

Biodiversity and Biocomplexity of the Protists and an Overview of Their Significant Roles in Maintenance of Our Biosphere

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Summary. The ubiquitous and very numerous protists, eukaryotic organisms mostly unicellular in structure and small in size, play numerous roles of importance that are often neglected or overlooked in biodiversity, biocomplexity, and conservation considerations of life on planet Earth. The present review article reminds readers, who hopefully include general biologists and other scientists as well as persons engaged directly in research activities that primarily involve solely protists (e.g. diverse studies on species belonging mainly to many individual groups of algae or protozoa), of such roles whether they be in areas directly or indirectly beneficial to human comfort and survival or in ones deleterious to our health and welfare. Matters become complex when multiple interactions are part of the overall picture (e.g. in food webs or in symbiotic relationships). Clearly, our far from complete knowledge of protistan taxonomic and phylogenetic interrelationships, as well as of their ecology, physiology, biochemistry, and molecular and evolutionary biology, hinders rapid progress in better understanding of their multiple roles in sustaining today's biosphere.

Key words: algae, complexity, conservation, diversity, lower fungi, protists, protozoa.

INTRODUCTION

It may not be generally realized that protists - eukaryotic organisms embracing what are classically known as the protozoa, the algae, and the so-called lower fungi - are far more speciose than the viruses and the prokaryotes (essentially the bacteria *sensu lato*), the two latter groups so widely hailed as the most important (or even only!) microorganisms seriously affecting the lives of the more visible (so-called higher)

organisms, the plants and the animals of the world. Many such tiny microbes (i.e. bacteria) are indeed highly important to the well-being of the latter, including humans. But there is also an immense assemblage of *protistan* microorganisms (representing dozens of phyla, scores of classes, hundreds of orders) that taxonomically far outnumbers the totals of known species of viruses and prokaryotes and that likewise has a major impact on us and on the sustainability of our world (see very brief preliminary note, a letter to the Editor of *BioScience*, by Corliss 2001).

The primary purpose of this article is to highlight some of the characteristics, actions, and interactions of the protists *sensu lato* that often seem to have been neglected in addressing the pressing problems of biodiversity,

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biocomplexity, and conservation, issues now in the forefront of public attention as well as representing topics of widespread biological research efforts. Scores of major publications and reviews dealing with such subjects have appeared since the stimulating pioneering essays of E.O. Wilson (e.g. see his 1992 book and references to his early papers therein), but they give scant mention, if any, to the significance of our predominantly unicellular lower eukaryotes.

A second aim of this overview presentation, persistently urged by protistological colleagues who have seen my preliminary note (cited above), is to offer an annotated guide (space limitations unfortunately require it to be a rather brief one) to the pertinent growing literature on protists in such highly diverse fields as systematics, ecology, parasitology, morphology, cell biology, evolutionary biology, and even paleontology. I have also tried to keep in mind the importance of *not* neglecting either of two seemingly disparate areas, the one involving essentially ubiquitous free-living forms (so numerous everywhere in ecological niches surrounding us) and the other devoted to symbiotic and especially parasitic species (e.g. the causative agents of malarias, trypanosomiasis, leishmaniasis, and the like).

TAXONOMICALLY, WHAT ARE THE PROTISTS?

Because taxonomy has often been heralded as the core of biodiversity, by Wilson and other biologists, we must pay some attention to it here, although space restrictions forbid detailed treatment. Arguments will long continue among classificational specialists, cladists, and molecularly oriented evolutionary biologists over the exact boundaries of both long and more recently recognized assemblages of protists (see especially discussions in Sleigh 1989; Karpov 1990; Margulis *et al.* 1990; O'Kelly 1993; Cavalier-Smith 1993, 1998a,b, 2000a, 2002; Corliss 1994a, 1998, 2000a; Blackwell and Powell 1995, 2001; Hausmann and Hülsmann 1996; Margulis 1996; Norton *et al.* 1996; Andersen 1998; Barnes 1998; Coombs *et al.* 1998; Vickerman 1998; Patterson 1999, 2002; Alimov 2000; Atkins *et al.* 2000; Johnson 2000; Leadbeater and Green 2000; Ben Ali *et al.* 2001; Simpson and Patterson 2001; Lee *et al.* 2002).

For most of our needs here, the protozoa - or protozoan protists - at the level of a kingdom PROTOZOA (written throughout this paper, when employed as a taxonomic name, in all capital letters to highlight its

supraphylum rank; this is also done for the other four kingdoms of organisms very briefly referred to below), may be considered as comprising the majority (but not all!) of those groups embraced by the classically long-familiar vernacular names (after Kudo 1966) of amoebae (rhizopods *s. l.* and the actinopods, many of both groups known only as fossil forms, plus the heliozoa); flagellates (diverse zooflagellates, including also the choanozoa and the opalinids, plus some so-called phytoflagellates); sporozoa *s. l.* (all symbiotic or parasitic, embracing the telosporidians, acnidosporidians, and cnidosporidians: the last composed of the microsporidians + myxosporidians); and ciliates (holotrichs, spirotrichs, peritrichs, suctorians, *in toto* the most diverse and speciose of all in extant forms: Corliss 1979, de Puytorac 1994, Lynn and Small 2002). There are numerous known species of these largely microscopic unicellular forms, many times the number recognized for bacteria and viruses; and their populations in nature exceed by several orders of magnitude those of all taxa of multicellular organisms combined.

Originally a taxonomic subcategory of the animals, as a *phylum* Protozoa, some former "protozoan" taxa in the above list appear today in other than just the relatively newly recognized formal *kingdom* PROTOZOA (refined and reduced in size, less paraphyletic in composition and thus more meaningful: Cavalier-Smith 1993, Corliss 1994a). For example, some zoosporic protists, a few slime molds *s. l.*, the opalinid infusorians, and various "phytoflagellates" (but not dinoflagellates and euglenoids) have been relocated to positions in the CHROMISTA (see below). The remarkable *Volvax* (Kirk 1998) is to be found with the chlorophytes in the PLANTAE. The microsporidians are in the FUNGI (Canning 1998, Cavalier-Smith 1998a) and the myxosporidians in the ANIMALIA (Siddall *et al.* 1995, Anderson 1998, Kent *et al.* 2001). Yet there are still (Corliss 2000a) some 83,000 protists embraced by the newly defined kingdom PROTOZOA, including extinct forms (e.g. among foraminiferans and radiolarians) known from fossil material; and probably many more are awaiting discovery.

The algae or algal protists have long been considered informally mainly as embracing pigmented (plus some non-pigmented and/or amoeboid) species classically assigned to such groups (often at the rank of class) as the cyanophytes (the blue-greens, but now recognized as prokaryotes), euglenoids, dinoflagellates, cryptophytes, chlorophytes (the greens), chrysophytes (the golden or yellow-greens), heterokonts (or chromophytes,

chromobionts), haptomonads (prymnesiophytes), phaeophytes (or fucophytes, the browns), rhodophytes (the reds), and charophytes (stoneworts, and now including the desmids), plus a few other small groups: see Andersen (1992, 1996). Such protists, never contained in a single top-level taxon of their own (having always been attached to a taxonomic subcategory of plants), are distributed among multiple kingdoms now, with many allocated to the kingdom CHROMISTA. [To be noted: The popular “stramenopiles” of Patterson (1989, 2002) and other phylogenetic cladists (e.g. Leipe *et al.* 1996) are basically the refined/redefined heterokonts of traditional phycologists and as such are thus mostly identical to the major portion of Cavalier-Smith’s (1981, 1986, 1989, 1998a, 2002) assemblage of the chromists. Therefore, in my opinion, the name “Stramenopila” of some authors is essentially a synonym of CHROMISTA. But see the recent scholarly reviews by Medlin *et al.* (1997) and Blackwell and Powell (2000).]

Mostly because of the incredible numbers of the chrysophyte diatoms (extant and extinct), the algal protists outnumber by several tens of thousands of species even the large assemblage of protozoan forms discussed briefly above. The chromists, today circumscribed as an independent kingdom, include about 107,000 species, but with >90% being diatoms. The groups now transferred (back) to the PLANTAE (essentially the greens, the reds, and the stoneworts *s. l.*) contain an additional 21,000 species; and those (the euglenoids *s. l.* and dinoflagellates) assigned to our PROTOZOA number some 6,000 species (Cavalier-Smith 1998a, Corliss 2000a).

