

Why the World Needs Protists!¹

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ABSTRACT. In this brief review, literature references are given to researchers—involving diverse species of protists—that support the author's firm conviction that the biological world of today absolutely requires the presence of numerous of these generally small and unicelled organisms if it is to survive. Examples supplied come from areas within the field of protistology *sensu lato* as widely separated as basic phycological research on photosynthesis and protozoological/medical/biomedical investigations on malaria and other pathogens of human beings. Emphasis is primarily on the most relevant works of the past 10–15 years, although historically highly significant papers of older vintage require at least indirect—and occasionally direct—citation.

Key Words. Algae, biocartels, historical references, other eukaryotic groups containing protistan taxa, protists, protozoa, symbionts, taxonomic, ecological, and evolutionary implications.

APPROPRIATE on this Golden Anniversary of the founding of the *Journal of Protozoology* (name changed to the *Journal of Eukaryotic Microbiology* in 1993) are reviews of advances in research on the protists during the past 50 years, including revelation of the roles played by our journal in publicizing such advances. Contents of the present paper—lead-off one in the Symposium planned over a year ago for the joint meeting in Oregon, in June 2003, of the Society of Protozoologists and the Phycological Society of America—naturally overlap to a certain, although generally very limited, degree the specific topics of those that follow it, *viz.*, the ones by Jeremy Young (2004) on culture collections, David Asai (2004) on dynein function in *Tetrahymena*, Melanie Cushion (2004) on comparative genomics of *Pneumocystis*, David Caron (2004) on contributions of molecular biology and immunology to protistan ecology, and Mark Farmer (2004) on a revised classification of the protists, not to mention the rousing introductory remarks by then Society President Lynn Rothschild (2004).

Chief organizer of the Symposium, Wayne Coats of the Smithsonian Environmental Research Center in Edgewater, Maryland, deserves special appreciation from the seven participants mentioned above for his always encouraging aid and his sage advice.

Finally, our gratitude also to *Journal* Editor-in-Chief Denis Lynn (2003, 2004) who, along with able Managing Editor Portia Holt, has most kindly set aside issue number 1, of Volume 51 of our illustrious *Journal*, as the Jubilee Number, half of it to fittingly contain (most of) our full-paper contributions in celebration of advances in protozoology and protistology during the past half-century.

EXPLOSION IN THE RECENT LITERATURE

In very recent years, even just months ago, we have been witnessing an explosion in the biological (and beyond!) literature with respect to topics involving the biodiversity, biocomplexity, and conservation of organisms, both prokaryotic and eukaryotic in body organization, with attention to their complex interrelationships and their effects on the well-being of each other (which includes human beings, at the alleged top of the Tree of Life). Entire organizations, both national and international (some are governmental agencies), have sponsored major

meetings and special symposia concerned with interactions of different groups of organisms, often with inclusion of attention to protistan species. Journals have invited panels of researchers to contribute articles, whether or not based on participation in specific society-sponsored symposia. New journals, giving sole attention to the subjects mentioned above, have sprung up within the past decade and a half.

Respected outlets of research on molecular, cellular, microbiological, and protistological (phycological, protozoological, fungal) topics have expanded coverage of sophisticated “cutting-edge” papers, many featuring free-living or symbiotic ciliates, flagellates, sarcodines, or sporozoa. Widely publicized newsletters and web-sites have appeared. Encyclopedias have added or expanded their entries on protists. Fresh editions of biological textbooks have added sections on the roles in Nature of these generally minute and often unicellular eukaryotic microorganisms.

In support of such positive statements, consider the following scores of selected citations to the burgeoning literature in the areas or outlets mentioned above. They are arranged alphabetically by author, editor, or convener and are presented below in several separate subsections for greater ease in reading. Most of them have been published within the past 10–15 years, many since the turn of the 21st century. Some, if edited books with separate chapters, may be cited (again) in appropriate subsequent sections of this paper, although, more likely, only certain chosen individual contributions *within* them are *there* directly mentioned. A few specific older references (often classics in their fields which, in my opinion, are still of lasting pertinence today) are not neglected. Lead author's name, date of the work, and an indication of the general subject matter are given on the following pages; and, of course, in the Literature Cited section more complete information is to be found if the reader desires to have it.

Collections of papers in book-form or as special section of a journal. First, let us consider recent collections of papers, invited and often of a review nature, which appear as books or as a special section of some specific journal. These works deal wholly or to a significant degree with protistological information. For example, see: G.H. Coombs et al., editors (1998) [one of seven books dealing solely with protists sponsored and published by or for the Systematics Association of UK: the others, in chronological order, are Irvine and John (1984), Leadbeater and Riding (1986), Green et al. (1989), Patterson and Larsen (1992), Green and Leadbeater (1994), and most recently Leadbeater and Green (2000)]; E.L. Cooper, organizer (2003), symposium on Comparative Immunology; R.A. Dewel & J.P.S. Smith III, organizers (2003), symposium on New Perspectives on the Origin of Metazoan Complexity; F.W. Harrison & J.O. Corliss, editors (1991), Vol. 1 of book series on Microscopic Anatomy of Invertebrates; L.A. Katz, editor (1999a), Evolutionary Relationships Among Eukaryotes; B. Kirsop & D.L.

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Hawksworth, editors (1994), *The Biodiversity of Microorganisms and the Role of Microbial Resource Centres*; J.J. Lee et al., editors (2002), *An Illustrated Guide to the Protozoa*, 2nd ed., 2 vols.; C.A. Lembi & R.J. Waaland, editors (1988), *Algae and Human Affairs*.

Also see: L. Margulis, J.O. Corliss et al., editors (1990), *Handbook of Protoctista*; L. Margulis & R. Fester, editors (1991), *Symbiosis as a Source of Evolutionary Innovation*; L. Margulis et al., editors (2000), *Environmental Evolution: Effects of the Origin and Evolution of Life on Planet Earth*, 2nd ed.; L. Margulis and K.V. Schwartz (1998), *Five Kingdoms: an Illustrated Guide to the Phyla of Life on Earth*, 3rd ed.; K.J. Peterson & G.E. Budd, organizers (2003), symposium on *The Cambrian Explosion: Putting the Pieces Together*; P.H. Raven & T. Williams, editors (2000), *Nature and Human Society: the Quest for a Sustainable World*; M.L. Reaka-Kulda et al., editors (1997), *Biodiversity II: Understanding and Protecting Our Biological Resources*; L. Rothschild & A. Lister, editors (2003), *Evolution on Planet Earth: the Impact of the Physical Environment*; I.W. Sherman, editor (1998), *Malaria: Parasite Biology, Pathogenesis, and Protection*; A.M. Sugden et al., “introducers” (2003), “The Tree of Life,” a multi-authored Special Section of *Science*, an AAAS publication, Vol. 300 (issue of 13 June 2003), with considerable attention to prokaryotes and “lower” eukaryotes (e.g. protists); K. Vickerman et al., editors (2000), *A Century of Protozoology in Britain* (see especially the broad-but-detailed historical overview by Vickerman 2000b, alone, on p. 16–128); M.H. Wake & J.S. Pearse, organizers (2003), symposium on *The Promise of Integrative Biology*; E.O. Wilson & F.M. Peters, editors (1988), *BioDiversity* (the National Academy of Sciences, USA, publication that “kicked off” the worldwide awareness of the planet Earth’s need to appreciate its dependence, its very survival, on maintenance of the diversity of life populating it).

Commercially “independent” publications including textbooks. Secondly, let us consider publications that might be viewed as “independent” from a commercial point of view—i.e. they are generally *not* financially or “spiritually” directly supported or sponsored by a specific society or institution. This category includes some textbooks, the authorships/editorships and titles of which are interspersed alphabetically among the other entries below. Today there are growing numbers of all such productions on the market, serving as major sources of information on protists (along with that on other organisms), often stressing the ecological *sensu lato* relationships of unicellular and multicellular populations to each other and to the physical world in which they and we live.

