of freshwater by 4% (Koehler 1922, Fetter 1926, Taneda 1987, Kuroda and Kamiya 1989). This corresponds to a force of  $10^{-10}$  N and a pressure gradient across the lower membrane of slightly below 0.1 Pa. Gravitropism in plant roots employs forces and pressure gradients of this magnitude (Volkman 1974). If we assume tentatively that the force of  $10^{-10}$  N deforms a

sensitive receptor over a distance of 1 nm, the work done or energy exerted on the receptor is  $10^{-19}$  J. This exceeds the energy of thermal noise by a factor of 50. Thus, from the physicist's viewpoint, the energetic preconditions for cellular gravitransduction are reasonable.

Where can gravity attack a ciliate cell? The viscoelastic properties of the cytoplasm may be modelled by a series of dashpots and springs. The lower membrane of a cell is the first candidate of outward deformation by gravity but, due to charging of the cytoplasmic "spring", also the upper membrane may be pulled inward after some delay. If gravity can induce mechanical deformations of the cell membrane, we are on less speculative grounds because the distributions of mechanosensitivity in ciliates such as *Paramecium*, *Stylonychia* and *Didinium* are comparatively well studied. Figure 1 shows the pattern of distributions of depolarizing mechanosensitivity, as mediated by somatic Ca channel conductances, and hyperpolarizing mechanosensitivity, as mediated by somatic K channel conductances (Ogura and Machemer 1980). If we assume that this pattern applies to static loads as well as to pulse stimulation, we can predict that a downward swimming *Paramecium* is depolarized due to activation of Ca-mechanoreceptor channels. When *Paramecium* swims upward, it is hyperpolarized because of K-mechanoreceptor channel activation. For horizontally swimming paramecia this scheme predicts a full cancelling of depolarizing and hyperpolarizing gravisensory input because the summed

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mechanoreceptor conductances give a Ca-K conductance ratio equivalent to that of the *Paramecium* resting potential.

Unfortunately, it is difficult to directly measure persistent gravity- and position-dependent small potential offsets in single cells. We employ an indirect method of assessing gravireceptor potentials: the velocity of free swimming cells. It is established that small positive shifts from the resting potential depress ciliary frequency and the rate of forward swimming in *Paramecium*; small negative shifts from the resting potential raise the ciliary frequency so that the forward swimming velocity goes up (see Machemer 1986). In other words, the electrophysiological hypothesis of gravireception predicts that active ciliary propulsion in upward swimming paramecia exceeds propulsion in horizontal cells, whereas ciliary propulsion in downward swimming cells is reduced as compared to horizontal swimmers (Machemer et al. 1991). We call this gravity-induced modulation of the rate of locomotion gravikinesis.

In a world of gravitational pull, it is not easy to measure the rate of active propulsion of a cell. A *Paramecium* that adds an increment ( $\Delta_U$ ) to the propulsion rate (P) during upward swimming from activation of K channels, settles at the same time at the rate of sedimentation (S). The vector sum of these velocities ( $V_U$ ) gives the observable swimming velocity. In vertically moving cells, the equation is:

$$V_U = P - S + \Delta_U \quad (1)$$

The same reasoning applies to vertically downward swimmers, where Ca channel activation induces a subtraction from P by the amount  $\Delta$ , and S adds to that difference:

$$V_D = P + S - \Delta_D \quad (2)$$

In order to assess the gravikinetic response,  $\Delta$ , we need to determine three variables: the observed swimming velocity, the sedimentation rate and the rate of intrinsic propulsion, as being unaffected by gravity. For convenience in experimentation, we have, as a first attempt, ignored the value of the propulsion rate using the difference of the equations of vertically downward swimming and vertically upward swimming cells. In the resulting simple equation, P has been eliminated, and the value of  $\Delta$  equals the arithmetic mean of  $\Delta$  during downward ( $V_D$ ) and upward swimming ( $V_U$ ):

$$(V_D - V_U)/2 = S - \Delta \quad (3)$$

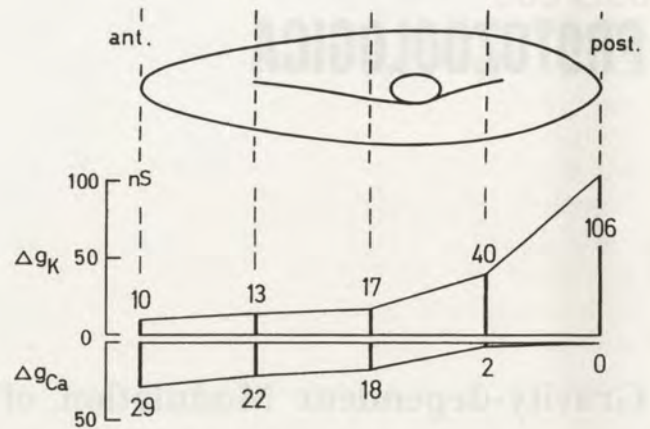


Fig. 1. *Paramecium* mechanoreceptor conductances of the cell soma as revealed by topographically defined pulse stimulation (modified after Ogura and Machemer 1980). Along the antero-posterior axis of the cell two gradients of  $Ca^{2+}$ -dependent depolarizing mechanosensitivity and  $K^+$ -dependent hyperpolarizing mechanosensitivity overlap. A mechanically induced conductance ratio,  $\Delta g_{Ca}/\Delta g_K$ , determines the polarity and amplitude of the resulting mechanoreceptor potential (conductance ratio of resting potential: near 2.3). Behavioural data suggest that overall static deformation of the "lower" soma membrane by gravitational pressure affects a similar or even the same system of mechanically sensitive channels

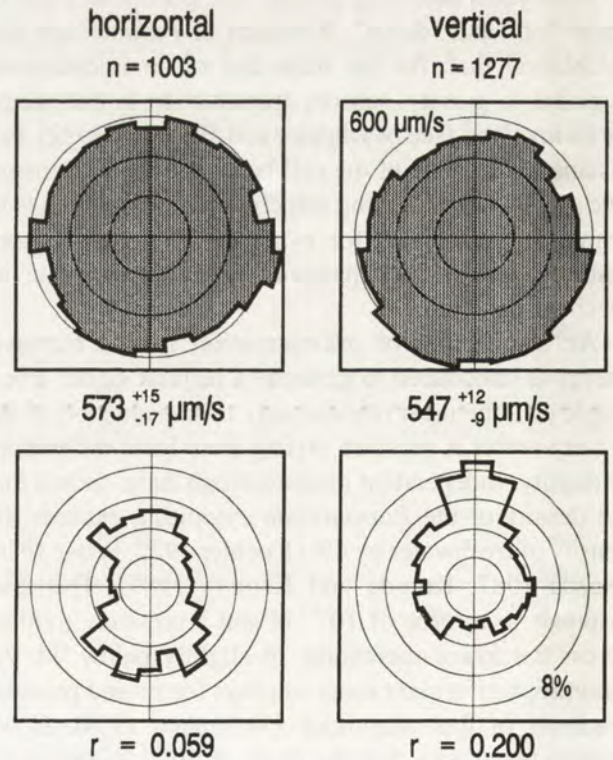


Fig. 2. Swimming velocities (upper panel) and orientations (lower panel) of *Paramecium* in horizontally and vertically oriented volumes of the experimental chamber (30 x 18 x 1.6 mm). The polar histograms suggest a downward velocity bias and upward orientation bias of cells swimming in the vertical plane. Note scaling of velocity ( $\mu m/s$ ) and orientation (% of total cell count, n). r - direction coefficient (Batschelet 1981). Modified after Machemer et al. 1993