The so-called lower fungi, conventionally a small group in the kingdom FUNGI (although they, like the algae, long represented just a taxonomic subcategory of plants), have in the past embraced the myxomycetes *s. l.*, the labyrinthulids *s. l.*, the oomycetes, the hyphochytrids, and the chytrids. The groups vernacularly just named and together totaling some 3,000 species are today quite widely separated, with only the chytrids, 900 species, remaining in the FUNGI proper; although to them, also as “lower fungi” of a sort, have now been added some 800 species of microsporidians, removed from their classical protozoan status.

The grand total of described-to-date protists, no matter how classified, reaches at least 213,000 species distributed among about three dozen phyla (see Table 2 of Corliss 2000a) belonging to the five eukaryotic kingdoms - the PROTOZOA, the CHROMISTA, the PLANTAE, the FUNGI, the ANIMALIA - recognized by Cavalier-Smith (1998a, 2002) and the author (Corliss

1998, 2000a). These kingdoms are not universally accepted, although their hierarchical ranked structures are convenient (“user-friendly”) for non-protistologically oriented biologists, for students, and for other scientists, as well as for indicating their relationships to groups of past conventional schemes of classification still in wide usage around the world.

The principal opponents to the serviceable taxonomic framework or Linnean System used in this review (one allegedly accepting paraphyletic and occasionally polyphyletic assemblages and susceptible to some subjectivity) are the cladists (champions of Phylogenetic Systematics), led mainly by Patterson (1994, 1999, 2002), who favor division of all organisms into *clades*, phylogenetic lines defined objectively by synapomorphies, innovative or unique derived characters or features (subjectively chosen?) held in common - or if absent, presumably secondarily lost - by all species comprising a given unit (Wiley 1981). The main problem to this alternative approach, as I see it, is the complete incompatibility of hierarchically arranged, named higher taxa with a system of clades, sister clades, etc. (Mayr 1990, 1997; Corliss 1994a, 1998, 2000a). Can the two approaches ever be integrated? Patterson (2002) himself confesses, “Unfortunately, we still lack the plans [to create a lasting systematic edifice] which will come in the form of a robust and probably molecular understanding of evolutionary relationships among [protozoan] taxa...”

I feel obliged to repeat my statement made eight years ago on pages of this journal (Corliss 1994a), “We are frustratingly trapped between existing classifications of protists that are recognized to be faulty and some future scheme (hopefully closer to the ideal natural system long awaited) not yet available.” Thus, also *still* true, “The current status of the megasystematics of the protozoa and their nearby relatives is unsettled, in a state of flux” (Corliss 1998). Ideal solutions seem to depend on revelations yet to appear.

As stated above, today I find it acceptable to consider the species of protists as distributable among all five kingdoms of the supraprotozoan (empire or domain) Eukaryota. The once attractive idea of an isolated/separate kingdom for the protists alone (called “PROTISTA” or “PROTOCTISTA”: see especially Whittaker 1969, Margulis 1974, Whittaker and Margulis 1978, Margulis *et al.* 1990, Margulis and Schwartz 1998) has been widely abandoned by research workers in protistology, pedagogically convenient and popular though it was (and often still is!): see Sogin *et al.* (1996), Bardele (1997), Ragan (1997), Andersen (1998), Cavalier-Smith

(1998a, 2002), Corliss (1998, 2000a), Lipscomb *et al.* (1998), Schlegel (1998), and other relevant earlier papers, including Rothschild (1989) on nomenclature for such a group.

For a little further clarification of the taxonomic matter of (my acceptance of) the appearance of protists in all five eukaryotic kingdoms, let me briefly make an additional comment or two here. Although *all* members of the kingdoms PROTOZOA and CHROMISTA may be considered as true protists, the protists or superficially protist-like forms often associated with the *other* kingdoms (FUNGI, PLANTAE, ANIMALIA, where mostly *multicellular* species predominate) fall into *three* broad categories. This point can be best illustrated using the fungi *sensu lato* as an example, but it is essentially true for the plant and animal assemblages as well. (1) There are true *fungus* protists or *protistan fungi* (e.g. chytrids and microsporidians, the latter formerly considered to be unique protozoa). (2) There are *fungus-like* protists (e.g. members of Cavalier-Smith's chromistan phylum Pseudofungi). (3) There are *protist-like* fungi (e.g. *Pneumocystis* and some species of *Saccharomyces*, two true fungal genera *not*, incidentally, closely related to one another).

These distinctions need to be kept in mind. One could add here that the ubiquitous protists even have superficial "look-alikes" (pseudo-protists) among the *prokaryotes*, too (e.g. species of the cyanobacteria, still often known as "the blue-green algae" and more frequently studied by phycologists than by bacteriologists).

Numbers and kinds of species of protists

As a kind of footnote to our taxonomic discussions on the preceding pages, I should briefly mention the "species problem" in protistology (see especially Andersen 2000), but it is a vast subject mostly beyond pertinence to the main topics of this paper. Taxonomists and ecologists, however, are keenly interested in the proper identification of the diverse forms involved in their researches, and arguments of ubiquity versus endemism, not trivial matters, depend in part on concepts of the nature of a species at the level of the lower eukaryotes. Such controversial problems are not made any easier by either the legitimate concerns of nomenclaturists (worried about synonymies, etc.) or the sobering predictions of census- or inventory-takers who estimate that protistan species-yet-to-be-described are probably at least two or three times greater than those named and cata-

logued to date. Finally, add to this the present furor over newly proposed codes of biological nomenclature, documents that purport to bring a measure of order out of the continuing chaos related to some of the just-listed woes (and also extending taxonomically upward well above the level of species).

Selected major works on those matters (above) are the following. For the "species problem" overall: Hammond (1995), Norton *et al.* (1996), Claridge *et al.* (1997), Howard and Berlocher (1998), Corliss (2000a), May (2000), Wheeler and Meier (2000). For ubiquity *versus* endemism: Finlay *et al.* (1996, 1998, 2001), Foissner (1997, 1998, 2000a,b), Finlay (1998), Finlay and Fenchel (1999), Foissner *et al.* (1999), Esteban *et al.* (2000, 2001), Finlay (2002). For discussions over changes of or in the codes of nomenclature: Hawksworth (1992), Patterson and Larsen (1992), Corliss (1993, 1994b, 1995, 2000a), Hawksworth *et al.* (1994), Blackwell and Powell (1999), Forey (2001), de Queiroz (2001).

GENERAL CHARACTERISTICS OF PROTISTS

The principal structural, physiological, and ecological features characteristic of protistan species overall separate them from other major assemblages of micro- and macroorganisms. But the "constellation of characters" principle (Corliss 1976) needs to be applied here. There is no single derived feature (a synapomorphy, if you will) conveniently setting them apart. If there were, then we should have justification for recognizing a unique kingdom here (e.g. "PROTISTA"), but the very fact that we do not have such an isolated character has been and is still the main reason for rejecting the Margulis proposal, first made years ago (Margulis 1974), of her artificial "kingdom Protoctista" (see above). Recall also that many protists are, simultaneously, *both* single, independent, complex cells *and* functionally complete, whole organisms: these terms are not mutually exclusive (Corliss 1989a). But no multicelled-multitissued organism can lay claim to exhibition of such a dual condition of life.

Thus we should consider briefly major morphological, ecological, physiological, behavioral, and evolutionary characteristics of protists, some of which indeed - alone or in combination - serve as unique features separating individual protistan phyla (and/or lower taxa) one from another and from members of still other phyla comprising the five kingdoms of eukaryotic organisms accepted by the writer. Space does not permit an exhaustive listing

of citations, but a limited number to the most recent and/or comprehensive publications appear in each of the following subsections.