For example, see: C.J. Alexopoulos et al. (1996), *Introductory Mycology*, 4th ed.; A.F. Alimov, editor (2000), *Protista* (in Russian); R.S.K. Barnes, editor (1998), *The Diversity of Living Organisms*; D. Bhattacharya, editor (1997), *Origins of Algae and Their Plastids*; H.C. Bold and M.J. Wynne (1985), *Introduction to the Algae: Structure and Reproduction*, 2nd ed. (aging but still most useful); J.O. Corliss (1979), *The Ciliated Protozoa: Characterization, Classification, and Guide to the Literature*, 2nd ed. (out of date; but 3rd ed. with D.H. Lynn, under contract with expected appearance in 2004); T. Fenchel and B.J. Finlay (1995), *Ecology and Evolution in Anoxic Worlds*; L.E. Graham and L.W. Wilcox (2000), *Algae*; B. Groombridge and M.D. Jenkins (2002), *World Atlas of Biodiversity* (with emphasis on education and conservation); K. Hausmann & P.C. Bradbury, editors (1996), *Ciliates: Cells As Organisms*; K. Hausmann and N. Hülsmann (1996), *Protozoology*; K. Hausmann & B.P. Kremer, editors (1994), *Extremophile: Mikroorganismen in ausgefallenen Lebensräumen*; D.L. Kirk (1998), *Volvox: Molecular-Genetic Origins of Multicellularity and Cel-*

lular Differentiation (see also Kirk 2003); A.H. Knoll (2003), *Life on a Young Planet: the First Three Billion Years of Evolution on Earth*; R.E. Lee (1999), *Phycology*, 3rd ed.; J.H. Lipps, editor (1993), *Fossil Prokaryotes and Protists*.

Also see: L. Margulis (1993), *Symbiosis in Cell Evolution*, 2nd ed.; L. Margulis (1998), *Symbiotic Planet: A New Look at Evolution*; W.C. Marquardt et al. (2000), *Parasitology and Vector Biology*, 2nd ed.; E. Mayr (1997), *This is Biology: The Science of the Living World*; D. Moore (2001), *Slayers, Saviors, Servants, and Sex: An Exposé of Kingdom Fungi*; S. Paracer and V. Ahmadian (2000), *Symbiosis: An Introduction to Biological Associations*, 2nd ed.; D.J. Patterson & J.O. Corliss, editors (1989), *Progress in Protistology* (4th and last vol. in short-lived series; 1st–3rd, years 1986–1987, were edited by Corliss & Patterson); P. de Puytorac et al. (1987), *Précis de Protistologie*; M. Ridley (2000), *Genome: the Autobiography of a Species in 23 Chapters*; L.J. Rothschild & A. Lister, editors (2003), *Evolution on Planet Earth: The Impact of the Physical Environment*; C.D. Sandgren et al., editors (1995), *Chrysochyte Algae: Ecology, Phylogeny and Development*; J. Sapp (1994), *Evolution by Association: A History of Symbiosis*; J. Seckbach, editor (2002), *Symbiosis: Mechanisms and Model Systems*; Yun-fen Shen et al. (1995), *Monitoring of River Pollution* (most recent in series of research monographs by Shen and students or young colleagues *and* mostly in English; preceded by three huge others appearing in years 1976, 1983, 1990, all solely in Chinese, on freshwater protozoa—and a few other “lower” invertebrates—associated mostly with stream pollution, wastewater treatment plants, and biomonitoring techniques); Yun-fen Shen, editor-in-chief (1999), *Protozoology* (first general textbook of protozoology ever published in People’s Republic of China and entirely in Chinese language!); M.A. Sleight (1989), *Protozoa and Other Protists*, 2nd ed. (aging, but still very useful); W. Song, editor-in-chief (1992), *Progress in Protozoology* (in Chinese); F.J.R. Taylor, editor (1987a), *The Biology of Dinoflagellates*; S.C. Tiwari & S.D. Sharma, editors (2002), *Microbial Diversity: Status and Potential Applications*; C. van den Hoek et al. (1995), *Algae: An Introduction to Phycology*; R.G. Wetzel (2000a), *Limnology: Lake and River Ecosystems*, 3rd ed. (good attention to roles of protists); E.O. Wilson (2002), *The Future of Life*; E.O. Wilson and D.L. Perlman (2000), *Conserving Earth’s Biodiversity*; C. Zimmer (2000), *Parasite Rex: Inside the Bizarre World of Nature’s Most Dangerous Creatures* (emphasizes the “downside” of symbiotic relationships).

Key separate/individual papers, invited reviews not in book-form. Thirdly, and finally, I invite the reader to note several key separate papers (*not* appearing as books), often lengthy single-authored invited reviews rich in bibliographic references to the literature practically to the date of their own paper’s appearance. The longish list, starting in the *second* paragraph below, deliberately *excludes* any works—by the same authors—that are parts of *any* of the edited books and collections cited in the two preceding subsections of this overview offering. But a goodly number of *such* papers would certainly, themselves, also qualify for simultaneous inclusion *here*. The latter should at least be given brief consideration now, but (to save space) without citation of their titles (but many are available in my Literature Cited section, below). So, your attention is directed to the immediately following inserted paragraph. Alphabetically, the authors—a number of the works of whom *are* cited, as appropriate, in subsequent sections of the present paper—include A. Adoutte, R.A. Andersen, C.L. Anderson, O. Roger Anderson, C. Bacchi, G.F. Ball, S.S. Bamforth, G.W. Beakes, J. Beisson, E.C. Bovee, P.C. Bradbury, G. Brugerolle, E.U. Canning, T. Cavalier-Smith, R.E. Clopton, G.H. Coombs, J.O. Corliss, G. Deroux, J.D. Dodge, J. Dragesco, M.J. Dykstra,

T.D. Edlind, J.T. Ellis, C. and J. Febvre, T. Fenchel, B.J. Finlay, I. and W. Foissner, J. Frankel, J. Grain, J.C. Green, J.H.P. Hackstein, R.P. Hall, D.L. Hawksworth, J.R. Haynes, P. Heywood, K. Hiwatashi, G.G. Holz, Jr., D.S. Horner, R. Hovasse, C.J. Howe, S.H. Hutner, K.W. Jeon, J.F. de Jonckheere, E.S. Kaneshiro, M.L. Kent, G.W. Kidder, P. Kugrens, M. Laval-Peuto-Moreau, J. Laybourn-Parry, B.S.C. Leadbeater, J.J. Lee, R.E. Lee, G.F. Leedale, N.D. Levine, J. Lom, D.H. Lynn, R.M. May, E. Mayr, S.M.M. McCready, M.F. Melkonian, J.-P. Mignot, Ø. Moestrup, M. Müller, D.L. Nanney, J.R. Nilsson, C. O'Kelly, E. Orias, N.R. Pace, F.C. Page, D.J. Patterson, J. Pawlowski, F.O. Perkins, D.R. Pitelka, H. Philippe, J.R. Preer, H.R. Preisig, D.M. Prescott, L. Provasoli, P.H. Raven, B. and P. Sattir, F.L. Schuster, G.R. Seaman, D. Simberloff, E.M. Simon, A.G.B. Simpson, M.A. Sleigh, E.B. Small, M.L. Sogin, T.M. Sonneborn, M.-O. Soyer-Gobillard, O. Tendal, W. Trager, J. Vávra, K. Vickerman, R.A. Virginia, N. Vørs, D.H. Wall, N.E. Williams, E.O. Wilson, R.J.M. Wilson. Note that many of the persons just cited have already had *other* works of theirs cited in preceding—as well as in following—sections of the present paper. Not surprisingly, a goodly number of the names are of contributors to the J.J. Lee et al. (2002) volumes of the 2nd edition of the "Illustrated Guide to the Protozoa," persons authoring chapters mainly on the taxonomy (and general biology) of all genera of a given group plus a brief historically-oriented account of knowledge (often limited to the pre-1997 literature) on that group. The majority of the *additional* names included above come, again not surprisingly, from the *other* recent major book, the chapters of which are devoted solely to protists, viz., Coombs et al. (1998) on evolutionary relationships among protozoa, a production whose pre-WW-II's unforgettable predecessor was the classic "Blue Bible," edited by G.N. Calkins and F.M. Summers (1941).