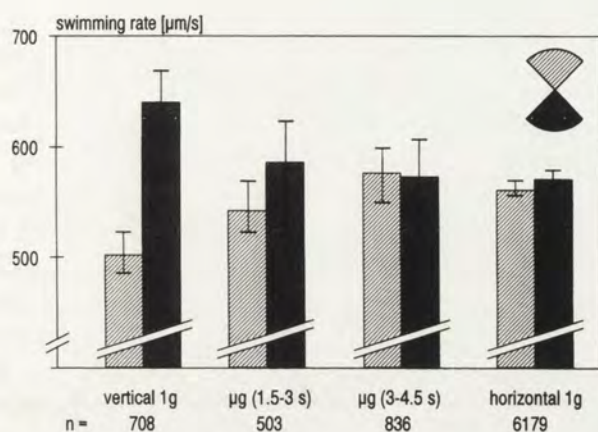


Fig. 3. Relaxation of differences in vertical velocities of *Paramecium* following transition from normal gravity (1g) to weightlessness ( $\mu\text{g}$ ) in the drop tower (light shading: upward swimmers; heavy shading: downward swimmers). Median velocities within "upward" and "downward"  $90^\circ$  sectors were determined during two periods (1.5-3 s; 3-4.5 s) after start of free fall. Comparison with horizontal velocity of same population within same sectors shows that velocity under weightlessness corresponds to horizontal velocity at 1g. Note interruption of velocity scale (Machemer et al. 1992)

With equation 3, it takes measurements of easily accessible parameters to determine gravikinesis: the velocities of downward and upward swimming, and the sedimentation rate. Note that with the electrophysiological hypothesis, the sign of gravikinesis in *Paramecium* is inverse to sedimentation. We have used both the simple difference equation (3) and the more specific original equations (1, 2). The propulsion rate,  $P$ , can be determined in the absence of gravity such as during free fall in the vacuum tube of a drop tower. The sedimentation rate can be modulated using, for instance, hypergravity conditions in a centrifuge. We have performed these types of experiments in different ciliates. I will now briefly summarize some of our experiments and conclusions.

How is the sedimentation rate determined? We immobilize cells using up to 1 mM  $\text{NiCl}_2$  in experimental solution. Individual variations of sedimentation rates of *Paramecium caudatum* are quite large, but mean values are near  $90 \mu\text{m/s}$  at 1 g. Applying hypergravity of up to 5.4 g, the sedimentation rate of *Paramecium* rose in a quasilinear fashion beyond  $300 \mu\text{m/s}$  (correlation coefficient 0.995). We cannot infer the sedimentation rates below 1 g because a linear regression of data points did not intersect with zero velocity and zero gravity.

How are the velocities of cells measured? Several strategies exist. We record on video tape fields including 100 to 300 cells and evaluate by hand tracks from digitized, superimposed fields. Typical tracking times

are 2 to 4 seconds. Linear calibration of the field, and time of swimming, give the velocity. Fields were evaluated quantitatively by hand. This allows us to distinguish between continuously swimming cells and those, which perform reversals.

Swimming velocities were represented by polar histograms. In Fig. 2 the upper panel shows polar distributions of velocities of the same population of cells recorded horizontally (left) and vertically at 1 g (right). There was no preferred direction in horizontal swimming rates. On the other hand, the upward swimmers were slower, and the downward swimmers faster than at horizontal orientation. In the same population, velocity medians of all vertical rates differed from the medians of all horizontal rates suggesting in vertically oriented cells the existence of a gravikinetik response superimposed on sedimentation.

A quantitative determination of the graviresponse is possible defining sectors of more or less vertical orientation. Figure 3 gives the evaluation of a free-fall ex-

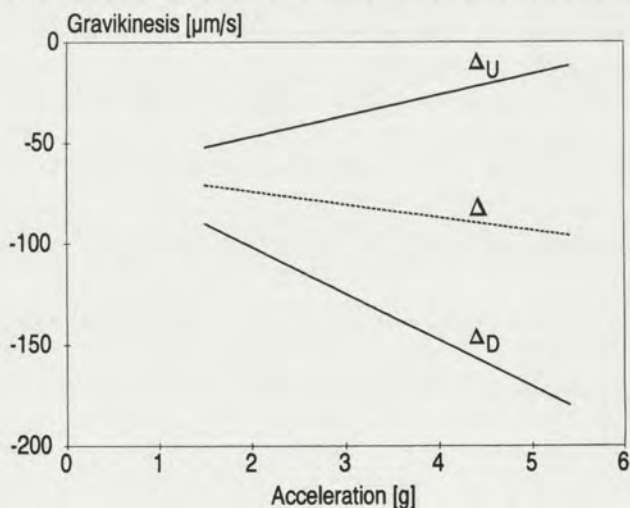


Fig. 4. Gravikinesis in *Paramecium* as a function of acceleration. Swimming and sedimentation velocities at 5 different values of hypergravity between 1.5g and 5.4g were used to calculate gravikinesis ( $\Delta$ ; equation 3). The intersection near 0g of linear regressions of upward (corr. coeff. 0.99) and downward velocity (corr. coeff. 0.96) were employed for approximation of the intrinsic propulsion velocity ( $P$ ) and gravikinesis of upward ( $\Delta_U$ ) and downward swimming cells ( $\Delta_D$ ; equations 1, 2). The data suggest that  $\Delta$  grows with rising acceleration because the increase in gravikinesis of downward swimmers outweighs the decrease in gravikinesis of upward swimmers (Bräucker et al. unpublished). Note that (1) the sign of gravikinesis is negative in the full range of hypergravity tested and (2) regressions do not tend to intersect with the origin of the diagram. Gravikinesis of *Paramecium* at 1g is between  $-20 \mu\text{m/s}$  and  $-90 \mu\text{m/s}$  according to the published literature (see Machemer and Bräucker 1992)



periment of *Paramecium*, which we have done in the 140m-drop tower of Bremen. A significant difference in rates of upward and downward swimmers at 1 g decayed with the beginning of the free fall and was absent after about 5 s. This would be expected for conditions under weightlessness, where intrinsic propulsion alone determines the swimming rate. Interestingly, the swimming rates during free fall coincided with the rates of horizontal swimmers at normal gravity. Our conclusion is that - corresponding to predictions from the distribution of mechanically sensitive receptors in *Paramecium* - horizontal swimming rates at normal gravity are equal to the value of  $P$ . With the rates of swimming under weightlessness ( $P$ ), sedimentation ( $S$ ) and vertical up and down swimming at 1 g ( $V_U$ ,  $V_D$ ) given, the gravikinetic responses can be determined in detail. In all experiments  $\Delta_U$  and  $\Delta_D$  had a negative sign, and their absolute values differed from each other. The mean gravikinetic response ( $\Delta$ ) in *Paramecium* was small, ranging near 50  $\mu\text{m/s}$  which is about 5% of the active propulsion rate.

I will now briefly summarize experiments using artificially raised gravity. We have mentioned a sedimentation rate growing with the  $g$ -vector. With gravity rising more than fivefold, the downward swimming rates of 3 days old *Paramecium* increased, and the upward swimming rates strongly declined. Interestingly, the horizontal swimming velocities were virtually unchanged even at raised gravity. Using the intersection of linear regressions of downward and upward swimming rates for approximation of the gravity-free propulsion ( $P$ ), and the regression lines of sedimentation, upward and downward swimming, we calculate the gravity-dependent kinetic responses of *Paramecium* (Fig. 4). It is seen that negative values of gravikinesis, that is an active motor response antagonizing sedimentation, persisted or even grew well beyond 150  $\mu\text{m/s}$  with 5-fold gravity.