Main morphological/structural features

Primarily because of continuous development of improvements in methods of microscopy and cytology and the relatively recent advent of molecular approaches, we can today analyze and amass data on scores of protistan characteristics of great value in comparative morphological and taxonomic studies. Such features range from body shapes (all kinds) and sizes (usual range 2–2000 μm , with notable exceptions to several meters in length) and exhibited symmetries (bilateral, radial, etc.) to nuclear numbers and nuclear characteristics (centrioles, spindle fibers, telomeres, etc.), kinds of endo- or exocytoskeletal structures, extrusive organelles (of diverse sorts), stalks (contractile with myonemes or non-contractile) and diverse other attachment or adhesive accoutrements, pigments, cortical alveoli, and contractile vacuoles to numerous kinds of specific cytoplasmic inclusions [e.g. endoplasmic reticulum, ribosomes, lysosomes, mitochondria/chondriosomes (with lamellar, discoid, vesicular, or tubular cristae), hydrogenosomes, Golgi bodies/dictyosomes, peroxisomes, plastids (e.g. chloroplasts, typically with stacked thylakoids and pyrenoid bodies), cyanelles, eyespots/stigmata, and carbohydrate/lipid/protein food reserves].

Even a brief list must be extended to include locomotory and feeding apparatuses, often involving pseudopodia of various kinds, flagella (some with mastigonemes), cilia and their subparts (including basal bodies/kinetosomes) and their compound derivatives (membranelles, cirri, etc.). Some protists have a highly structured oral apparatus (which may include sucking tentacles) for particulate food ingestion, while others are able to obtain nourishment by absorption directly through the cell membrane, with and without the use of exoenzymes. Still others have the machinery to engage in photosynthesis, an activity often essential for their very survival. Numerous species secrete or otherwise construct enveloping walls, sheaths, scales, thecae, loricae, tests, or shells, sometimes with “exit” pores and often of complex chemical and/or structural composition. Many such forms are easily fossilized (e.g. among dinoflagellates, foraminiferans, radiolarians, diatoms, ciliates). Cysts and/or spores, serving as dispersal or protective forms, are not uncommon in full life cycles of numerous species

from a large number of different taxa of protists (Corliss 2000b).

Organizationally, cells of protists may remain independent or be grouped together in chains, filaments, plasmodia, coenobia, or colonies (gregaloid, discoid, spheroid, arboroid/dendroid) of various kinds and sizes and for varying periods of time under specific environmental circumstances. Some colonial species (e.g. the peritrich ciliate *Ophrydium*: see Duval and Margulis 1995) are members of a consortium formed by sharing their own microcosm temporarily or permanently with other organisms. Other protists are truly multicellular, at least at some stage, but they seldom form more than one somatic tissue. Polymorphism is common in many protistan life cycles.

Such elaborations of cytoarchitectural diversity and complexity as those mentioned above - and the list is far from exhaustive - are, *in toto*, unique among all living things on Earth. Recall that they occur within - or are produced by - basically a *single cell* (see Figs 1-3).

Most of the structures listed are familiar to protistologists. But for the benefit of other readers and for details and examples of specific protistan taxa involved, the following publications by specialists are offered, works that also serve as excellent sources of numerous individual papers from both the recent and the older - often still indispensable in protistology - research literature: Grell (1973), Corliss (1979), Grassé (1984), Irvine and John (1984), Bold and Wynne (1985), Lee *et al.* (1985, 2002), Kristiansen and Andersen (1986), de Puytorac *et al.* (1987), Green *et al.* (1989), Sleigh (1989), Margulis *et al.* (1990), Harrison and Corliss (1991), Melkonian *et al.* (1991), Patterson and Larsen (1991), Perkins (1991), Hori (1993a,b, 1994), Müller (1993), Wetherbee *et al.* (1994), van den Hoek *et al.* (1995), Alexopoulos *et al.* (1996), Hausmann and Bradbury (1996), Hausmann and Hülsmann (1996), Lee (1999).

Ecological characteristics

Protists are cosmopolitan in overall distribution, although obviously symbiotic forms are limited to ranges of their hosts. In similar habitats or niches, many of the same species may be found in abundance worldwide. Most protozoa play roles as phagotrophs (particulate consumers), many algae as phototrophs (primary producers), most fungi as saprotrophs (decomposers). But there is considerable overlapping in nutritional modes

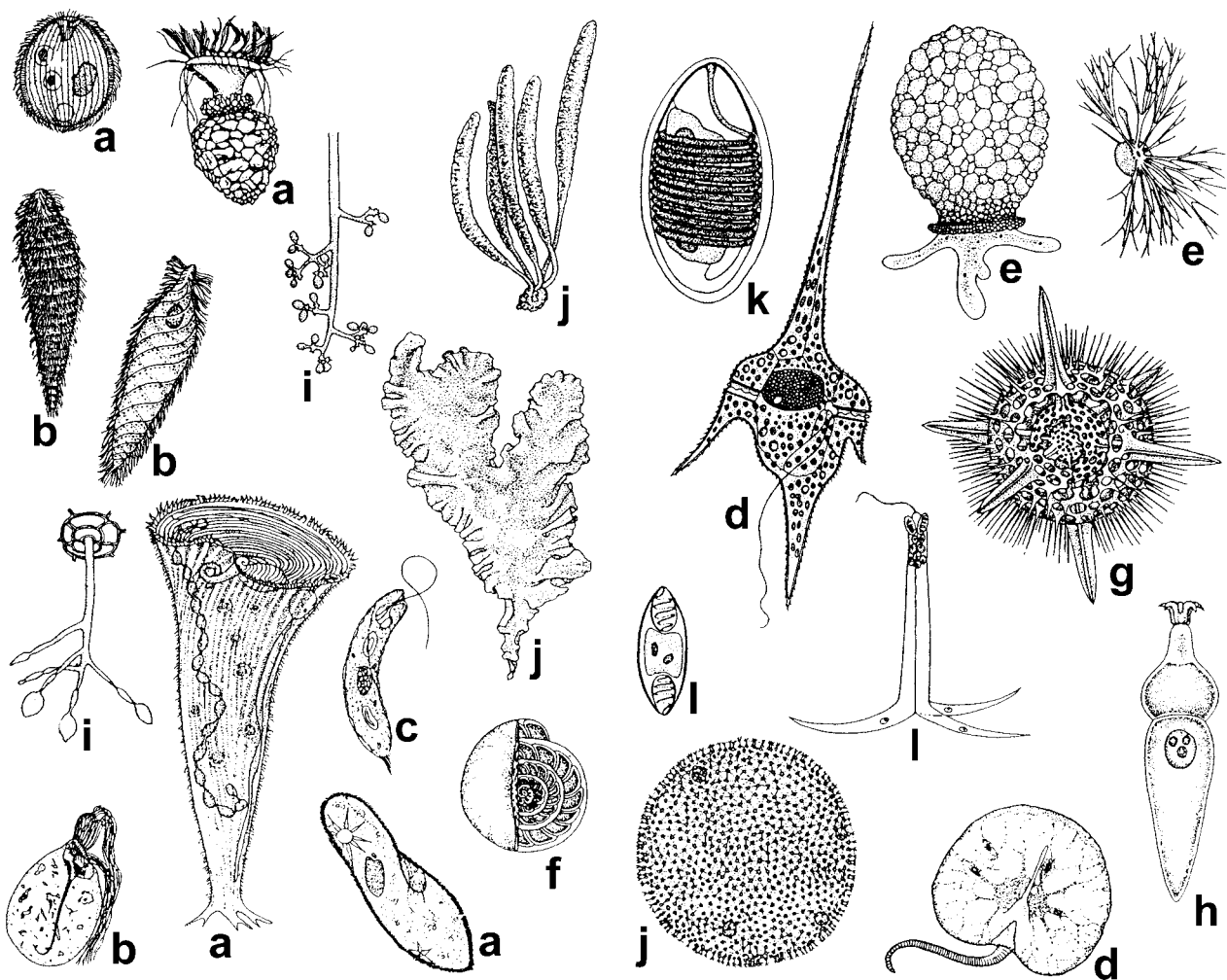


Fig. 1. Diversity among protists, as shown in figures (not drawn to scale) of selected representatives from the five eukaryotic kingdoms. Protozoan protists: **a** - Four examples of common free-living ciliates. **b** - Three symbiotic colorless flagellates. **c** - One photosynthetic euglenoid. **d** - Two free-living (upper figure freshwater, lower marine) dinoflagellates. **e** - Two testaceous amoebae, with differing pseudopodia. **f** - One foraminiferan (a nummulite shell). **g** - One radiolarian, showing complexity of skeleton. **h** - One cephaline gregarine sporozoon, with epimerite. Chromistan protists: **i** - Two saprozoic pseudofungi. Plant protists: **j** - Two marine algae (second known as "sea lettuce") and (lowest figure) one freshwater volvocine coenobium. Fungal protists: **k** - One microsporidian (spore, *greatly* enlarged). Animal protists: **l** - Two myxosporidians (a bipolar spore and a trivalved epispore). [All 23 figures modified from ones used in Corliss (1991) which, in turn, had been redrawn from multiple, widely scattered, sources in the protistological literature of the past century.]

among protists overall, and it is clear that the protistan role in ecosystem regulation stems from their diversity in ways of feeding as well as in body size and location (of aquatic forms) in the water column.