To return (after the interruptive but necessary paragraph immediately above) to my listing of key individual papers with titles supplied for readers' benefit, see: R.A. Andersen (1992), Diversity of eukaryotic algae; R.A. Andersen (1998), What to do with protists?; R.A. Andersen (2003), A historical review of heterokont phylogeny; S.L. Baldauf et al. (2000), A kingdom-level phylogeny of eukaryotes based on combined protein data; T. Cavalier-Smith (1993), Kingdom Protozoa and its 18 phyla; T. Cavalier-Smith (1998a), A revised six-kingdom system of life; T. Cavalier-Smith (2002), The phagotrophic origin of eukaryotes and phylogenetic classification of Protozoa; M.J. Chapman et al. (2000), Centrioles and kinetosomes: form, function, and evolution; J.O. Corliss (1989), The protozoan and the cell: a brief twentieth century overview; J.O. Corliss (1992), Historically important events, discoveries, and works in protozoology from the mid-17th to the mid-20th century (includes, among biographies of other—relatively recent—leaders, brief accounts of our very earliest protistological heroes, such as van Leeuwenhoek, Joblot, Hill, Baker, Trembley, O.F. Müller, Ehrenberg, Dujardin, Gruby, Lambl, De Bary, Nägeli, Rabenhorst, Kützing, and C.A. and J.G. Agardh, explorers who fearlessly marched across uncharted landscapes 200+ years ago motivated only by their restless zeal and their burning curiosity about thithertofore unseen life, and generally with only an early type of microscope as faithful travel companion); J.O. Corliss (1994), an interim utilitarian ("user-friendly") hierarchical classification and characterization of the protists; J.O. Corliss (2000b), A commentary on D.A. Windsor's recent heuristic biocartel concept; J.O. Corliss (2002), Biodiversity and biocomplexity of the protists and an overview of their significant roles in maintenance of our biosphere; B.J. Finlay (2002), Global dispersal of free-living microbial eukaryote species; B.J. Finlay and G.F. Esteban (1998), Freshwater protozoa: biodiversity and

ecological function; B.J. Finlay et al. (1996), Biodiversity at the microbial level: the number of free-living ciliates in the biosphere; W. Foissner (1994b), Soil protozoa as bioindicators in ecosystems under human influence; W. Foissner (1998), An updated compilation of world soil ciliates (Protozoa, Ciliophora), with ecological notes, new records, and descriptions of new species; W. Foissner et al. (1999), Identification and ecology of limnetic plankton ciliates; M.W. Gray et al. (1999), Mitochondrial evolution; E.S. Kaneshiro (2002), Is *Pneumocystis* a plant?; A.H. Knoll (1992), The early evolution of eukaryotes: a geological perspective; S. Köhler et al. (1997), A plastid of probable green algal origin in apicomplexan parasites; J.J. Lee & J.O. Corliss, symposiarchs (1985), Symposium on symbiosis in protozoa.

Also see: L. Margulis (1996), Archaeal-eubacterial mergers in the origin of Eukarya: a phylogenetic classification of life; L. Margulis et al. (2000), The chimeric eukaryote: origin of the nucleus from the karyomastigont in amitochondriate protists; M. Melkonian (2001), Systematics and evolution of the algae. I. Genomics meets phylogeny; M. Müller (1993), The hydrogenosome; M. Müller (1996), Energy metabolism of amitochondriate protists, an evolutionary puzzle; T.A. Norton et al. (1996), Algal biodiversity; C.J. O'Kelly (1993), Relationships of algae to other protists; E. Orias, symposiarch (2000), Symposium on the genomics of free-living microbial eukaryotes: state of the art and promise; D.J. Patterson (1994), Protozoa: evolution and systematics; J. Pawlowski and M. Holzmann (2002), Molecular phylogeny of Foraminifera—a review; M.A. Ragan (1997), A third kingdom of eukaryotic life: history of an idea; I.B. Raikov (1995a), Structure and genetic organization of the polyploid macronucleus of ciliates: a comparative review; I.B. Raikov (1995b), The dinoflagellate nucleus and chromosomes: mesokaryote concept reconsidered; L.J. Rothschild (1989) Protozoa, Protista, Protocista: what's in a name?; J.D. Silberman et al. (2002), Retortamonad flagellates are closely related to diplomonads—implications for the history of mitochondrial function in eukaryote evolution; P.C. Silva (1993), Continuity, an essential ingredient of modern taxonomy.

Also see: A.G.B. Simpson and D.J. Patterson (2001), On core jakobids and excavate taxa: the ultrastructure of *Jakoba incarcerata*; A.G.B. Simpson and A.J. Roger (2002), Eukaryotic evolution: getting to the root of the problem; A.G.B. Simpson, A.J. Roger et al. (2002), Evolutionary history of "early-diverging" eukaryotes: the excavate taxon *Carpodidomonas* is a close relative of *Giardia*; A.G.B. Simpson, R. Radek et al. (2002), How oxymonads lost their groove: an ultrastructural comparison of *Monocercomonoides* and excavate taxa; M.L. Sogin (1991), Early evolution and the origin of eukaryotes; M.L. Sogin et al. (1996), Ancestral relationships of the major eukaryotic lineages; F.J.R. Taylor (1987b), An overview of the status of evolutionary cell symbiosis theories; F.J.R. Taylor (2003), The collapse of the two-kingdom system, the rise of Protistology and the founding of the International Society of Evolutionary Protistology (ISEP); W. Trager (2002), Loose ends: axenic culture, parasitophorous vacuoles, bird malaria; Y. Van de Peer et al. (2000), An updated and comprehensive rRNA phylogeny of (crown) eukaryotes based on rate-calibrated evolutionary distances; K. Vickerman (1992), The diversity and ecological significance of Protozoa; K. Vickerman (1997), Landmarks in trypanosome research; R.H. Whittaker and L. Margulis (1978), Protist classification and the kingdoms of organisms; A. Wier et al. (2002), Spirochete and protist symbionts of a termite (*Mastotermes electrodominicus*) in Miocene amber; D.A. Windsor (2000a), Biocartels—units of ecology and evolution based on host-symbiont interrelationships; C.R. Woese (1994), There must be a prokaryote somewhere: microbiology's search

Table 1. Protistan phyla/divisions assignable to the five non-bacterial kingdoms of life recognized and tentatively accepted by the author (data mostly from Corliss 2000a, 2002). See text and also Cavalier-Smith (1998a,b, 2000a, 2002) for some details.