Is the gravikinetic behaviour of *Paramecium* representative of many or even all ciliates? In order to answer this question, we investigate the electrophysiology and behaviour in different ciliates. Here, I will briefly mention the graviresponses in *Didinium*, which is a well known predator of *Paramecium*. *Didinium* differs from *Paramecium* in that it does not generate hyperpolarizing receptor potentials with posterior mechanostimulation (Pernberg, unpublished observations), and its cilia do not respond to hyperpolarization under voltage clamp (Mogami et al. 1990). An implication of this finding is

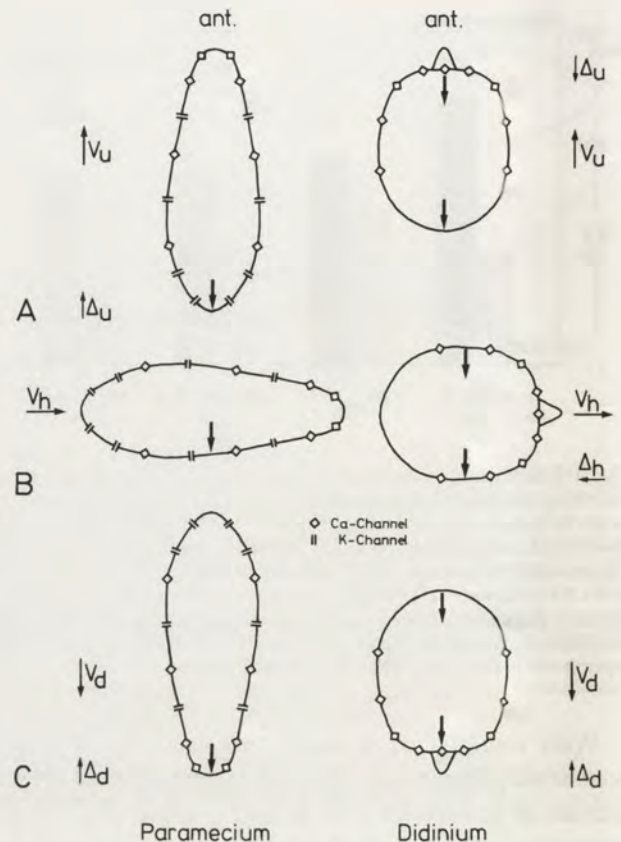


Fig. 5. *Paramecium* and *Didinium* gravikinesis compared diagrammatically. Cells are depicted as swimming upward (A), horizontally (B) and downward (C; ant. = anterior cell end). Two classes of gravireceptor channels are included in the membrane with gradient-type distributions: Ca-channels ( $\circ$ ) and K-channels ( $|$ ). Heavy arrows give presumed area of membrane deformation due to inside-outside density differences. Light arrows: forward swimming rates ( $V_U$ ,  $V_H$ ,  $V_D$ ) and inferred gravikinetic components ( $\Delta_U$ ,  $\Delta_H$ ,  $\Delta_D$ ) incorporated in the observed velocities. Note that a gravikinetic response can add to or subtract from the intrinsic cell propulsion. In *Paramecium* gravikinesis always acts to reduce effects of sedimentation. Data in *Didinium* suggest that hyperpolarizing gravireceptor channels are absent; therefore, propulsion is slightly depressed under gravity irrespective of orientation (Bräucker et al. unpublished)

that we cannot expect a gravikinesis from hyperpolarization-dependent ciliary activation.

The swimming rates of *Didinium* at normal gravity, horizontal and vertical rates, and the swimming rates during weightlessness were investigated. Horizontal swimmers of opposite field sectors swam at the same rate at 1 g. After about 5 s of weightlessness during free fall in the drop tower, the vertical velocity differences subsided as expected. However, the swimming rates during the free fall were significantly higher than the horizontal swimming rates. This suggests, in agreement with the electrophysiological hypothesis of gravikinesis, that in horizontally swimming *Didinium* at normal gravity, the excitatory motor component of gravistimula-



tion, hyperpolarization, is missing, whereas the inhibitory motor component, depolarization, persists. Removal of the inhibitory depolarization under weightlessness conditions, therefore, speeded up *Didinium*.

I close this short presentation with a scheme which attempts to explain the observed gravikinetic behaviour of *Paramecium* and *Didinium* at the level of membrane channels (Fig. 5). In upward swimming *Paramecium*, gravity acts to open gravireceptor K channels at the posterior cell end, the cell hyperpolarizes and the cilia, by raising the frequency of their beating, generate an increment in upward swimming rate,  $\Delta_U$ , which antagonizes sedimentation. In horizontally swimming *Paramecium*, both gravireceptor K and Ca channels are activated with a conductance ratio which corresponds to that of the resting potential. Hence, no change in ciliary frequency occurs. In downward swimming *Paramecium*, anterior gravireceptor Ca channels activate; the membrane depolarizes depressing the rate of ciliary beating. This decrement in downward swimming rate,  $\Delta_D$ , antagonizes sedimentation.

Our data in *Didinium* agree with the general scheme of *Paramecium* with two exceptions: (1) there exist no hyperpolarizing gravireceptor channels; (2) gravity-induced inward as well as outward deformation of the membrane can generate depolarizing gravireceptor potentials. Thus, with the pull of gravity, swimming in any direction is slightly inhibited. Only under conditions of weightlessness is this inhibition of ciliary activity removed so that the *Didinium* cell swims faster than at terrestrial gravity.

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## Effects of Solar Radiation on Motility, Orientation, Pigmentation and Photosynthesis in a Green Dinoflagellate *Gymnodinium*

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**Summary.** The effects of solar radiation on motility, orientation to light and gravity as well as pigmentation and photosynthetic and respiratory oxygen exchange have been analyzed in the dinoflagellate, *Gymnodinium*, Y-100. Exposure to unfiltered solar irradiation impaired motility (percentage of motile cells) within 130 min while the average swimming velocity of the remaining motile cells was hardly affected. The cells show exclusive positive phototaxis, the precision of which decreases strongly with exposure time to solar radiation. In a vertical cuvette the cells show positive gravitaxis which soon becomes random after short exposure times; longer exposure causes the cells to switch to positive gravitaxis, which may be an escape mechanism from excessive radiation. The photosynthetic pigments are gradually bleached by solar radiation. Photosynthetic oxygen production is impaired even on a shorter time scale, while respiration is not as much affected.

**Key words.** Dinoflagellate, gravitaxis, *Gymnodinium*, photosynthesis, phototaxis, solar radiation, swimming velocity.

### INTRODUCTION

Dinoflagellates are among the most important biomass producers in the oceans (Taylor 1987). Most photosynthetic dinoflagellates are capable of active movement and optimize their position in the water column by orienting with respect to external factors. Many phytoplankton organisms cannot tolerate bright solar radiation encountered at the surface and their pigments are bleached within hours or days (Nultsch and Agel 1986, Häder et al. 1988). On the other hand, they cannot move too far down in the water column because of their dependence on sunlight for energetic reasons.

Thus, they optimize their position, finding a compromise between optimal photosynthesis and pigment bleaching.

Some freshwater and marine organisms use positive phototaxis at low fluency rates to move upward in the water column (Eggersdorfer and Häder 1991a, b). Often the upward movement by positive phototaxis is supported by negative gravitaxis (Häder and Liu 1990a, b). In some cases the upward movement is balanced by a downward movement mediated by negative phototaxis at high fluence rates (Rhiel et al. 1988). In contrast, several freshwater and marine dinoflagellates have been found to show diaphototaxis (movement perpendicular to the incident light beam) at higher fluence rates which is an effective means to stay at a selected level (Liu et al. 1990, Eggersdorfer and Häder 1991a). On top of these orientation mechanisms many phytoplankton organisms undergo vertical diurnal migrations, and

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dinoflagellates have been found to move up to 15 m up and down the water column (Burns and Rosa 1980).

In addition to phototaxis (orientation with respect to the light direction, Diehn et al. 1977) some organisms use photokinesis (dependence of the swimming velocity on the steady state light intensity, Wolken and Shin 1958) and/or both step-up and step-down photophobic responses (transient directional changes upon sudden changes in the fluence rate, Doughty and Diehn 1983, 1984). In addition to light, other organisms have been found to utilize different physical and chemical external stimuli to orient within their microhabitat such as chemical and thermal gradients (MacNab 1985, Poff 1985), the magnetic field of the earth (Esquivel and de Barros 1986) and even electric currents (Mast 1911).