Free-living species have a very broad distribution, as mentioned above. They live as planktonic or benthic forms in oceans, seas, rocky intertidal pools, hydrothermal vents, tropical reefs, estuaries, fjords, bays and harbors, lakes, rivers, streams, creeks, subterranean waters, caves, thermal springs, briny pools, lagoons, bogs and marshes, freshwater ponds, rain puddles, swimming

pools, bird baths, ice and snow, desert sands, sewage treatment plants, reservoirs, beach sands and intertidal mud flats, sediments, moss, forest litter (and on bark and leaves of trees and bushes), arable soils, and so on. Bonafide endemic forms may not be as common as generally thought in the past, but more studies need to be carried out on this continuing controversial topic, one of major importance (see below). Note that habitats may include niches manifesting extreme ranges in temperature, oxygen, water and mineral content, salinity, pH, atmospheric pressure, radiation, etc. (see the informa-



Fig. 2. Scanning electron microscope image of a giant cannibalistic protozoan, a hypotrichous ciliate (*Onychodromus quadricornutus*), caught in act of devouring one of its small congeners (latter still visible on floor of gaping oral opening of the hunter). The predator has also sprouted spurs on its rear dorsal surface (a phenotypic change as defense/protection from still larger carnivores in its habitat) in response to a chemical signal emitted from its foes. [SEM kindly provided to the author (with permission to use at any time), some years ago, by protistological colleague Barry Wicklow, Saint Anselm College, Manchester, NH, USA.]

tive and stimulating review by Rothschild and Mancinelli 2001).

Symbiotic species (benign or pathogenic) are common in or on sponges, bryozoa, all kinds of arthropods, worms of diverse taxonomic sorts, members of all higher phyla and classes of invertebrates and vertebrates, wild or domesticated, including humans among the many mammals infected. Plants of all kinds also serve as hosts, everywhere. Free-living *or* symbiotic protists may themselves house ecto- or endosymbionts, viruses, bacteria, and/or other protists or even micrometazoa. One of the most fascinating relationships is that of protists (free-living in anaerobic habitats or parasitic in diverse hosts) that are physiologically dependent on methanogenic archaean bacteria dwelling within their cytoplasm as hydrogenosomes (of some sort).

There is abundant literature on the ecology of protists. Many references cited above (under morphology) contain information also relevant here. Some additional works on mostly free-living species: Poljansky and Cheissin (1965), Bamforth (1985), Dragesco and Dragesco-Kernéis (1986), Fenchel (1987), Foissner (1987, 1991), Anderson (1988), Patterson *et al.* (1989), Page (1991), Patterson and Larsen (1991), Sleight (1991),

Andersen (1992), Laybourn-Parry (1992), Vickerman (1992), Darbyshire (1994), John (1994), Fenchel and Finlay (1995), Sandgren *et al.* (1995), Finlay and Fenchel (1996, 1999), Finlay and Esteban (1998), Lee and Patterson (1998), Boltovskoy (1999), Wetzel (2001a). On mostly symbiotic forms: Kreier and Baker (1991-1995), Krylov (1993-1994), Ashford and Crewe (1998), Marquardt *et al.* (2000), Zimmer (2000). And on symbionts of protists: Jeon (1983), Hovasse (1984a,b), Preer and Preer (1984), Reisser (1986), Wang and Wang (1991), Görtz (1996, 2001), Hackstein *et al.* (2001, 2002).

Physiological, biochemical, and behavioral traits

The protists overall exhibit a great number of functions, reactions, tropisms, taxes, circadian and tidal rhythms, modes of food-gathering, means of locomotion, internal cycles, polymorphism, morphogenetics of fission, en- and excystation, and so on, sometimes unique, sometimes mimicking general known properties or reactions of some of their descendants, the multicelled/multitissued organisms of our biosphere. Nuclei have two main functions, replication of genetic material and release of information to the biosynthetic machinery of

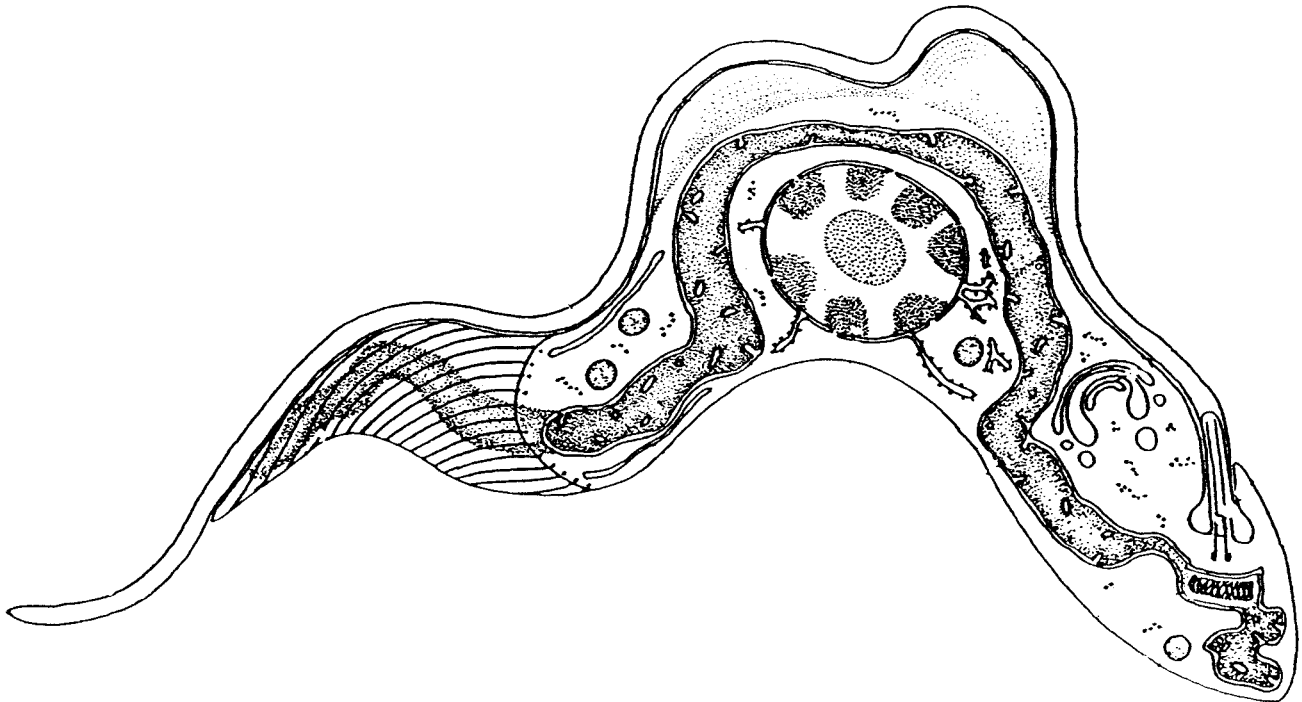


Fig. 3. Composite semidiagrammatic drawing from transmission electron micrographs of a trypanosome (*Trypanosoma rhodesiense*) highly virulent in humans. In the intermediate bloodstream form portrayed may be seen a diversity of (unlabeled) ultrastructural features characteristic of these protists (see review of their fine structure in Vickerman *et al.* 1991). The vector is the tsetse fly. [Figure modified from a drawing kindly provided to the author many years ago (with permission to use at any time) by protistological colleague Keith Vickerman, Glasgow University, UK.]

the cell. Exhibition of specialized adaptations to particular environments or habitats is widespread. Study of trophic dynamics of protists today involves sophisticated approaches at cellular, biotechnical, and molecular levels. In the case of symbionts or parasites, accommodating to changes in hosts' reactions is likely more common than yet recognized.