Kingdom	Principal phyla/divisions includable in each	Comments
PROTOZOA	Apicomplexa (= Sporozoa), Dinzoa, Ciliophora; Euglenozoa, Sarcodina: Rhizopoda/Amoebozoa, Archameobae, Mycetozoa, Foraminifera; Actinopoda: Heliozoa, Radiozoa; Zooflagellata: Percolozoa, Trichomonadida, Parabasala	First three grouped phylogenetically and taxonomically as the Alveolata by many workers. Euglenids here, but other familiar greens elsewhere in Chromista or Plantae.
CHROMISTA	Chrysophyta, Diatomeae, Phaeophyta, Raphidophyta, Cryptomonada, Bicosoecae, Dictyochae, Pseudofungi, Labyrinthomorpha, Haptomonada, Opalinata	Chromista itself is essentially the equivalent of Patterson's Stramenopila or the Chromophyta/Heterokonta of the older botanical/phycological literature.
PLANTAE	Chlorophyta, Prasinophyta, Glaucophyta, Rhodophyta, Ulvophyta, Charophyta	Bulk (ex. Chrysophyta <i>s.l.</i> and euglenids) of traditional greens and reds are here; blue-greens are bacteria, thus not considered algae.
FUNGI	Chytridiomycota, Microspora	Both phyla only recently here.
ANIMALIA	Choanozoa ⁺ , Myxozoa	Choanoflagellates a "missing link" between "higher" Animalia and Fungi; myxosporidians, with pluricellular stages, better classified as primitive invertebrate.

for itself; C.R. Woese et al. (1990), Towards a natural system of organisms: proposal for the domains Archaea, Bacteria, and Eucarya.

TAXONOMY AND PHYLOGENY OF "PROTISTS"

Before writing further about the "protists," I need to give the reader at least a very brief idea of what I mean by the term. Aware of (the title of) the paper, appearing elsewhere in this volume, by respected colleague Mark Farmer (2003), I do not intend to encroach on his topic. We may or may not agree on some solutions to the knotty problems involved, ones made even knottier by recognition that the very definition of a species (Claridge et al. 1997, Hammond 1995, Stork 1993, Wheeler and Meier 2000)—a relevant factor—remains controversial at the level of the so-called "lower" eukaryotes (Andersen 2004, Corliss 2000a, Finlay 2002, Finlay and Esteban 2001). And I'll not even mention here the myriad associated nomenclatural problems, but see pertinent references to modern critics—of cladistics as well as systematics—in the bibliographies of Corliss (1995, 2002); and see the fourth paragraph of this section (below).

Suffice it to say here that I am still in general agreement with conclusions of mine quite fully discussed recently in several major review papers (Corliss 1994, 1998, 2000a, 2002), that the protists *sensu lato* appear in all five of what I consider to be acceptable kingdoms (names shown totally in CAPITAL letters here and in Table 1) of eukaryotes, viz., the PROTOZOA (as refined/redefined by Cavalier-Smith, 1998a,b, 2002), the CHROMISTA (of Cavalier-Smith, but basically the stramenopiles of Patterson, 1994, 1999, 2002, or even the emended chromophytes or heterokonts of the older botanical literature: see Andersen, 2003, for an invaluable history of names for this entire group of what I'm calling the chromists *sensu lato*, and Ben Ali et al. 2002, for its evolutionary relationships as determined by combined rRNA analyses), the FUNGI, the PLANTAE, and the ANIMALIA. See Table 1 for a simple listing, without nomenclatural details, of protistan (or protistan-like) phyla or divisions that I tentatively assign to these five kingdoms of organisms (also see Cavalier-Smith 2000a for some relevant details).

Incidentally, one could even say that the protists have "look-alikes" among the prokaryotes, in appreciation of the fact that "blue-green algae" (cyanobacteria) are still called that by many botanists and are undeniably more frequently studied by

phycologists than by bacteriologists. So they are not entirely excluded from this paper.

Serious critics of any or all taxonomic schemes or evolutionary arrangements involving the protists still abound today. To cite but a dozen or so of the most recent works of some such persons directly, see Blackwell and Powell (2000), Hausmann and Hülsmann (1999), Hawksworth et al. (1994), Lipscomb et al. (1998), Melkonian (2001), Patterson (2002), Philippe and Adoutte (1998), Ragan (1997), Schlegel (1998, 2003), Seravin (2001), Sogin et al. (1996), Van de Peer et al. (2000), Vickerman (1998).

My own concern about the taxonomic arrangement of protistan groups in Table 1 is that, while trying to adapt/apply the "protist perspective" (Corliss 1986) to knowledge of modern times, I am still conscientiously resolved to bridge, for clarity and in a user-friendly way (for the benefit of teachers, students, general biologists, and scientists from other areas), the ever-widening gap between more classical schemes of classification and very recent proposals, especially those of cladistic phylogeneticists.

By the way, the incredible size range of protists—from species with a diameter of only 1 μm to the giant seaweeds or elongated slime molds with lengths of several+ meters—still bothers some biologists, whose feelings we must ignore. Great size differences exist in much more confined taxonomic eukaryotic metazoan/metaphytan units (shrew/whale among mammals, hummingbird/ostrich among birds, tiny plants to redwoods, etc.) and even among prokaryotic organisms (e.g. among cyanobacteria).

KINDS OF BIOTIC INTERACTIONS

In the "good old days" it was easy to recognize seemingly clear-cut distinctions concerning actions/reactions among all organisms. Roughly, they were either free-living (and fed upon other free-living forms, and/or themselves served as food for others in the chain) or lived symbiotic/parasitic lives (endo- or ecto- in their location in/on hosts and showing different degrees of beneficence or harmfulness to said hosts). Excellent and popular little books, such as those by William Trager (1969), titled "Symbiosis," and John Baker (1969), "Parasitic Protozoa," informed non-specialists about the general subject, including interactions of symbionts and hosts, taxonomy of the protists, etc., with numerous well chosen illustrations of points made. The acknowledged classic in this genre of handbooks, however,

remains the earlier production by Maurice Caullery (1905), “Le Parasitisme et la Symbiose” (not to mention *his* predecessor De Bary 1879!). Rapid advances in biochemical and ultrastructural studies, plus the then newer field of molecular biology, allowed Baker and Trager—and others of that era (e.g. authors of standard textbooks of parasitology) to predict (often quite correctly) some of the surprises that lay in store for the “symbiology” of the 1970’s and beyond.

Today, with far more sophisticated approaches in morphological (including ultrastructural and molecular techniques), physiological, chemical, and ecological researches, we realize that the picture is far from being so simple as it seemed 40–50 years ago. Independence or dependence or interdependence of organisms is directly or indirectly affected by multiple factors of their environment *sensu lato* and is subject to minor or major fluctuations over time due to causes ranging from changes in climate or other physical factors to genetic shifts in their genomes or in those of nearby others (including intimately associated organisms: see the following paragraph). Examples are highlighted in the remainder of this brief overview paper, where we find that the two (and the number could be larger!) major categories I have chosen to try to present separately (phototrophic + anoxic forms vs. symbiotic *s.l.* forms) have a strong—and thus inconvenient!?!—overlapping in contents, as will be noted. However, the examples described (all too briefly) serve as strong support of my general theme of the indispensability of protists in sustaining all life on the planet Earth.

A further word needs to be said concerning special “endosymbionts” which also are, or have become, “normal” cytoplasmic or nuclear constituents of the (host) cell. The idea of an extracellular origin for “regular” cell organelles has been around for scores of years: see Mereschkowsky (1905, 1910) for chloroplasts, Wallin (1927) for mitochondria, Margulis (= Sagan 1967) for cilia and flagella (and later papers, even the nucleus); and see subsequent early reviews on “eukaryogenesis” in Raven (1970), Stanier (1970), D.L. Taylor (1970), F.J.R. Taylor (1974), and especially the highly stimulating—if, in part, controversial—book-length treatment by Margulis (1970). These and other works started an “explosion in the literature” not unlike the “second” explosion of the 1990’s (and still in progress) claimed here on early pages of *this* paper. The present situation’s explosion has been brought about in large measure by the tremendous refinements in probing the molecular genetics and thus the molecular intimacies of the bodies and cell parts of bacteria and protists in relation to invaded host cells and *their* nuclei and cytoplasm.