Enhanced solar radiation has been shown to impair motility and swimming velocity in a number of flagellates and also gliding organisms. In addition, the orientation mechanisms with respect to light are affected (Häder and Worrest 1991). The degree of inhibition is lower, when the short wavelength radiation is removed by cut-off filters or by inserting an artificial layer of ozone. Furthermore, artificial ultraviolet radiation has been found to induce similar effects (Häder and Häder 1990a, Häder et al. 1990), indicating that the ultraviolet component is a major stress factor for phytoplankton organisms. Similarly, gravitaxis was affected in a number of flagellates (Häder and Liu 1990a, b), indicating that the orientation is mediated by an active physiological receptor organelle rather than by a passive physical process (Brinkmann 1968).

Many UV-B effects are caused by DNA absorption (Yamamoto et al. 1983), leading to the formation of thymine dimers. However, for some responses DNA could be ruled out as a primary UV-B target and also photodynamic reactions were found not to be involved (Hirosawa and Miyachi 1983, Häder et al. 1986), suggesting that specific proteins of the photoreceptor and motor organelles were affected by increased ultraviolet radiation. And indeed, spectroscopic and biochemical studies have revealed that specific proteins were destroyed under the influence of ultraviolet radiation (Häder and Brodhun 1991, Zündorf and Häder 1991, Häberlein and Häder 1992). In addition, the chromophoric groups of the pigments are bleached as shown by spectroscopic investigations. Pigment bleaching and other damages of the photosynthetic apparatus result in reduced photosynthetic oxygen production (Zündorf and Häder 1991). Especially sites in photosystem II have been identified as primary UV-B targets (Renger et al. 1989).

Any inhibition of motility and orientation of phytoplankton organisms by solar ultraviolet radiation is bound to be detrimental for growth and survival of the population in its habitat. Furthermore, any increase in solar UV-B radiation due to a partial reduction of the stratospheric ozone layer caused by the production and emission of anthropogenic gaseous pollutants such as CFCs (Madronich et al. 1991) bears the risk of reducing the biomass production of phytoplankton.

The aim of this paper is to characterize the effects of solar ultraviolet radiation on motility and the orientation strategies with respect to light and gravity in the marine dinoflagellate, Y-100. Furthermore, the effects of solar radiation on pigmentation and photosynthesis are studied.

## MATERIALS AND METHODS

### Organism and culture

The dinoflagellate, *Gymnodinium* Y-100, was a gift from Dr. Elbrächter and used for all experiments described in this article. The cells were inoculated into 40 ml of a medium described recently (Guillard and Ryther 1962) kept in 100 ml Erlenmeyer flasks. The cultures were grown for about 1-2 weeks under continuous light of about  $2.5 \text{ W m}^{-2}$  from mixed cool white and warm tone fluorescent lamps at about  $23^\circ \text{ C}$ . Cell suspensions were removed from the cultures and subjected to solar irradiation in their growth medium.

### Solar irradiation

Cell suspensions were exposed to solar radiation in open plastic Petri dishes at the research station Quinta de Sao Pedro, Monte de Caparica, south of Lisbon ( $38^\circ$  North) on sunny days between 20.07. and 1.08.1992 between 10.30 and 15.00 h local time. The organisms were placed inside a temperature controlled growth chamber, the Plexiglas roof of which transmitted  $>92\%$  of solar radiation between 280 and 750 nm. The spectral distribution and the fluence rates of solar radiation were measured by the group of Prof. Tevini with a double monochromator spectroradiometer (model 742, Optronic, Orlando, Fla.).

### Image analysis of motility and orientation

Samples were taken at regular time intervals during exposure to solar radiation for motility and orientation measurements. Gravitaxis of the flagellates was meas-



ured in darkness in a flat glass cuvette (60x8x0.17 mm inner dimensions) placed on the stage of a horizontally oriented microscope (Olympus BH2) with a 2.5x objective. A dark field condenser was used to enhance the contrast and the microscope light beam was filtered through an infrared cut-off filter (RG 715, Schott & Gen., Mainz, FRG) to be used as an IR measuring beam. Infrared monitoring of the cells allowed to avoid orientation of the cells with respect to the measurement beam; furthermore, the cells in the microscope focus did not produce oxygen photosynthetically which otherwise might have attracted cells from the outside due to their pronounced aerotaxis. The image of the moving cells was recorded by an infrared sensitive CCD b/w camera (LHD 0600, Philips, The Netherlands) mounted on top of the microscope. The video signal was digitized on line in real time by a framegrabber (Matrox, PIP 1024, Quebec, Canada) accommodated in an IBM AT compatible microcomputer (Deskpro 386/25, Compaq, Scotland). Digitization was performed with a spatial resolution of 512x512 pixels at 256 possible grey levels. The software package has been written in the computer language C (Häder and Vogel 1991) but time critical calculations such as the determination of position and outline of the organisms were performed in Assembly language using the chain code algorithm (Freeman 1974, 1980). The raw data were stored in form of movement vectors of the cells reflecting the individual swimming speed and the deviation from the stimulus direction. Subsequent programs were developed for statistical and mathematical analysis to quantify the precision of orientation. The computer program also recorded the percentage of motile cells.

Phototaxis was measured with the same hardware and software system as gravitaxis in a horizontal cuvette placed on the stage of a vertically oriented microscope. The actinic light beam was produced from a 250 W slide projector equipped with a 24 V quartz halogen bulb (Kindermann Universal, Wetzlar, Germany) and entered the cuvette at an angle of 12° above the surface. The irradiance was measured with a Mavolux radiometer (Gossen, Erlangen, FRG).

### Absorption spectroscopy

*In vivo* absorption spectra were measured with a dual beam spectrophotometer (UV240, Shimadzu, Düsseldorf, Germany). The cells were immobilized in a 0.7% agar prepared from medium. Two quartz cuvettes were filled bubble free with the same suspension and

closed with lids and parafilm to avoid evaporation and thus volume changes. A baseline was determined with a cuvette each in the sample and reference compartment, respectively, to abolish all possible optical differences between the two. Subsequently the sample cuvette was exposed to solar radiation and difference spectra were recorded at regular time intervals. By this method the bleached pigments appear as negative peaks. Another advantage of this method is that exclusively real absorption changes are detected while differences in scattering are excluded.

### Photosynthetic oxygen production

Photosynthetic oxygen production was measured in a Plexiglas cylinder with 20 mm inner diameter thermally stabilized by a water jacket connected to a thermostat (25 °C, RMT6, Dr. Wobser GmbH, Lauda-Königshofen, Germany). The sample compartment held 5 ml cell suspension agitated by a magnetic stirrer and was sealed with a Clark electrode (Yellow Springs Instruments, Yellow Springs, Ohio, USA) (Dubinsky et al. 1987). The electrode was connected via a custom-made polarizer (Estabrook 1967) with a recorder (PM 8262, Philips). Calibration was done with 10 mM sodium dithionite for the 0% oxygen saturation and the 100% value was measured after bubbling air through the medium. Photosynthesis was induced by white light produced from a 250 W slide projector with a 24 V quartz halogen bulb (Kindermann Universal).

All experiments were repeated at least four times on different days. However, as in ecological experiments day-to-day changes in visible and specifically ultraviolet radiation levels are unavoidable the data were not averaged and the standard error calculated but rather representative single experiments are shown.