Numerous protists seem to be limited to asexual modes of reproduction, by binary or multiple fission (e.g. palintomy) or by budding. This does allow stability of an established genotype, at least for some generations. With respect to sexuality (whether cross- or self-fertilization is involved), diversity of patterns within or among major protistan groups has been claimed to dwarf that of the combined multicellular members of the kingdoms of plants, animals, and fungi (Dini and Corliss 2001). Stages of senescence and rejuvenescence, as well as "natural" death, have long been recognized (since the most insightful studies of Maupas in the late 1800s) in aging populations of some ciliated protozoan lines (Simon and Nanney 1979, Smith-Sonneborn 1981, Bell 1988, Dini and Nyberg 1993), although immortality is still consid-

ered a general feature of most species of protists. Temporary dormancy, in resting or transfer stages of the life cycle - so essential to viral and prokaryotic forms - is also common among many protistan groups (Henis 1987, Corliss 2000b).

Biochemical investigations on protists (Coombs and North 1991) continue apace: consult any protistological journal or scores of other specialized biological outlets that are published every month. Molecular studies are the current rage: see Raikov (1989) for a review of their early application to research on the nuclear genome of diverse protists, and papers in the symposium chaired by Orias (2000) for the state of the art today in genomic sequencing in protists. But works in both of these domains, biochemistry and molecular biology, are generally - except for their application to protistan systematics and phylogeny - well beyond coverage in the present overview.

In ethological research, the ciliates have probably been subjected to more study than any other major taxon of protists (Miyake 1996, Ricci 1996, Ricci and Erra 2001). In modern times, researches on their sometimes

highly complex pheromone- or gamone-induced characteristics run from the early perceptive observations by Grell (1951) on pairs engaged in a prenuptial dance of the hypotrich *Stylonychia* to the signal-induced defensive phenotypic changes in other hypotrichs described by Wicklow (1997) (see Fig. 2). Equally amazing are the reactions of some epibiotic/phoretic ciliates (e.g. among peritrich, chonotrich, and apostome groups) to invertebrate hosts' molting cycle hormones. The protists are induced to temporarily vacate their spots of attachment to the host's exoskeleton, which becomes unsuitable when shed; and then their motile stages - in due time - swim and reattach to the reconstituted host body (Corliss 1979).

Evolutionary and phylogenetic considerations

Some groups of the largely unicellular protists have surely served as transition forms (what I have called "gap-bridgers") from the structurally simpler bacterial prokaryotes to the complex multicelled-multitissued eukaryotes represented today by most contemporary species of plants, fungi, and animals (Corliss 1987, 1989b; Bardele 1997; Hausmann and Hülsmann 1999). During the last quarter of the past century, research on the phenomenon of eukaryogenesis has led many biologists to recognition of a distinct interdisciplinary field of protistology (Corliss 1986), an exciting and growing area exploiting fully what I have labeled "the protist perspective" (Margulis *et al.* 1990; Patterson and Larsen 1991; Patterson 1994, 1999; Cavalier-Smith 1995; Kristiansen and Cronberg 1996; Andersen 1998; Leadbeater and Green 2000).

In cases of many invertebrate and vertebrate animals and various plant groups, study of fossil lines has led to an understanding of evolution and evolutionary processes in those organisms. But in general this has not been possible for assemblages of protists, due largely to the relative simplicity of their remains - often limited to merely external coverings (tests, loricae, impregnated thecae, etc.) or silicifiable or calcifiable external or internal scales, spicules, spines, etc. Nevertheless, >100,000 protist species have been described solely as extinct forms (e.g. 89% of the foraminiferans, 65% of the radiolarians, 70% of haptomonads, 60% of diatoms, 55% of the dinoflagellates, 25% of prasinophytes, 15% of chrysophytes, 15% of rhodophytes, 2.5% of charophytes, and 2.5% of ciliates: Corliss 2000a), so they can hardly be ignored from consideration when one is illustrating protistan biodiversity and its usefulness in

the biosphere. Major references to literature on extinct protists are included in these compendia: Tappan (1980), Haynes (1981), Anderson (1983), Taylor (1987a), Round *et al.* (1990), Fensome *et al.* (1993), Lipps (1993), Green and Leadbeater (1994); and individual papers continue to appear in many appropriate journals.

Multiauthored considerations of evolution in diverse groups of mostly extant protists have recently appeared (e.g. Coombs *et al.* 1998, Katz 1999, Fast *et al.* 2002); but Cavalier-Smith (1990) has attempted to integrate the living and fossil evidence in his essay on "microorganism megaevolution," and Knoll (1992) has taken a geological perspective in recognizing a "terminal crown" group of eukaryotes in which he places the bulk of the protists. Barr (1992), Alexopoulos *et al.* (1996), and Beakes (1998) have presented mycologists' views of relationships among eukaryotic kingdoms; and Seravin (2001) has introduced the concept of "counter-directional morphological evolution" in his construction of a megasystem for protists and other eukaryotes. Pawlowski and Holzmann (2002) have published an up to date review on the molecular phylogeny of extant foraminiferans.

Highly visible in today's literature, whether the group under examination is at the lowest (strain, species) or highest (class, phylum, kingdom) taxonomic level, are molecular phylogenetic/evolutionary trees and cladograms - dramatic illustrations of protist biodiversity. Such dendrograms have been constructed employing most often the small subunit rRNA genes but also protein coding genes (see historical overviews in Sogin and Hinkle 1997, Schlegel 1998, Baldauf *et al.* 2000, Melkonian 2001, Cavalier-Smith 2002). All such approaches using molecular markers are said to have unique weaknesses as well as strengths (Edlind 1998, Lipscomb *et al.* 1998, Philippe and Adoutte 1998, Van de Peer *et al.* 2000). Yet, with eventual refinements, which Vickerman (1998) has cautiously implied are on the way, molecular-phylogenetic approaches should serve a major role in solving many of our currently vexatious problems in understanding the evolution of protists.

ROLES OF PROTISTS IN NATURE AND IN RESEARCH

Having demonstrated the taxonomic diversity and structural and functional complexity of protists (and the need to increase our knowledge in such areas), we now turn our attention to their actions and reactions with

respect to each other, to bacterial populations, and especially to the higher eukaryotes with which they share the biosphere. The pivotal roles played by protists in ecosystem functions, for example, are often simply not appreciated, as recently emphasized in a brief but significant note by Wetzel (2001b: a letter to the Editor of *BioScience* commenting on Corliss 2001).

It will generally be convenient to largely separate consideration of free-living protists (photosynthetic and non-photosynthetic) from that of symbiotic (especially parasitic) forms, although there is overlapping in functions 'twixt the two groups. And certainly members of such strictly artificial assemblages are not always separable on taxonomic grounds. Incidentally, of aid to experimental studies of protists of all kinds are the international culture collections of free-living and parasitic species, both of actively living populations of carefully identified, sometimes "pure" (axenic), strains and/or of cryopreserved material revivable on request. The availability of these authenticated stocks to researchers everywhere provides an indispensable source of highly reliable experimental material, model cells, if you will. For latest information on four major collections, see Nerad (1993), Starr and Zeikus (1993), Andersen *et al.* (1997), and Catalogue of the UKNCC (2001). Andersen (1996) and Norton *et al.* (1996) have supplied a highly useful list of the names and addresses of 73 culture collections around the world that maintain strains of algal protists mostly through perpetual subculturing of living stocks. See, too, Richmond's (1986) useful handbook on microalgal mass culturing techniques, Lee and Soldo's (1992) multiauthored protocols in protozoology, Simon and Nerad's (1996) review, and Colwell's (1975) early collection of workers' papers stressing the value of the accessibility of refined collections in all areas of biological research during that time's strongly emerging Era of Molecular Biology.

Type slide collections, of fixed and stained material, are also helpful to experimentalists, and to taxonomists and ecologists as well. Often type specimens are kept in personal collections, although major museums and herbaria in various countries are expected to house official material available internationally for comparative studies and identification purposes on proper request (e.g. see Cole 1994).