Recall also that human beings everywhere are intricately involved in “biotic interactions,” our lives and actions intertwined with those of practically all other organisms and with the physical world we share as well (Penn 2003, Wilson 1984, 2002). After all, for either better or worse, our very presence/existence as a part of Nature makes imperative our inclusion in studies of the mysteries of Nature, as Max Planck, a Nobel Laureate in Physics, is said to have once philosophized early in the 20th century.

Some additional literature references to the matters mentioned briefly in this section are made in the following sections. And the reader has already seen a number of pertinent ones among the review works cited on early pages of this paper.

As we move to abbreviated treatment of major examples of the “indispensability” of protists, I must sorrowfully mention that lack of space precludes a deserved inclusion in *this* paper of still another important area in which these microorganisms play a role also invaluable to the welfare of the world, viz., their use as research tools—microscopic “guinea pigs,” if you will—in problems ranging from studies of pollution to inves-

tigations of diseases in multicellular organisms including humans. In such respects, it is very good news to report that the number of protist genera now with a sequenced genome of one or more of its species has risen dramatically since my little tally of only two years ago (Corliss 2002). Thanks primarily to two protistological colleagues—Bob Andersen and Geoff McFadden—I can here add (most with certainty) algal genera *Chlamydomonas*, *Emiliania*, *Thalassiosira*; (zoo)flagellate genera *Giardia*, *Leishmania*, *Trypanosoma*, and very likely, by now, one or more species of trichomonads; mycetozoon/myxomycete cellular slime mold genus *Dictyostelium*; amitochondrial rhizopodial/foraminiferan genera, one or two; unique fungal genus *Pneumocystis*; microsporidian/fungal genus *Encephalitozoon*; sporozoon/apicomplexan genera *Babesia*, *Cryptosporidium*, *Eimeria*, *Plasmodium*, *Theileria*, *Toxoplasma*; ciliate genera *Paramecium*, *Tetrahymena*, plus possibly some stichotrichs. Such protists are research tools *par excellence!*

Hopefully, fellow Symposium author Jeremy Young (2003) will include some aspects of the worthiness of protists in research on problems of “higher” organisms in his treatment of the value of culture collections; and references of my own occur occasionally on later pages (e.g. under my extensive Section on Symbiosis, below). But I am inserting the following brief paragraph in order to add mention *here* of several *other* relevant and helpful reviews of recent years.

A number of phycologists, mycologists, and protozoologists (not to forget the bacteriologists for whom cultures have long been an absolute requirement) have lately been strongly (re)stressing the advisability, even the necessity, of carefully monitored collections of living protists and accurately labeled slide collections of fixed material for use in comparative taxonomy and in a wide range of basic research projects that are directly related to the welfare of all life on Earth. Painstaking and continuous maintenance of such collections is imperative, and adequate funding of such activities is required. High quality results from on-going and proposed ecological, nutritional, medical, and molecular studies of protists (properly using existing collections) are benefiting—or are expected to benefit—all of us mightily. See Aescht (1994), Andersen (1996, 1998), Andersen, Blackburn, et al. (1997), Andersen, Morton, and Sexton (1997), Catalogue of the UK National Culture Collection (UKNCC) (2001), Cole (1994), Foissner (1994a), Foissner and Berger (1996), Jassby (1988), Lee and Soldo (1992), Lembi and Waaland (1988), Nerad (1993), Norton, Melkonian, and Andersen (1996), Potter et al. (1997), Starr and Zeikus (1993), and many relevant references within these several publications. The classic here is E.G. Pringsheim’s (1946) little book on culturing of free-living and mostly photosynthetic protists; for various mostly parasitic forms, see the series of volumes by Hutner and Lwoff, years 1951–1964 (first one edited by Lwoff 1951, alone; last by Hutner 1964, alone) and historically important references therein. For freshwater algae and cyanobacteria, a still-used compact book is that of 40 years ago by G.W. Prescott (1962). Finally, for an excellent up-to-date summary on culture collections of protists around the world and their continuing and growing value in diverse modern research fields, see the news item in the journal *Protist* last year by B. Surek (2002), who was reporting on the highly successful international meeting held, fittingly, at (Pringsheim’s) Göttingen University, in September 2002.

INDISPENSABILITY OF PHOTOOXYTROPIC AND ANOXIC PROTISTS

Dominating role of photosynthetic protists. If one were limited to mention of a single “*most significant*” role that protists play in support of all life on the planet Earth today, an

excellent choice would surely be the exhibition of photosynthesis by many of them. Without the activities of chlorophyll-possessing algal and protozoan protists (forget trees and other green things that, after all, are only minor evolutionary offshoots of algae!), survival of everything else, even the hardy and ubiquitous insects and the truly cosmopolitan bacteria of the kinds identifiable today, could not last beyond a few (or few hundred?) centuries.

We have learned only in recent years that these oxygenic phototrophic protists (including the prokaryotic blue-green algae)—often of such an inconspicuous size yet with such striking biochemical and physiological versatility—provide 40% of the primary productivity on Earth in essentially fresh-water environments and almost 100% in marine ecosystems. One needs to keep in mind that a huge percentage of our planet's surface is covered by water. The oft-cited solid figure of 71%, exclusive of freshwater and terrestrial sources, was carefully calculated by Andersen (1992). Water constitutes 99% of the living space on Earth according to Norton et al. (1996). And the figures rise to > 99% (W. Foissner, pers. commun.) if one includes the bound-water around soil particles (including those of "dry" desert sands and covering mats there), on plant and animal surfaces (above and below ground), in/on ice and snow particles, and including/counting anoxic as well as oxygenated biotopes or niches of the world.

Relatively weak is our knowledge of protists of soils *sensu lato* compared with that of those in open aquatic biotopes, freshwater and marine. But modern researches, especially those being carried out today in highly industrious laboratories mostly in Australia, Great Britain, and central Europe, are showing that the contributions of eukaryotic microorganisms in soils are far from negligible with respect to biogeochemical cycles and nutrient recycling in general. For example, see Bernard and Fenchel (1995), Bernard, Simpson, and Patterson (2000), Esteban et al. (2000), Ettl (2001), Feest (1987), Finlay (2001, 2002), Finlay and Esteban (1998, 2001), Finlay et al. (2001), Finlay et al. (1996), Foissner (1987, 1988, 1992a,b, 1993, 1994a-c, 1995, 1996, 1997, 1998, 1999a,b, 2000a,b), Foissner, Agatha, and Berger (2002), Foissner, Blatterer, and Foissner (1988), Song and Wilbert (1989), Tiwari and Sharma (2002). Recall that the classic work in this area was H. Sandon's (1927) little book, in which attention was really first called to the abundance and significant roles played by the protists in soils from around the world. Grandori and Grandori's (1934) large monograph deserves mention as well; and Foissner's (1987) long invited review paper may be recognized, in effect, as the *modern classic* in the field.

The roles of protists in restricting bacterial and fungal growth in such habitats are also highly significant, whether the protists are light-sensitive or anaerobic/anoxic. An excellent source of information and of references to the literature is Wetzel's (2001a) book. That noted limnologist also treats subjects mostly beyond space-consideration here: for example, the major roles of freshwater microbial phototrophs in blooms (phenomena that can upset the delicate balance of Nature wherever they occur) and their positive uses in biomonitoring and bioremedial operations of many kinds. With respect to blooms, including especially toxic ones in near-shore *marine* biotopes (where effects on both fish and shellfish—and their human consumers—seem to be on the rise), see the important review by Hallegraeff (1993).