### RESULTS

In the horizontal cuvette the cells showed a high precision of phototactic orientation when irradiated laterally at an irradiance of 50 W m<sup>-2</sup> (Fig. 1a). The Rayleigh test (Batschelet 1965, 1981) gave an r-value of 0.70. When exposed to unfiltered solar radiation this high precision of orientation was maintained for about 40 min. After 75 min the r-value of phototactic orientation had decreased to 0.51 (Fig. 1b) and after 105 min to 0.25 (Fig. 1c). After 125 min the motile cells moved completely randomly as indicated by the standard Rayleigh test for directionality (Fig. 1d). Quantification



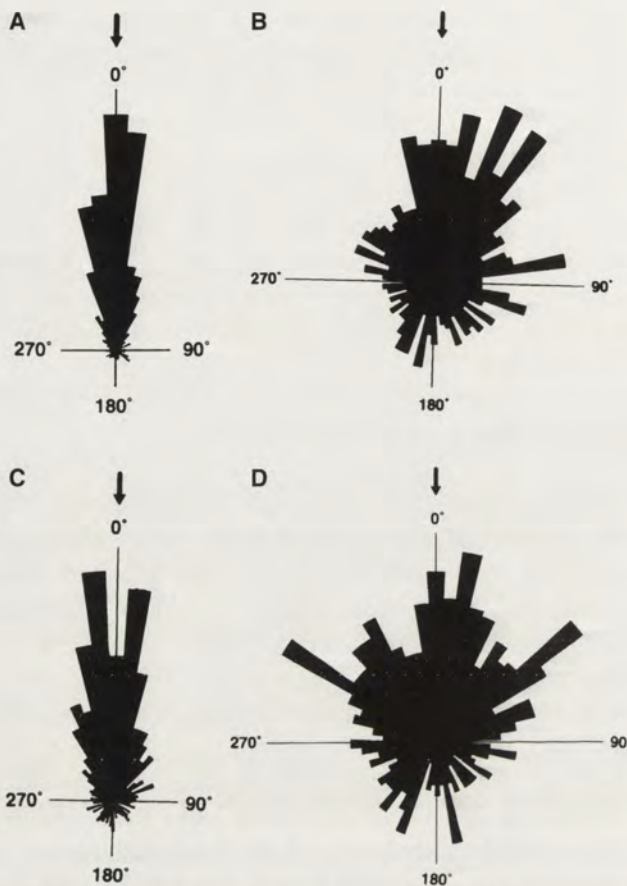


Fig. 1. Histograms of positive phototaxis to  $50 \text{ W m}^{-2}$  in *Gymnodinium* after 0 (a), 75 (b), 105 (c) and 125 (d) min of unfiltered solar radiation

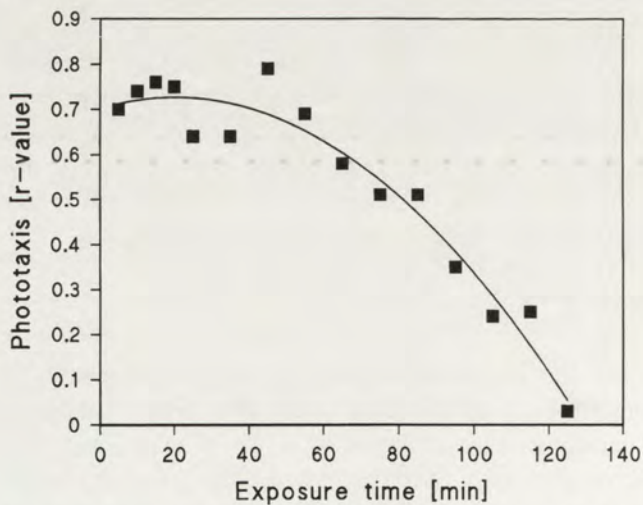


Fig. 2. Dependence of the precision of positive phototaxis ( $50 \text{ W m}^{-2}$ ) quantified by the Rayleigh test (r-value) of *Gymnodinium* on the exposure time to solar radiation

of the phototaxis data showed a steady decline of orientation with time (Fig. 2). Not exposed control cells continued to show a high precision of orientation for at

least the same time (data not shown). The percentage of motile cells decreased steadily with increasing exposure time (Fig. 3), while the average swimming velocity of the motile fraction was not as much affected (Fig. 4). When the UV component of solar radiation is removed by a GG 400 cut-off filter the effect of solar radiation on orientation and motility is less dramatic even though also visible radiation affects these processes (data not shown). When the cells were exposed to a point that their motility had decreased to zero there was no regeneration even when the cells were kept for 24 h in darkness or dim white light indicating that there is no reversibility after UV exposure. After short term exposure (10 min) there was a partial recovery after 24 h.

In a vertical cuvette the cells showed negative gravitaxis (upward movement in the water column) with an r-value of about 0.35. Even after short exposure to unfiltered solar radiation the precision of gravitactic orientation declined (Fig. 5) and the cells moved randomly. Visual inspection of the moving track indicated that the cells actually moved in a random fashion as opposed to half of the cells moving upward and half downward. After about 100 min the cells started moving downward in the water column (positive gravitaxis) with increasing r-values until after 160 min no motile cell was found. The downward movement is mediated by active swimming and not by passive sedimentation. Control populations kept in darkness continued to show negative gravitaxis with a high degree of precision for several hours (data not shown).

Absorption difference spectra showed a gradual bleaching of the photosynthetic pigments, specifically in the absorption range of the carotenoids and the chlorophylls (Fig. 6). Furthermore there is a gradual decrease in absorption at shorter wavelengths, indicating a loss in scattering. Not exposed controls did not show any detectable changes in absorption over the same period of time. Photosynthetic oxygen production was affected even more rapidly than the bleaching of photosynthetic pigments (Fig. 7). When exposed to solar radiation photosynthesis decreased drastically and after 10 min no net oxygen evolution was found. Subsequently, the oxygen uptake increased. This result is supported by respiration measurements showing only a moderate inhibition. When the solar radiation was filtered through a GG 400 cut-off filter (which removes the UV component from solar radiation) photosynthesis was affected much less and the net oxygen production fell to zero only after 18 min. Likewise, respiration was



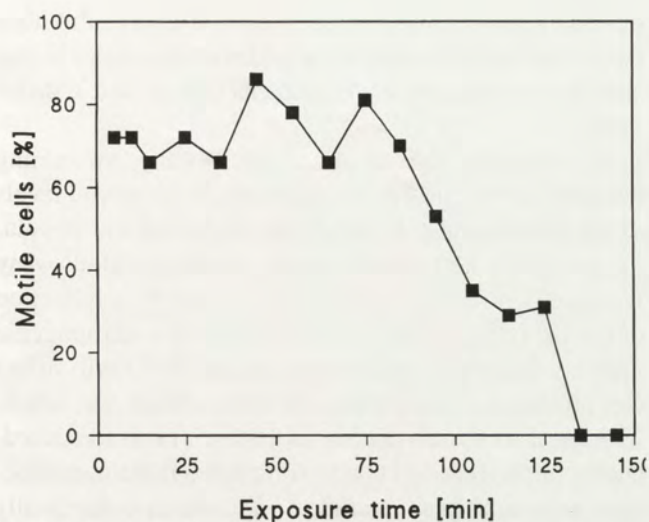


Fig. 3. Effects of unfiltered solar radiation on the percentage of motile cells in *Gymnodinium*

less affected by solar radiation when the UV component was removed. After short term exposure there was some recovery: oxygen production commenced within about 30 min. After long term exposure no recovery could be observed within the next few hours.

## DISCUSSION

In the water column, the dinoflagellate, *Gymnodinium* Y-100, moves upward by using light as an external stimulus (positive phototaxis). The precision of orientation increases with light intensity (Tirlapur et al. 1993). In contrast to other flagellates, which show positive phototaxis at low fluence rates and negative one at higher (Häder et al. 1988), this organism shows exclusively positive phototaxis. Other dinoflagellates, both marine and freshwater, use a different strategy of orientation and show a positive phototaxis at low fluence rates but diaphototaxis (movement perpendicular to the incident light beam) at higher, which effectively keeps the cells at a level of suitable light intensities (Liu et al. 1990, Eggersdorfer and Häder 1991a). Gravitactic orientation is similar to that of many other flagellates being negative in unstressed cells (Häder and Liu 1990a, b).