Roles and functions of free-living forms

Free-living (in the broadest sense) species, representing at least 85% of all non-fossil protists (therefore

>86,000 species, according to my counts and estimates: Corliss 2000a), occur in majority numbers in more than two-thirds of the major phyla. Representatives of such groups may exhibit, with overlapping, all the principal kinds of nutrition: ingestive, absorptive, photosynthetic.

Pigmented algal protists, if we include the prokaryotic blue-greens here, are said to provide 40% of global photosynthesis (carbon fixation and oxygen production) on Earth and nearly 100% of the primary production in marine systems (Andersen 1998). More poorly known is the contribution of algal photosynthesis in soils, forests, and tundra, but it is surely a major factor in life there as well (Ettl and Gaertner 1995).

Non-photosynthetic protists, particularly as represented by freely swimming flagellates and ciliates, are the most important consumers of bacteria in both aquatic and terrestrial ecosystems, having major functions in organic carbon utilization and nutrient cycling in general (Foissner 1987, Finlay and Esteban 1998, Wetzel 2001a). The ciliates, the most abundant phagotrophs in the biosphere (Finlay *et al.* 1998), exhibit high feeding rates on not only the bacterial populations but also on algae and other protists and even on the particulate detritus (the "snow" of lakes and oceans that includes fecal material from metazoa: Silver *et al.* 1984, Grossart and Simon 1993). The flagellates, typically smaller but much more abundant than ciliates and often mixotrophic in their nutrition, occupy both planktonic and benthic levels and feed on other microorganisms while also fixing carbon photosynthetically. According to figures in Wetzel (2001a,b), such flagellates are a dominant mortality factor for the bacterioplankton and frequently remove 20-60% of the algal picoplankton as well.

Protists are actively involved in essential food chains and webs, and thus in the well-known "microbial loop" of modern ecologists; as a result, they affect the health and very survival of a multiplicity of organisms including, ultimately, the carnivorous and herbivorous mammals (including humans) at the top of the nutritional chain. Flagellates and ciliates (less often amoebae), species typically <100µm in length, serve as both major decomposers and mediators of nutrient recycling in ecosystems (Patterson and Larsen 1991; Reid *et al.* 1991; Wetzel 2001a,b). Besides the open water systems of ponds and lakes and oceans, the many sewage disposal, waterworks, aquacultural, and soils operations in the world also benefit by this often perhaps little known protistan control of bacterial populations (Sieburth 1979, Capriulo 1990, Curds 1992, Arndt 1993, Foissner 1994, Sherr and

Sherr 1994, Anderson 1996, Foissner and Berger 1996, Moriarty 1997, Andersen 1998, Finlay and Maberly 2000, Ettl 2001).

Rhizopod, foraminiferan, and testaceous amoebae are involved in soil, fresh-water, and marine environments, too (Feest 1987, Foissner 1987, Arndt 1993, Ekelund and Rønn 1994, Wanner 1999, Finlay *et al.* 2001, Anderson 2002, Smith and Coupe 2002), but often in less well understood ways than are ciliates and flagellates. For the marine ecosystems especially, the revelations of Grell on the “plasmoidal protists of the sea” should be consulted (e.g. Grell 1985, 1995; Grell *et al.* 1990; Grell and Schüller 1991).

Some protists (free-living or symbiotic forms), like their metaphyten and metazoan descendants, are invasive species (Elton 2000), often causing a significant loss of biodiversity among native organisms inhabiting the locales invaded and thus upsetting the delicate balance of nature established there. A very recent example is to be found among species of the plant protist *Caulerpa*, a tropical green algal seaweed discovered just a year or two ago flourishing abundantly in a marine lagoon near San Diego, CA. Rather drastic control methods, intended to serve as a worldwide model, have been put in place to eradicate the fearsome intruder there (Withgott 2002).

The direct economic importance of free-living protists should also be briefly mentioned. Their involvements as food and industrial and medical products are many. Some 500 species of algae (processed or unprocessed, mainly seaweeds) are devoured by humans directly, with still other algal products appearing in commercially prepared foods (e.g. the gelatin in puddings, ice cream, etc.). And in modern mariculture, finfish and shellfish are routinely fed on phytoplankton. In industry, algal hydrocolloids are widely used; and recall that diatomite, fossilized diatom frustules, are the abrasive bases in many scrubbing and cleaning compounds, including toothpaste (Andersen 1996, 1998; Lembi and Waaland 1988). *Preersatz* blackboard chalk was composed mostly of tiny foraminiferan shells, mined directly from natural deposits. This brings to mind T.H. Huxley’s famous address, “On a Piece of Chalk,” delivered in 1868: now see the lecture/paper by J.J. Lee (1993) for *his* updated version on the same topic.

The helpful role of protists in soils, especially in restricting over-populations of bacteria and fungi and recycling nutrients, should not be overlooked, nor the

parts they play in biomonitoring and bioremediation of polluted waters and shores everywhere (Foissner *et al.* 1991-1995; Cairns *et al.* 1992; Wetzel 2001a). Habitat loss is caused mostly by human activities that result in widespread depauperization (often total loss) of species diversity, so conservation of “good” microorganisms is imperative if we are to maintain a beneficial balance in this world between nature and human beings.

Medically, algal agars and agaroses (phycocolloids) are widely used, especially in culture media and in specialized instruments (e.g. for gel electrophoresis, affinity chromatography, etc.). Human heart disease is reduced when certain fatty acids are included in the diet: these are available in/from marine fish, but their origin is in the phytoplankton (especially chrysophyte algal protists) consumed by the fish (Lembi and Waaland 1988). A large number of free-living protists, especially ciliates such as *Tetrahymena* (Frankel 2000) and a variety of pigmented and non-pigmented flagellates, are grown in axenic culture (see above); these organisms are particularly valuable in medical and biomedical research projects, both of an applied and experimental nature. They serve as perfect eukaryotic micro-size “guinea pigs” in a host of investigations ranging from toxicity studies to drug testing and beyond. They also have been used as assay organisms and pharmacological tools of value (Hutner *et al.* 1972), and as ideal microorganisms in modern molecular and genetic studies of diverse sorts (Gall 1986, Simon 1992, Asai and Forney 2000). Several growth factors (= vitamins) have owed their discovery long ago to researches on cultured strains of *Tetrahymena* and of the parasitic flagellate *Trichomonas* (see references in Hutner *et al.* 1972).

Exciting is the report, just now published in *Science* and in news outlets around the world, about a *very* recent decision of the National Human Genomic Research Institute of the U.S.A. The NHGRI has released an announcement that next on its Priority List of actions that will be taken is deciphering the genome of selected members of six taxonomically widely separated groups of organisms. Among these top chosen few are some protists: the ciliate *Tetrahymena thermophila* and several fungal or fungus-like protistan species.

The value of use of fossil protists in the petroleum industry needs to be noted. Carefully identified species of foraminiferans can be used to determine the ages of the strata penetrated by the exploring drills, thus serving as a guide to the potential richness of discovered oil and