With additional regard to both organismal biodiversity in soils and bioremedial work, the recent paper by Wall and Virginia (2000) should be also consulted, keeping in mind that these biologists were considering primarily metazoan invertebrates and treating the problem from a conservationist's point

of view. See, too, the recent papers by Anderson (2002, 2003) on the involvement of free-living sarcodinids (amoebae and amoebflagellates) in maintaining an ecological balance among soil microbial communities. Incidentally, often forgotten as "soil communities" are the more or less permanent "tree-top islands" of accumulated soil, litter/debris, and various "epiphytic" (often wind-borne) organisms including, of course, protists of diverse types (algae, protozoa, lower fungi: some likely unique species), in the canopies of tropical rain forest trees, several meters up from the ground (Wardle 2002). More identification work for the belabored taxonomists, whose ranks are already being depleted by increasing lack of grant monies sufficient to carry out their research programs.

The information given in immediately preceding paragraphs, some of it surely quite startling to the general biologist, emphasizes the indispensability of light-absorbing protists to maintenance and survival of life on Earth, and I have hardly yet mentioned (mostly reserved for below) their significant roles in *symbiotic* associations. *Other* general references of great help to the reader would be the series of reviews and/or research papers (always so rich in pertinent citations to the literature) of prolific phycologist-protistologist R.A. Andersen, often published with his students and/or other young colleagues. For example, for selected quite recent ones clearly relevant here, see Andersen (1992, 1998, 2003), Andersen, Saunders, et al. (1993), Karlson et al. (1996), Kawachi et al. (2002), Medlin et al. (1997), Norton, Melkonian, and Andersen (1996), Saunders et al. (1995), Wetherbee, Andersen, and Pickett-Heaps (1994).

I am omitting detailed consideration here of the "blue-green algae" (more properly, the cyanobacteria) and some other groups truly bacterial in nature, but might very briefly remind the reader that the phototrophs (plus anoxic forms as well) among *them* have always also served important roles in the Earth's current and past survival.

Dominating role of anoxic protists. If one were limited to mention of a single "*most significant*" role that protists play in support of all life on the planet Earth, *another* excellent choice would be the exhibition of the *anoxic* way of life. These protists (and numerous bacteria, not particularly covered here) are often associated with other organisms (especially the so-called evolutionarily "higher" ones) and are thus mostly left to consideration in the inevitably overlapping large "Symbiosis" section, which follows. But also see brief remarks about roles of free-living soil *sensu lato* protists of all kinds, above.

There is space here only to give brief mention to the fascinating (though somewhat still controversial and of possible polyphyletic origin from ancient methanogenic bacteria) hydrogenosomes, symbiotic organelles occurring in amitochondriate and often anaerobic/anoxic species of taxonomically diverse groups of protists ranging from various parasitic flagellates and fungal forms to free-living amoebflagellates and ciliates (Brugerolle and Müller 2000, Cavalier-Smith 1998b, 2000b, 2002, Fenchel and Finlay 1995, Finlay and Esteban 1998, Finlay and Fenchel 1993, Hackstein et al. 2002, Martin and Müller 1998, Müller 1993, 1996, 1998, Vickerman 2000a). Another exciting organelle, the apicoplast of certain sporozoa, derived independently from quite a different symbiont, fits somewhat into this same "mysterious" category. It is treated below in the "Symbiosis" section (mostly in subpart "endosymbiogenesis"): see references to its literature there.

Highly significant is the fact that anoxic protists (and bacteria) played indispensable roles in altering Earth's environment chemically in aeons past when oxygen had not even been a significant part of the atmosphere (but once an oxygenated atmosphere appeared, anoxic areas still remained, of course). Other kinds of life, many long since extinct, could not have

survived in their day without such anoxic forms' not only leaving appropriate gases (methane, N₂O, sulfuric acids, etc.) but also contributing to the build-up of sedimentary rocks, shells, calcium (coral reefs, invertebrate skeletons, etc.), etc., some such deposits destined to become liquid or solid fuels in much later aeons (see chapters in Lembi and Waaland 1988).

Appropriate to add here is at least brief mention of the *extremophiles* among protists. Protistan species as well as numerous bacteria are, or await to be, found in extremely harsh (at least from our point of view) types of habitats: very hot springs, very cold (cavities in ice) locales (e.g. polar pools), high pressure places (e.g. oceanic hydrothermal vents), volcanoes, very dry deserts, mat-covered sulfurous muds, very wet and smelly bogs, etc., etc. (see Hausmann and Kremer 1994, Horikoshi and Grant 1998, Rothschild and Mancinelli 2001, and references within these relatively recent publications). Regarding a specific "cold" locale, it is well to keep in mind that 40% of the Earth's land mass is covered with snow for at least a part of every year and, as only recently realized, that snowy blanket contains or covers *active* fungal-like protists and protist-like fungi that are producing CO₂ which, on reaching the free atmosphere, adds to the winter production of greenhouse gases causing increased global warming, a matter of grave concern to us all.

INDISPENSABILITY OF SYMBIOTIC AND ENDOSYMBIOGENETIC PROTISTS

The term symbiosis *sensu lato* may be, and has been, defined in different ways by different workers, depending largely on what aspect of the interrelationship (in our case, protists *s. l.* and their hosts) the author wishes to emphasize; and there is unavoidable overlapping among any categories chosen. The most intimate of all are the situations in which the genetic systems/mechanisms become merged, and if such an endosymbiotic merger is quite extreme the term now being popularized by the Margulis school (see especially Margulis and Chapman 1998, Margulis and Sagan 2002, Sagan and Margulis 2001) for that particular permanent condition is "sybiogenesis" (a term first introduced into the literature *early* in the 20th century by Mereschkovsky and virtually equivalent to the independently suggested synonymous term of "symbiogenesis" by Wallin in *mid*-20th century). The following five subsections are not particularly novel. They are mostly based on the simplified categorization intimated in a preceding section of this paper (beginning of "Kinds of Biotic Interactions"; also there see the references to Trager 1969 and Baker 1969, and others, related to the general taxonomic placement of protistan hosts of symbionts; finally, see my own relevant classificatory remarks in Corliss 2002).

However, a sixth, called endosymbiogenesis or endosymbiogenetics (see historical note, above) is additionally and separately included here because of the recency of its wide recognition as a matter of high significance and its potential importance in research in biomedical and medical fields (for one example of the latter: its use in drug-testing). Speaking of the great significance of endosymbiogenetics, Lynn Margulis and recent eager student associates feel strongly that such a very close relationship of "host" and "symbiont" leads over time to production of new organelles, cells, tissues, organs, and even species (see especially Chapman et al. 2000, Chapman and Margulis 1998, Margulis 1998, Margulis and Chapman 1998, Margulis, Matthews, and Hazelton 2000, Margulis and Sagan 1997, 2002). In fact, in their opinion, *all* eukaryotes are chimaeras and are products of sybiogenesis, *the* creative force of/in evolution.

So, once again, if we choose as a single "*most significant*"

role that protists play in support of life on Earth, our choice of symbiosis *s. l.*—fully realizing the inevitable overlapping with our *other* "most significant" picks (see above)—would not be amiss. It may surprise a goodly number of readers to learn that more than 14,000 kinds of protists (15% of all extant species: Corliss 2000a) exhibit a symbiotic way of life, and the symbiotic membership of nine separate protistan phyla (in four different kingdoms: see Taxonomy Section, above) is practically 100%!

(1) **Phoresis.** Strictly speaking, this condition is commonly illustrated by protistan species that are carried about, and thus indispensably dispersed from time to time to fresh locations, by a host organism which is typically/seemingly unaffected by its passenger. Actually, the situation can be more complicated, and the host itself may be either free-living (or in a free-living phase of its life cycle) or parasitic in or on some host of its own. Also, the carried form may have evolutionarily become intimately involved with its host at the genomic level, leading us to special subsection 6, below.