The orientation pattern of this organism is surprising, since both phototaxis and gravitaxis will take the cells to the surface, where they are exposed to the bright unfiltered solar radiation, which is known to bleach and eventually kill many phytoplankton organisms (Häder and Häder 1990b, Häder and Worrest 1991). However,

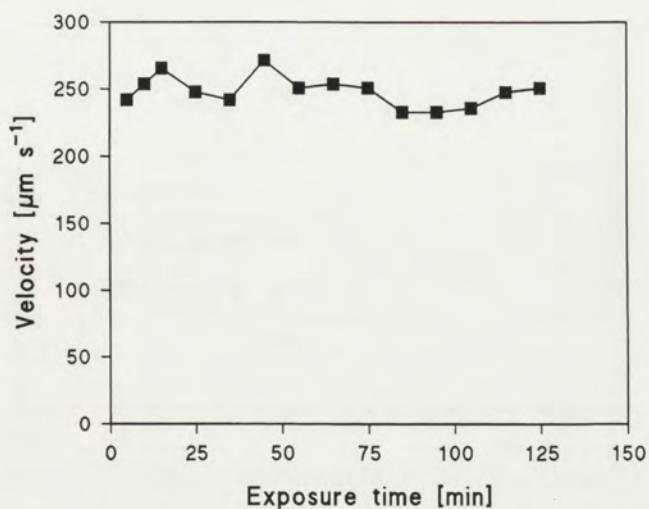


Fig. 4. Effects of unfiltered solar radiation on the average swimming velocity of motile cells in *Gymnodinium*

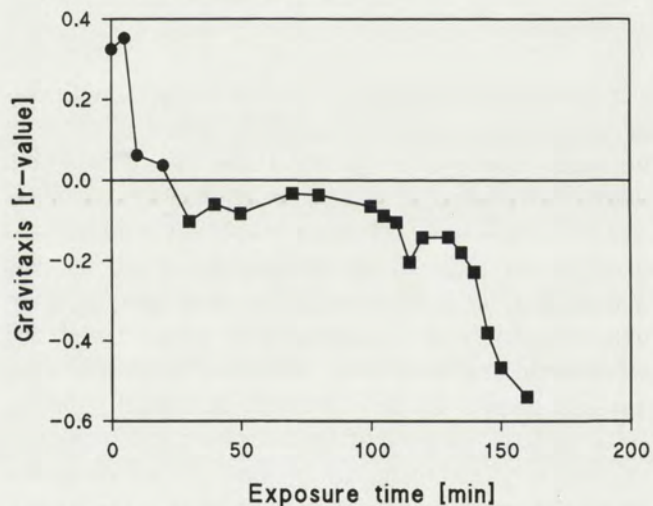


Fig. 5. Effects of unfiltered solar radiation on the direction and precision (r-value) of gravitactic orientation in *Gymnodinium*. Negative gravitaxis (circles) is plotted above zero and positive gravitaxis (squares) below (although, mathematically speaking, the r-value is always positive)

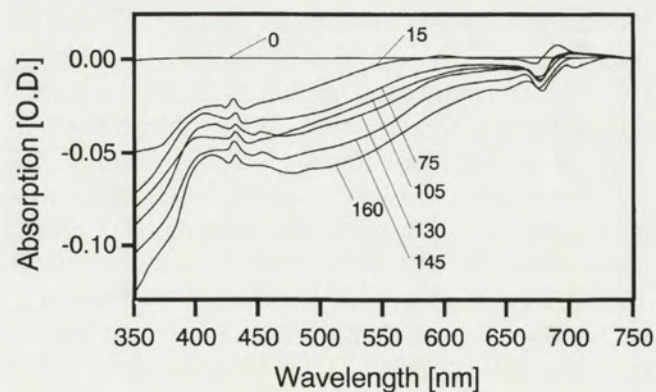


Fig. 6. Absorption difference spectra calculated by subtracting the spectrum of an unexposed sample from the spectra of samples exposed to solar radiation after increasing times



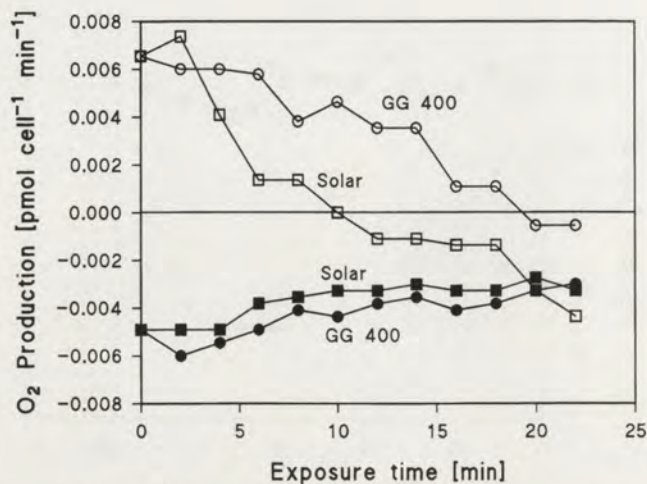


Fig. 7. Effects of unfiltered solar radiation (squares) and solar radiation from which the ultraviolet radiation has been removed (circles) on photosynthetic oxygen production (open symbols) elicited by a test light at  $333 \text{ W m}^{-2}$  and respiration (closed symbols) in *Gymnodinium*

a similar behavior has been found in another dinoflagellate, *Gyrodinium*, which exclusively moves upwards in the water column (Ekelund and Häder 1988) and which indeed is bleached by light at higher fluence rates.

This orientation mechanism is difficult to understand on an ecological basis since the current results indicate that motility and orientation mechanisms with respect to light and gravity are strongly affected by even moderate exposure to unfiltered solar radiation. This leads to the question of how the cells escape detrimental radiation at the surface. Some dinoflagellates have been observed to passively sediment when exposed to excessive ultraviolet radiation (Häder and Liu 1990a). In contrast, *Gymnodinium* Y-100 seems to utilize an active escape mechanism by downward swimming (positive gravitaxis).

This escape behavior is probably ecologically significant since photosynthesis is strongly affected by solar radiation. This inhibition is even more rapid than the effect on motility and orientation. Since the absorption difference spectra show massive bleaching only after longer exposure times it can be assumed that photosynthesis is affected by structural changes in the photosynthetic apparatus as has been detected also in higher plants (Renger et al. 1989, Tevini et al. 1989). The decrease in absorption at shorter wavelength may reflect a loss in scattering indicating a partial lysis of cells after extended periods of solar exposure. UV-B radiation is responsible for part of the inhibition by solar radiation as indicated by a study which used artificial ultraviolet radiation (Tirlapur et al. 1993). However, also

excessive UV-A and visible radiation exert inhibitory effects on motility, orientation and photosynthesis in this and other phytoplankton organisms (Häder and Worrest 1991).

In summary, the inhibition of motility, swimming velocity and orientation mechanisms by enhanced levels of solar radiation diminishes the ability of the populations to grow and survive under stress conditions. Any increase in solar UV-B radiation caused by a reduction of the ozone layer due to the emission of anthropogenic gaseous pollutants (Madronich et al. 1991) will affect the productivity and thus adversely affect the whole biological food web (El Sayed 1988). This is in accordance with the findings that *in situ* photosynthetic productivity of natural phytoplankton populations is drastically decreased under the Antarctic ozone hole (Smith et al. 1992, Vosjan et al. 1990, Karentz et al. 1991).