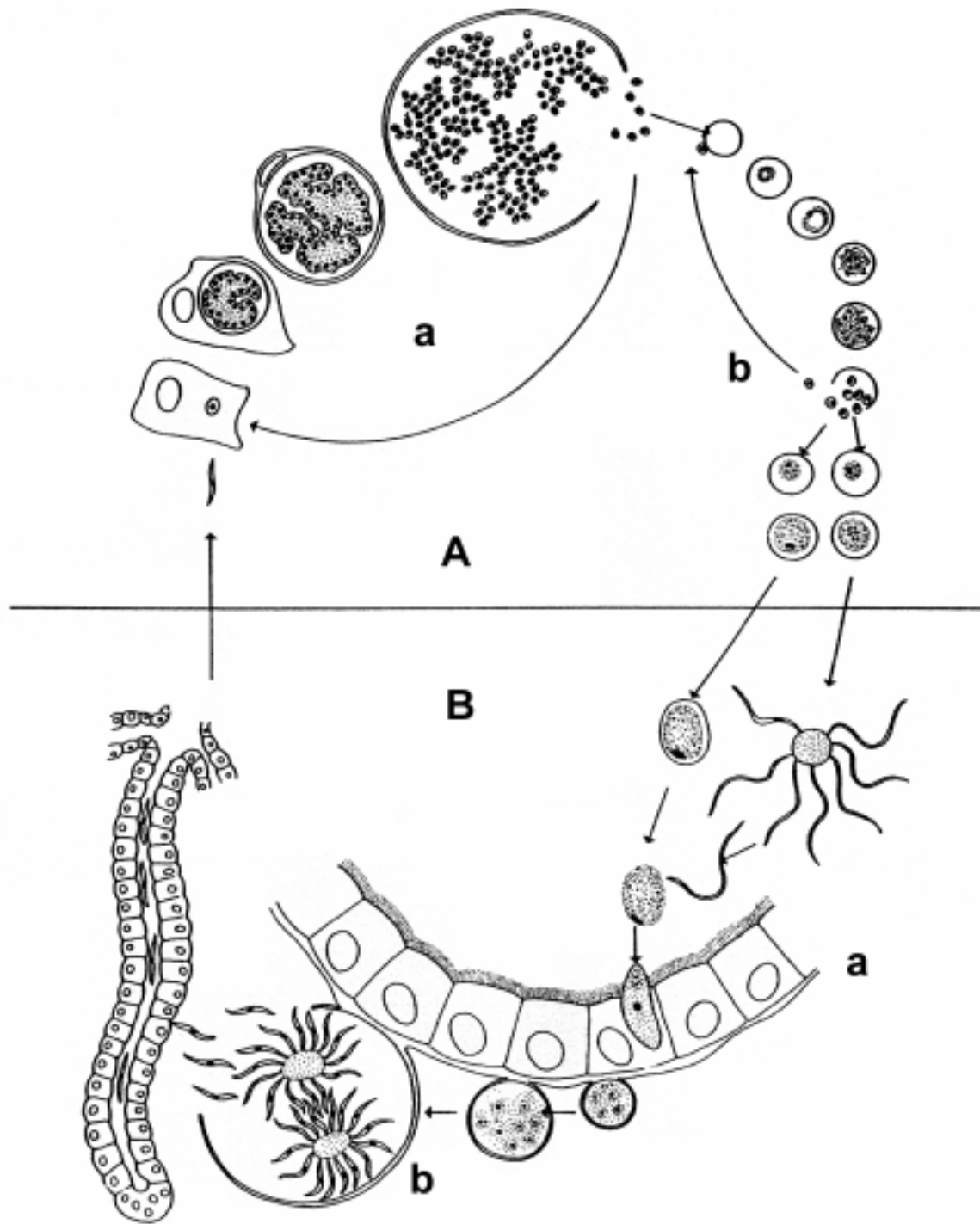


Fig. 4. Two-host life cycle of a sporozoan parasite, the malarial species *Plasmodium vivax* (pathogenic in humans), illustrating (semidiagrammatically, with unlabeled structural details but with all stages drawn roughly to the same scale) the complexities often found in host-protist relationships. **A** - Stages in the human host: **a** - Repeatable cycle in liver parenchyma cells; **b** - repeatable cycle in erythrocytes of the circulating bloodstream. **B** - Stages in the female anopheline mosquito vector, which has ingested macro- and microgametocytes along with the blood meal from her human victim: **a** - Production of macro- and microgametes in mosquito digestive tract and their fusion, followed by penetration of gut wall by motile zygote (ookinete); **b** - multiplication of sporozoites in the growing oocyst, rupture of oocyst membrane releasing sporozoites into hemolymph of mosquito body cavity, with their eventual migration to and penetration of the salivary glands, thus ready for inoculation through the mosquito proboscis into a fresh human host. [Figure modified from a drawing kindly provided to the author many years ago (with permission to use at any time), by protistological colleague Keith Vickerman, Glasgow University, UK.]

gas deposits (Cushman 1948). These commercially prized products - indispensable in an industrial world - are themselves derived from the breakdown, in aeons past, of fossilized photosynthetic protists (Andersen 1998).

Roles and functions of symbiotic forms

Because there is some confusion in the literature, I briefly offer here my own use or definitions of major terms for the principal kinds of relatively intimate partnerships of taxonomically distinct organisms, in this case, species of protists and their living hosts (other protists or, more commonly, higher eukaryotes). Symbiosis: a general overall term for such an association to any degree of closeness. Mutualism: an association of two organisms from which both the symbiont and the host derive a measure of benefit. Commensalism: an association in which only one partner, the symbiont, derives substantial benefit. Parasitism: usually a very intimate association in which the (ecto- or endo-) symbiont derives benefit at the expense of, but not necessarily fatal to, the host. If the host is also living a symbiotic existence, the phenomenon is known as hyperparasitism. Phoresis: in which one partner, the symphoriont or phoront, is carried about - and often dispersed - by the host without necessarily any (other) beneficial or destructive effect on either partner. Note that stalked protists, in particular, can also attach to substrates that are non-motile, even totally inanimate; the latter are not considered hosts, of course.

All such relationships described above may be temporary or permanent (depending on the organism/situation), obligate or facultative, and/or limited to certain stages in the life cycle of either partner. Diverse means of getting from an individual host to another, preferably a fresh one, are exhibited among parasitic protists: contamination of food or habitat, often by cysts or spores (very common), use of active (see Figs. 3, 4) or passive vectors (with or without multiplication therein), sexual intercourse, blood transfusions (and use of non-sterilized needles by drug-users), carnivory (including cannibalism), and transovarial or placental transfer.

Incidentally, symbioses may involve consortia of multiple organisms as well as often being confined to pairs, as mentioned briefly above under colony formation. Windsor (1997, 2000a) has called such an assembly a "biocartel," considering it a crucial unit in both ecology and evolution of all forms of life, a view reached independently but reminiscent of that of Margulis

(e.g. Margulis 1993, 1998; Margulis and Fester 1991).

Symbiotic species of protists, which reach a number of at least 14,000 (thus nearly 15% of all extant species) according to my counts (Corliss 2000a), occur throughout several phyla. The symbiotic membership of nine of these is practically 100%: the phyla Metamonada, Parabasala, and Sporozoa (syn. Apicomplexa) of the kingdom PROTOZOA; Opalinata, Labyrinthomorpha, and Pseudofungi of the CHROMISTA; Chytridiomycota (chytrids) and Microsporidia of the FUNGI; and Myxozoa (myxosporidians) of the ANIMALIA.

Symbiotic, especially parasitic, protists continually wreak havoc on humans' alleged control of the world's environment. Annually there are tremendous losses of farm produce, ranging from poultry and livestock to fruit orchards and grain and vegetable crops. In the latter cases, recall the massive epidemics (and their far-reaching consequences) of potato and grape blights in Ireland and France in the middle to late 19th century. Wildlife - both animal and plant - is also affected, of course. Economically, hundreds of millions of dollars are lost yearly in the U. S. A. alone through only partially controllable diseases of multicellular organisms, such as farmed birds, mammals, and plants (Levine 1973, 1985; Marquardt *et al.* 2000). Similar losses are encountered in the finfish and shellfish industries from the harmful actions of still other parasitic species (Perkins 1987, Lom and Dyková 1992, Hoffman 1999). And near-shore plants (e.g. eel grasses) and algae are often depopulated through destructive actions of fungal and fungus-like protists (e.g. chytrids and oomycetes).

Coccidian sporozoa (particularly species of the widespread genus *Eimeria*: Levine 1988, Allen and Fetterer 2002) and a number of flagellates (e.g. *Histomonas*) are among the main culprits (from the human point of view) in cases of poultry diseases. Myxosporidians, animal (cnidarian) protists often with two hosts (fish and an invertebrate: a larval chironomid "blood worm" or a bryozoon or some marine oligochaete annelid), are responsible for epidemics among marine and freshwater salmonid (and a few other) fishes around the world, with disastrous outbreaks occurring in netpen and maricultured commercial populations (Kent *et al.* 2001).

Blooms of (especially) algal protists are destructive in many aquatic ecosystems (Chrétiennot-Dinet 2001). Their occurrence when polluted lakes and coastal shores become eutrophic has long been viewed with dismay:

eutrophication usually reduces species biodiversity by the choking out of other life forms sharing the biotope (Norton *et al.* 1996, Wetzel 2001a). But their involvement in elimination of shellfish and finfish populations in the seas is compounded by their infection or contamination (via their toxins: note the “red tide” outbreaks of principally dinoflagellate species in many locations around the globe) of such hosts which, on consumption, can sometimes bring death to the non-alert human consumer (Taylor 1987a, Hallegraeff 1993).