Typically, phoreses have been thought of in connection with hosts that, themselves, are free-living: for example, many species of the stalked (sedentary) peritrich ciliates are transported about by freely swimming aquatic invertebrate or vertebrate hosts (for peritrichs associated with crustaceans, see recent lengthy reviews by Fernandez-Leborans and Tato-Porto 2000, and Morado and Small 1995). But, as suggested above, host organisms (at all taxonomic levels) may be parasites as well (thus, hyperparasitism) and may be vectors (so important!: see emphasis in Marquardt et al. 2000) between same or different hosts; or involved may be zoonoses—reservoir hosts in which the transferable symbiont is less highly pathogenic (classic reference: Hoare 1962). Then again, often resistant cysts or spores play a part in distributing the symbiont; but such stages in the life cycle (Henis 1987) are also known for free-living microorganisms, including algae and protozoa (Corliss and Esser 1974). The microbial ecology of cyst- and spore-producing protists demands further attention than it has received to date (a modern experimental approach is that of Gutiérrez et al. 2001, using a species of the well-known soil and edaphic ciliate *Colpoda*; the classic paper here, on anabiosis as it involves protists, is that of Keilin 1959).

(2) **Mutualism.** Traditionally, this has been defined as an association of two organisms from which both the symbiont and the host derive a measure of benefit. While this is generally true, in a broad sense, complications can arise at the intimate genetic level, leading to a kind of potential or realized competitiveness between host and symbiont, a condition not easily recognizable before the advent of today's refined molecular techniques. The viability of one or both members of the partnership can affect drastically many or even all members of the biological community in which the two are fellow-dwellers.

(3) **Commensalism.** This category has classically been defined as an association of two organisms in which only one partner, the symbiont, derives substantial benefit. At the molecular level, evolutionarily, however, the host may have tried (with or without success to date) to control its "free-loader" to the extent that the latter is influenced/conditioned to contribute something itself to its generous hosting partner. More research needs to be carried out in this interesting field, one that can be more complicated than generally thought.

(4) **Ectoparasitism.** The symbiont lives on the outside of its host, beneficently or harmfully and temporarily or permanently, depending on the particular organisms involved. Many years ago, so-called ectoparasitism was presumed to be the route by which, evolutionarily, endoparasitism was reached; then that notion was largely dismissed. Interestingly enough, the concept

has been revived by the Margulis school as the way that explains the appearance of certain *motile* elements ultrastructurally and molecularly recognizable today in many eukaryotic cells (Margulis 1996, 1997; Margulis, Dolan, and Guerrero 2000).

(5) **Endoparasitism.** This is the situation in which the symbiont dwells within the host organism; if the host is a metazoan (or metaphyton), then typically it often suffers (at least from the viewpoint of human beings) from the association, directly or indirectly. However, recall the dictum to all parasites: refrain from killing the goose that lays the golden egg; treat your host with some restraint if you wish to continue to derive benefit from having a cozy shelter in which to live and multiply!

Windsor's (1997, 2000a) widely overlooked hypothesis of the "biocartel" as a biological unit composed of a free-living host species and all its (ecto- as well as endo-) symbionts deserves mention here. He suggests that the biocartel is the crucial (indispensable?) unit in both the ecology and evolution of the multiple implicated taxonomic species, irrespective of their locations on any phylogenetic tree. The Biocartel Concept is reminiscent of some of the propositions of the Margulis school (see especially the references given above under "Ectoparasitism," further above in lines just preceding "Phoresis," and below in the category "Endosymbiogenesis").

Windsor further estimates that every eukaryotic species (and at this stage in his calculations he is thinking primarily of free-living vertebrate hosts) is parasitized by a sizeable number of taxonomically different symbionts, and he reasonably concludes from that "evidence" (presumed or known) that there are far more symbiotic species of life (at least of metazoa) on Earth than there are parasite-free forms. This is hard to deny!! Thus Windsor's concern on behalf of the symbionts is that possible independent mutations in the host might either render their bodies totally inhospitable to the parasite or, in other instances, over time, even cause total extinction of the host. Sometimes co-evolution (with parallel mutations?) of host and symbiont will save the day, but at other times it selfishly(?) increases growing antagonisms among members of the cartel. Yet, since many symbionts may indeed be supplying needed nutritional materials to the host, discord is not particularly advantageous to either/any member of the partnership. An uneasy balance!

From an exhaustive analysis of the pertinent literature, Windsor (2000a,b) reports that the biocartel of the American robin, despite its relatively small body size among vertebrates, has at least 94 species of symbionts, *not* counting prokaryotes or protists, the latter themselves representative of several phyla of parasitic flagellates, amoebae, and sporozoa. Round worms, flat worms, cestodes, acanthocephalans, ticks, fleas, flies, lice, and a couple of "parasitic" fellow avian species, comprise the nearly 100 members of that cartel of the robin knowable from his literature search to date. And add one for the robin itself!

An hypothesis related to his biocartel concept has been developed by Windsor (see especially 2000a,b) is that of "leveraged extinction." Briefly, he postulates that when a given host is caused to become extinct (at least one documented case is available in the evolutionary literature: see Stork and Lyal, 1993, who claim that when the passenger pigeon went extinct in 1914, so too did two species of its body lice), it takes its unique symbionts with it and jeopardizes the lives of still the other members of that cartel (who simultaneously may also be part of still other cartels). This is a very serious matter when the number of symbionts, even among vertebrates, far exceeds that of the hosts: the depletion of the latter organisms will cause a lag in the recovery of biodiversity and a slowing down of the basic process of speciation itself due to the exploitation of ecological opportunities. Windsor (2000b) concernedly asks (along

with other biologists these days), are we headed for, *or already in*, a sixth mass extinction of vertebrate life?

In the case of *Homo sapiens* (with a considerably bigger body size than the robin) there are ca. 400 members of the biocartel, exclusive of bacteria, with some 70–75 species being protists (figures from Ashford and Crewe 1998). Sites in and on our bodies (not to say that every individual human being is host to *all* of these possible parasites at the same time!) range from blood and other tissues to digestive tract and other body cavities and to cells of numerous kinds. Many are not harmful; some are even positively beneficial, for example, keeping bacterial numbers down in the digestive system by grazing or crowding. Incidentally, some of the classic works in this "beneficent" area include early observations by Cleveland (1934) and Grassé (1926) on protists symbiotic in wood-feeding roaches and termites, and by Hungate (1942) and Coleman (1960, 1963) on ciliates in ruminants. But among other fistulated vertebrates (beyond the ruminants and well before *their* usage) surely the most celebrated case is that of a young Canadian man accidentally shot through the mid-body, back in 1812! For many years he was determinably kept alive, cared for, and methodically experimented on through his naturally-caused fistula (reinforced in the opened state) by an American Army surgeon (see Beaumont 1833). The protists in the poor man's "gut" were helpful through their keeping *down* the numbers of bacteria, an over-population of which would be harmful to their host, as Beaumont demonstrated in his extensive physiological observations.

Among the many organisms that do or can affect our health quite *unfavorably* are, among the protists alone, various species of sporozoa, flagellates, amoebae, and ciliates. Consider the malarial sporozoa, which alone—as number one among our most harmful parasites—kill more than one million human beings every year, with as many as 500(!) additional millions weakened and made more susceptible to other infections that are often also eventually fatal. Surprisingly, in many parts of the world, more than half of the mortality caused by *Plasmodium falciparum* alone occurs in infants under the age of eight months (Sedegah et al. 2003). During the past decade or so, medical workers have suddenly appreciated that AIDS patients, with their compromised immune system, may actually have their death caused (or at least hastened) by secondary invaders including the protistan *Pneumocystis* (Kaneshiro 2002), the microsporidians *Encephalitozoon* and *Enterocytozoon* (Weiss 2001), and other opportunistic protists (the malarial species and various flagellates and amoebae: see Kaplan et al. 2000).