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## *In Vitro* Excystation of *Gregarina blattarum* Oocysts

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**Summary.** Excystation of sporozoites from *Gregarina blattarum* oocysts was observed with light and scanning electron microscopy. When digestive tracts extracts were added to oocysts, the sporozoites became activated and emerged. Two or three holes surrounded by projections were observed in the surface of oocyst walls just after sporozoites had excysted. Oocysts were able to excyst for at least 10 days after being desiccated.

**Key words.** *Gregarina blattarum*, gametocyst, oocyst, sporozoite, excystation, SEM.

### INTRODUCTION

It has been reported that the sporozoites of some gregarines excyst from oocysts after the addition of the host's digestive fluids (Canning 1956; Janardanan and Ramachandran 1979, 1982). We investigated the process of sporozoite excystation from the oocysts of *Gregarina blattarum* with light and scanning electron microscopy after adding the extracts from the digestive tract. The resistance of the oocysts to desiccation was also studied. Terminology used was that proposed by Levine (1971).

### MATERIALS AND METHODS

The cockroach, *Blattella germanica* used in this experiment came from a culture that has been maintained in our laboratory and originated from Fumakilla Inc., Japan.

Ten *B. germanica* were decapitated and dissected. The digestive tracts were removed, placed in 1 ml of Ringer's solution and homogenized with a glass microhomogenizer. The mixture was centrifuged at 2000 x g for 2 min and filtered with a Millipore filter with 0.45 µm pores. The filtrate was used as the extract of digestive tracts.

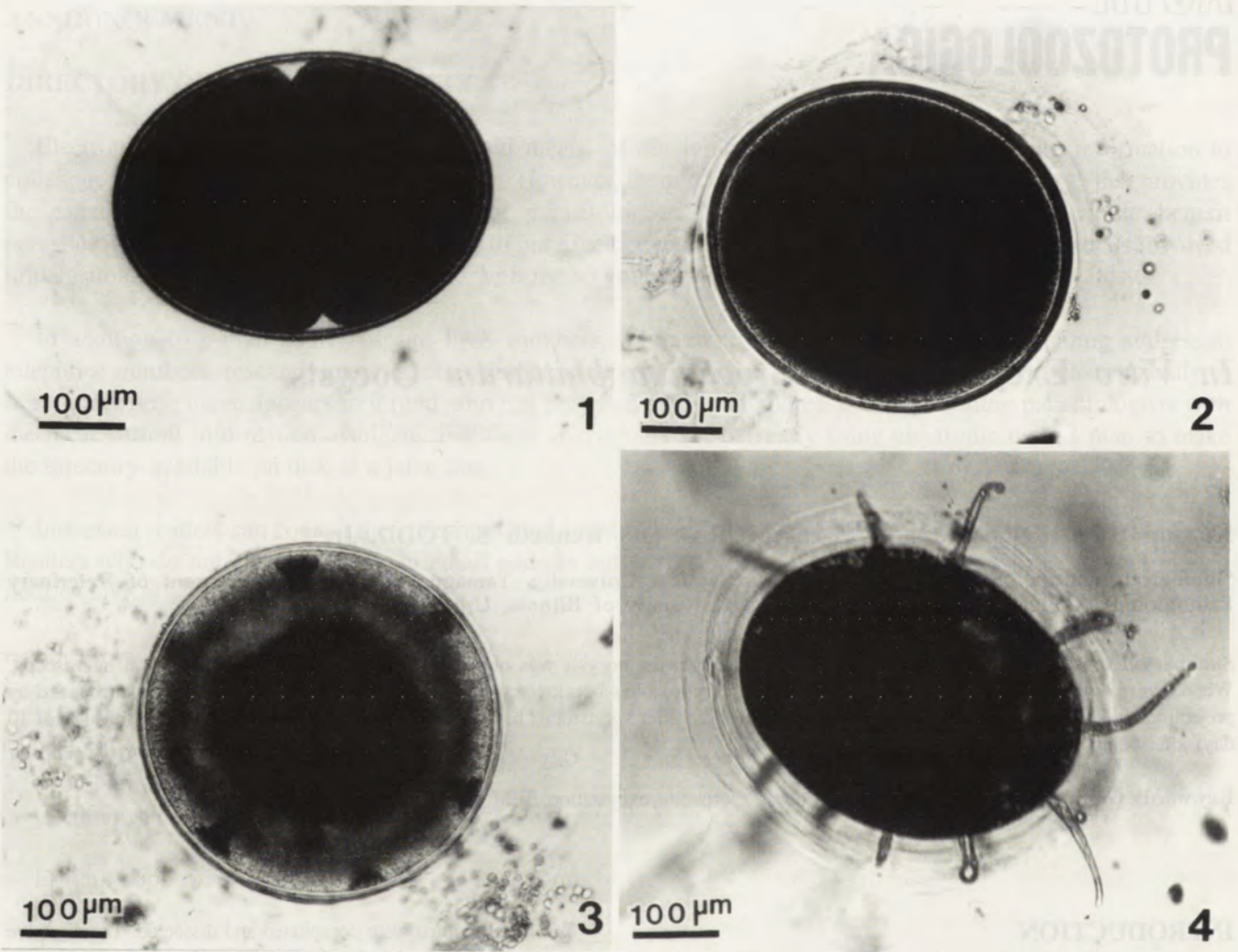
Gametocysts of *G. blattarum* were collected from the feces of *B. germanica* and placed in distilled water on a glass slide which was kept in a moist chamber for 2 or 3 days. The oocysts on the slide were divided. Each half was transferred to a different slide and two drops of Ringer's solution was added to one half and two drops of the digestive tract extract was added to the other half. The slides were covered with a cover-glass which was sealed around the edges with a balsam-paraffin resin. The samples were examined with a light microscope every 20 min.

The oocyst from which the sporozoites had excysted were examined with a scanning electron microscope. The specimens were prefixed in a 5% glutaraldehyde solution, rinsed several times with cacodylate buffer and dehydrated with an ethanol series. They were then placed in isoamylacetate and further dehydrated by the critical point method using CO<sub>2</sub> as the transition liquid. Dried samples were attached to aluminum stubs and sputtered with gold using a JEOL 40 unit. Specimens were observed with a JEOL T-300 scanning electron microscope.

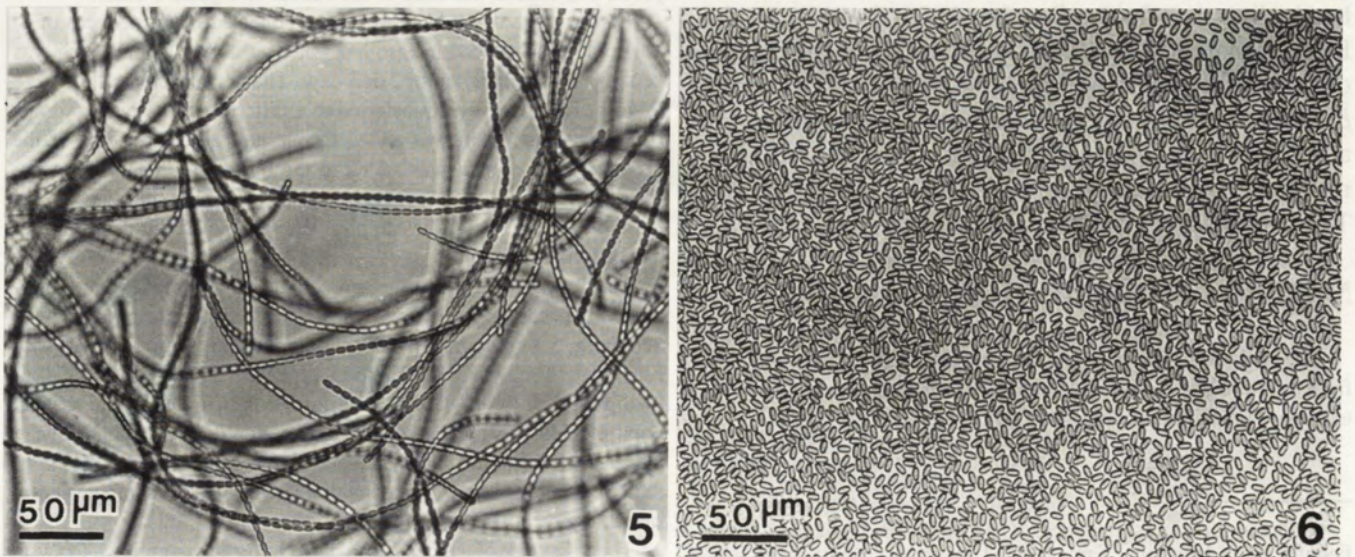
The resistance of the oocysts to desiccation was examined. Oocysts were transferred to 3 slides and each slide was dried for 1, 5 and 10