However, by no means are all symbiotic associations involving protists of a negative nature. While the better known mutualistic and phoretic examples are at least mildly beneficial, other - often more intimate - associations are even more helpful to the host. For example, the commensalistic protozoa thriving in body cavities and digestive tracts of many an animal, from insects to mammals (including humans), may be indispensable to a normal healthy life of their hosts. Besides often supplying essential growth factors, their control of potential overgrowth by other microorganisms, notably bacteria, is a highly beneficial activity. As known for nearly three-quarters of a century (Cleveland *et al.* 1934), termites and wood-feeding roaches require a population of protozoan protists to aid in digestion of the cellulose ingested by the host. In the case of ruminants (Hungate 1975), the associated protozoa go even further than just ingesting/digesting plant tissues; they also control the deleterious (if too large in population) prokaryotes by their grazing action (Bonhomme-Florentin 1994, Hobson and Stewart 1997, Russell and Rychlik 2001). Other cases involving non-pigmented protists could be cited.

Symbiotic photosynthetic algae are widespread in organisms extending from other protists through various invertebrate groups of animals, not to mention their serving as the all-important phycobiont moiety with certain fungi to give us lichens. The associations of fungal or fungus-like protists with roots of trees and other plants (including many cultivated legumes) are indispensable to the hosts' survival. In the intimate associations of algae with corals, the protists' photosynthetic activities are of primary importance to the whole marine reef community. In all such beneficial cases described above, plus the roles of endosymbionts in organismic evolution overall, discussion of the vast topics involved would require much more space than is possible here; but see the following: Margulis (1981, 1993, 1996), Goff (1983), Jeon (1983), Lee and Corliss (1985), Taylor (1987b), Margulis and Fester (1991), Sapp (1994),

Melkonian (1996), Hackstein (1997), Ossipov *et al.* (1997), Cavalier-Smith (2000b, 2002), Corliss (2000c), Inagaki *et al.* (2000), Margulis *et al.* (2000), Windsor (2000a), Zhang *et al.* (2000).

Protozoan parasites of human beings

Although a few algal protists may be directly or indirectly involved in causing occasional medical problems for humans (including protothecosis, a human skin lesion disease caused by the green alga *Prototheca*: see Jassby 1988), the most serious disease-causers are found among the protozoan protists. Some 70-75 species are “at home” in various parts of the human body, ranging from skin, teeth, nostrils, and eyes to favored more sheltered sites such as the digestive tract and associated structures, the circulatory system, sex organs, and brain tissue (Krylov 1993-1994; Ashford and Crewe 1998; Marquardt *et al.* 2000; Zimmer 2000). Naturally, all of such an impressive number are never found in a single person at the same time.

Some of these symbiotic protist species are much more common or more widely distributed than others; some are considerably more virulent than others; a few may ordinarily be relatively harmless commensals or even mutualistic forms; and a few others only opportunistic or occasional parasites. Nevertheless, I would guess that the high total of implicated species given above will come as an unpleasant surprise to most readers. Also, many people may not appreciate the impact of certain parasitic protozoa on the geopolitical history of the world. Consider the premature death (age 33), from malaria, of Alexander the Great, putative/poised conqueror of all known parts of Europe, Africa, and Asia in the 4th century B. C.

The periodically issued “death tables” of the World Health Organization (e.g. see WHO Report 2000) continue to show several protozoa high on the list as causative agents of some of the most serious human diseases in the world. Following the AIDS virus (causing nearly 2,700,000 deaths in 1999; and 25.3 million people were HIV-positive, with 4.7 million of the infections new, in the year 2000: UNAIDS/WHO 2000) and the bacterium responsible for tuberculosis (*ca* 1,700,000 fatalities in 1999), comes malaria (Fig. 4), caused by species of the sporozoan genus *Plasmodium* (Garnham 1966, an enduring classic in the field; Sherman 1998): well over one million deaths are recorded by WHO for the year 1999. Some 300-500 million people are affected by malarial world-wide, weakening many of those not killed

to the extent that they are susceptible to often fatal infections by various other parasites. Mainly because the blood-dwelling plasmodia involved (including those of the most deadly species, *P. falciparum*) have become resistant to drugs currently available and thus far no effective vaccine exists, the toll from malaria is alarmingly on the rise (Honigsbaum 2002). In fact, the spread of drug resistance in recent years by many pathogenic microorganisms is a looming crisis for the entire human race (Hunter *et al.* 1995).

For our struggle against the highly pathogenic *P. falciparum*, Hoffman (2000, 2001) is optimistic that we may finally be approaching an era in which we can hope to develop effective malaria vaccines. We have been aided greatly by our growing knowledge of the sequences of the genomes of *Homo sapiens* (the host), *P. falciparum* (the parasite), and *Anopheles gambiae* (the vector), by our industrious application of modern techniques of proteomics, molecular immunology, and vaccinology, and, finally, by our ability today to integrate the millions of resulting pieces of computer-generated data through the use of bioinformatics.

Hosts overall do not “stand still” while parasites evolve within their bodies: they, too, are constantly evolving, often developing counter-measures to offset gains made by their sometimes long-ago invaders (Kawecki 1998). At the same time, the members of the consortium or biocartel can co-evolve - or become extinct (Windsor 1996, 2000b), thus upsetting the balance of nature - as a unit, once again demonstrating the complexity of associations involving symbiotic protists.

Other tropical diseases of humans, for example, those caused by species of the flagellated protozoan genera *Trypanosoma* (see Fig. 3) and *Leishmania* (African sleeping sickness, Chagas’ disease, and visceral and cutaneous leishmaniases: see Hoare 1972; Lumsden and Evans 1976, 1979; Warren 1993), are also responsible for tens of thousands of deaths annually. Like malaria, insect vectors (tsetse flies, triatomid bugs, and sandflies here, rather than mosquitoes) transmit the parasitic organisms, both blood and tissue invaders. Effective vaccines, once again, are currently unavailable and other approaches to reducing human pain and fatalities from such afflictions are constantly being sought (Dumas *et al.* 1999). In addition, these trypanosomatids and other major protozoan parasites (including *Sarcocystis*, *Toxoplasma*, and *Trichomonas*) are participants in zoonoses (Hoare 1962), that is, diseases common to both humans and other mammals with the latter, often with

less debilitating infections, serving as reservoir hosts in the wild.

What WHO identifies, loosely, as “diarrheal diseases” cause over two million deaths per annum. One of the causal agents heavily involved is the species *Entamoeba histolytica*, along with other amoebae, and outbreaks are not limited to tropical areas of the world. Protists such as *Blastocystis*, *Balantidium*, *Dientamoeba*, *Giardia*, and *Trichomonas* could be listed here, too. With respect to deaths from the pandemic AIDS (see above), one should recall that compromising of the host immune system by the presence of HIV makes the body more susceptible to all sorts of infections by various *other* organisms, including bacteria, the protist-like fungus *Pneumocystis*, and several opportunistic protozoan parasites (including species of amoebae, flagellates, and sporozoa). Thus, the ultimate death of some persons with AIDS may have been caused by the activities of such *additional* pathogens, the discovered presence of which has been on the increase ever since the early recognition of the AIDS virus some 20 years ago (Kaplan *et al.* 2000).

CONCLUDING REMARKS

The biodiversity and biocomplexity of presently recognized species of the protists appear to be much greater than is generally appreciated by many biologists, let alone the laity. Their intimate and numerous interactions with other organisms, including humans, make imperative our becoming better informed about the multiple roles of these microorganisms in nature. Already many times more speciose than the bacteria and viruses combined and arguably equally ubiquitous, their effects—both beneficial and deleterious - on our biosphere cry out for considerable further investigation.

Thus, in today’s timely quest for a sustainable world (Reaka-Kulda *et al.* 1997, Raven and Williams 2000), it behooves us to learn more about the indispensable *eukaryotic* microorganisms that have been, are, and will continue to be an integral part of life, as we should mostly like to conserve it (Wilson and Perlman 2000), on our presently endangered planet.

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