One of our greatest medical challenges, incidentally, arises from the alarming spread of drug resistance among many pathogenic microorganisms, cause of a looming crisis for the entire human race (Honigsbaum 2002, Hunter et al. 1995; with the "modern classic" being Garnham 1966, who—in his weighty volume—pays deserved tributes to the early malarialogists of the end of the 19th century). And I am leaving to one side the economic (not to mention health) costliness of loss—due to infections by protists—of farm produce worldwide, foodstuff ranging from poultry and livestock to fruit orchards and grain and vegetable crops, and to fisheries (both marine and freshwater) of all kinds (see brief review in Corliss 2002; and see Perkins 1987, Lembi and Waaland 1988, and Sherman 1998).

But the reader's attention should be drawn again to the fact that not all symbiotic associations involving protists have purely negative effects on life. For example, commensalistic forms thriving in body cavities and digestive tracts of many animals may play indispensable roles in maintenance of the host's health, supplying growth factors and controlling potential overgrowth of bacteria in the same sites by grazing on them. Pro-

tistan associations with certain fungi give us the indispensable (and nearly indestructible!) lichens; other species are beneficially active in the soil in which are embedded tree and other plant roots. As pointed out on several earlier pages, the roles of protists in many kinds of soils remain largely unexplored, but their presence there may often be a beneficial one. There is growing evidence that photosynthetic forms are indispensable to marine reef communities (for references to the above topics see Corliss 2001, 2002, and Wetzel 2001a,b, reviews stressing the recent literature on the numerous beneficial roles played by protists in Nature). With specific regard to coral reefs, appropriate sections of the major review by Reaka-Kudla (1997) should be consulted. Of course at least partially dependent on the welfare of the reefs are innumerable “higher” organisms, especially certain major invertebrate groups and scores of species of fishes and other vertebrates including human beings at the so-called top of the food chain. An aging but still highly useful treatment is Taylor’s (1990) review of endosymbiosis in marine protozoa, recalling to mind Sieburth’s (1979) modern classic in the field of marine microbiology (with *its* emphasis, however, mostly on prokaryotes).

(6) Endosymbiogenesis. Permanent *genetic* intermixure/integration of cells and cell contents of “host” and “symbiont” (to the degree that, evolutionarily and taxonomically, can we—in cases of very ancient origins—really recognize exactly *which* one today should be called the “host” and *which* the “symbiont”?!?). Involved in such molecular intimacies are either gene-product transfers (proteins or RNAs synthesized from the genome of one biont required in the metabolism of the other biont—“biont” a far better term to use than “symbiont” or “host”) or direct gene transfers (genes of one biont transferred, with or without retention of copies, to the genome of the other biont). Relevant references here to one or the other of the kinds of gene or gene-product transfer research, works becoming *so* numerous during the past 8–10 years, are simply not possible to include in proper number in this highly space-restricted overview, although valiant (and successful!) attempts to give appropriate summaries via very recent News-of-Meetings reports of the journal *Protist* have been made by Dacks and Simpson (2002), Surek (2002), and Richards et al. (2003). So I have, myself, deliberately/arbitrarily singled out only the few (a scant two dozen) following papers, most chosen partly for their own rich bibliographies, from the very recent appropriate literature (years 1998–2003), showing the reader the diversity of organisms and kinds of approaches involved. Other papers of equal relevance appear in a subsequent paragraph devoted mainly to research publications on the fascinating “apicoplast” organelle being found in such medically important sporozoa as the malarian species.

So saying, see Baldauf (2003), Ben Ali et al. (2001), Cavalier-Smith (1999), Dacks and Doolittle (2002), Dolan et al. (2002), Doolittle (1999), Graves (2003), Ishida and Green (2002), Katz (1999b), Lynn et al. (1999), Martin et al. (1993), Ragan (2001), Rivera et al. (1998), Roger (1999), Silberman et al. (2002), Simpson, Lukes, and Roger (2002), Simpson, MacQuarrie, and Roger (2002), Simpson and Roger (2002), Stechmann and Cavalier-Smith (2002), Strüder-Kypke et al. (2000), Wakefield and Kemp (2001), Xoon et al. (2002), Zauner et al. (2000).

Laboratories or centers engaged in such intriguing “genetic” studies around the world are relatively few in number at the moment: but by the time of actual appearance of this paper, I suspect that number shall have doubled or tripled! Doubtless, the same may well go for numbers of journals serving as outlets for such research and for numbers of special meetings convened for discussions of such topics of growing biological and med-

ical interest. Incidentally, I have no room here to give you examples of even the best-known *classic* papers in the literature. If I did, I should certainly *not* omit citations to the discovery and subsequent brilliant revelations (by T.M. Sonneborn, J.R. Preer, G.H. Beale, A. Jurand, and still others) of the so-called “Kappa” particles in species of the ciliated protozoon *Paramecium*.

With respect to the apicoplastic organelle of Sporozoa mentioned above, it certainly serves as an excellent and strong example of genetic intimacy of two organisms at the unicellular level. Now known for half-a-dozen years as the “apicoplast” (a most apt term: see Köhler et al. 1997), this unique cellular inclusion is being studied by an increasing number of researchers everywhere and is the sole or a major topic represented in selected recent works of the following investigators: Bhattacharya (1997), Blackman (2003), Cavalier-Smith (2002), Chapman and Margulis (1998), Fast et al. (2001), Graham and Wilcox (2000), Hackstein et al. (1995), Jeon (2002), Köhler et al. (1997), Margulis (1996), McFadden and Roos (1999), Obornik et al. (2002), Richards et al. (2003), Sapp (1994), Trager (2002), R.J.M. Wilson (1998).

As the reader may recall, for a dozen years or so the Sporozoa (syn. Apicomplexa) has been a phylum of protists linked with the phyla of dinoflagellates and ciliates in a taxonomic higher-level group often known as the Alveolata because of their common possession of cortical alveolar spaces under the outer limiting cell membrane (otherwise these three major protistan phyla seem to be vastly unlike in many characteristics). The apicoplast, while itself colorless, resembles a green algal chloroplast in so many ways (see above references) that some biologists have allegedly asked, in all sincerity, whether or not the malarial genus *Plasmodium* should really be classified as a degenerate plant!

Very recently, it has been suggested—and generally agreed upon by serious students of the situation (*except* for members of the Margulis School: e.g. see Margulis and Chapman 1998, Margulis and Sagan 1997)—that, originally, the cell body of the sporozoan organism must have engulfed or was somehow invaded by a free-living green algal cell and then retained the *latter’s* chloroplasts (*and* membranes: e.g. see Cavalier-Smith 2000b), along with transfer of genic material to the nucleus of the apicomplexan (for literature, see the bulk of the 16 references given just above). With apparently eventual loss of the (unneeded) photosynthetic powers of the original algal plastid, however, the genes in the nucleus became quite necessary for *other* essential cellular processes required for survival of the whole sporozoan. Recall that the green algal cell itself had originally been *non*-photosynthetic and had acquired *its* plastid in the form of a cyanobacterial endosymbiont! Thus, the case so briefly outlined here represents an example of a secondary endosymbiotic phenomenon occurring in the apicomplexans, which comprise a very large and important protistan taxon and include species of *Eimeria*, *Toxoplasma*, and some *other* genera as well as the malarial *Plasmodium*.

The potential and demonstrated importance of studies on the apicoplast in ecological, taxonomic/phylogenetic, and biomedical/medical research is very clear, as I hope I’ve indicated—although too briefly?—on immediately preceding pages. With respect to medical research so vital for human health, in my choice of papers cited above some (of which McFadden and Roos 1999 is the earliest) explain modern drug-testing programs in detail. The opportunity to learn still more from all recent genomic revelations in our single-celled companions certainly guarantees an exciting future for all of us living as we do in a world that is full of indispensable protists!

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(See Introductory Section, page 2 of *this* paper, please)

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