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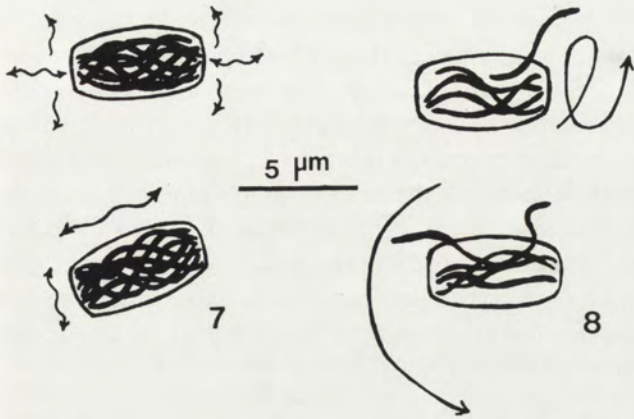


Figs. 1-4. *Gregarina blattarum* gametocyst. 1 - immature with a constriction, 2 - mature, 3 - mature with sporoducts inside the wall, 4 - sporoducts extended



Figs. 5-6. *Gregarina blattarum* oocyst. 5 - chains of oocyst just after extrusion, 6 - individual oocyst several hours after extrusion





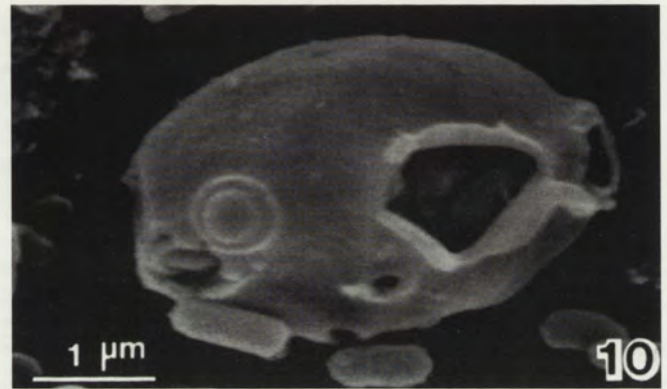
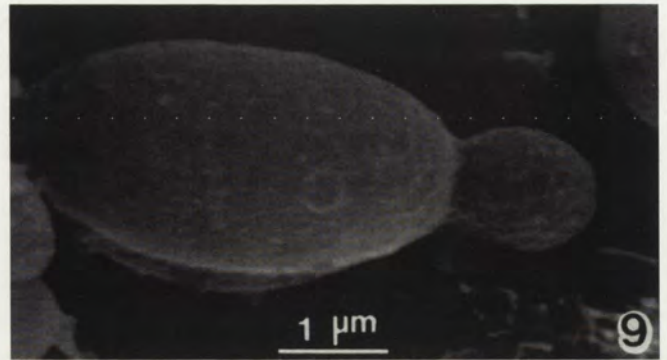
Figs. 7-8. *Gregarina blattarum* oocyst. 7 - vibrating oocyst 2 h after adding the digestive tract extract, 8 - rotational or spiral movement of oocyst 5 h after adding the extract. Sporozoites partially emerged from the oocyst

days. After desiccation the digestive tract extract was added and the oocysts were examined for excystation with light microscopy. The experiment was done in room temperature, approximately at 25°C.

**RESULTS**

Gametocyst were spherical to slightly ellipsoidal and had thick gelatinous walls. Immediately after passing in the feces of *B. germanica*, a constriction was clearly visible at the center of the gametocysts (Fig. 1). The stricture usually disappeared and the endoplasm became homogeneous within 5 h (Fig. 2). Oocysts and sporoducts were formed inside the gametocysts (Fig. 3). After 2-4 days of storage in a moist chamber the gametocysts formed 6-12 external sporoducts and the oocysts were extruded through them (Fig. 4). The oocysts were initially in chains but became separated within a few hours (Figs. 5, 6).

When Ringer's solution was added, oocysts remained unchanged for several hours. Two hours after the addition of digestive tract extract many oocysts began to move (Fig. 7). At that time the thread-like sporozoites were observed inside vibrating oocysts. After 5 h several oocysts began to rotate or spin. At that time, the sporozoites were partially outside the oocysts and violent movement of sporozoites caused a rotational or spiral movement of the oocysts (Fig. 8). The sporozoites were elongated cylinders and constricted at the middle (Fig. 11). Free sporozoites moved rapidly away from the oocysts. Oocysts from which the sporozoites had excysted had one or two protuberances on their surface



Figs. 9-10. *Gregarina blattarum* oocyst. 9 - oocyst with protuberance (SEM), 10 - oocyst with several holes (SEM)



Fig. 11. Excysted sporozoites (SEM)

and appeared transparent with light microscopy. The protuberances were observed with a scanning electron microscope (Fig. 9), and two or three holes were observed on the surface of the oocyst walls. The holes were irregularly distributed with some at the middle of the oocysts and others at the tips (Fig. 10).



The tolerance of the oocyst for desiccation was examined by adding digestive tract extracts. When the extract was added to the oocysts which were dried for 1, 5 or 10 days, the sporozoites excysted from the oocysts. It took a longer time compared to nondesiccated oocysts but they hatched normally. The oocysts which were dried for 5 or 10 days took 7 to 10 h to excyst.

## DISCUSSION

*Gregarina blattarum* is a typical cephaline gregarine (Siebold 1839, Watson 1916). It has a complex life cycle which includes sporozoites, cephalines, gamonts, gametocysts and oocysts. The different stages show structural changes which are adapted to an endogenous or exogenous environment. The gametocyst and oocyst stages are exogenous and produce multiple sporozoites.

Maturation of gametocysts and oocysts was observed with light microscopy. Oocysts of *G. korogi* have thick and homogeneous walls (Hoshide and Todd 1993) as does *G. blattarum*. The oocyst wall of *G. blattarum* was thick and protected sporozoites from external environmental conditions. Oocysts retained the ability to excyst after 10 days of desiccation. Janardanan and Ramachandran (1979, 1982, 1983) reported that the digestive fluids released the sporozoites from the oocyst on the gregarines that parasitized millipedes. The digestive tract extract affected the excystation of sporozoites, but we did not attempt to identify the active component. Some substance in digestive tracts activate sporozoites. The activated sporozoites bored holes in the wall of the oocyst and emerged through the holes. We found three breaks in the oocyst wall of *Gregarina korogi* and were of the opinion that the wall is split along the lines at the time of sporozoite excystation (Hoshide and Todd 1993). Sporozoites *G. blattarum* formed holes and emerged through the oocyst wall. The extract solution may ac-

tivate the sporozoites or weaken the wall of the oocyst. The property of activation by the extract of the digestive tract may be connected with host specificity.

One or two protuberances were observed on the surface of the oocyst shortly after excystation. The projections protruded from the inside and was the part of endoplasm of the oocyst which emerged with the sporozoites. The sporozoites were elongate cylinders and had constrictions at the middle of the bodies. The shape of the sporozoite of *G. blattarum* is similar to that of *Schneideria schneiderae* described by Da Cunha and Jurand (1978).

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