HAECKEL's Kingdom Protista and Current Concepts in Systematic Protistology

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Abstract

Ernst HAECKEL, one of the biological giants of the second half of the 19th century, boldly created a novel third kingdom of organisms, the Protista, to contain the largely microscopic and unicellular organisms that he believed should no longer be assigned to the long-dominating pair of kingdoms containing the macroscopic and multicellular plants and animals. This evolutionarily-based systematic concept, proposed in 1866 and refined in 1878 (and subsequent years), was controversial from its inception and, indeed, is still so today. Yet the idea was – and is – of much value, if only for focusing attention on the phylogenetic component of taxonomy and on the otherwise often ignored highly diverse groups of mostly microscopic eukaryotic organisms now widely known as "the protists" (consisting of the conventional algae, protozoa, and "lower" fungi). Discussed in this paper, beyond giving a historical background, are the attempts in the 20th century to improve the high-level systematic treatment of all protists. Current options, one of which may be considered particularly neoHaeckelian in nature, are presented in order to show that protistan megasystematics will remain in a state of flux until more data of relevance are available for detailed analyses. One of the major challenges facing workers in the field today is how to determine ways of including information from phylogenetic cladograms into ranked hierarchical schemes of classification (if retention of the latter into the future seems desirable), keeping in mind the varying uses or purposes to which such megasystems may ultimately be put. In a table, the author briefly presents his own skeletal arrangement of high-level protistan taxa that may be an improvement over those in the recent literature, with emphasis on the idea that the diversity of the protists is too great to be confined to a single kingdom and, thus, that their species require dispersal throughout all of the several kingdoms of the eukaryotic biotic world that are becoming widely recognized today.

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85-104

1
Introductory Remarks

Ernst [Heinrich] HAECKEL (1834-1919) was one of the most prolific and influential producers of publications in broad areas of the biological sciences, including evolution and systematics, during the latter half of the 19th century. This fact is attested to by the many diverse papers comprising the present special issue of the journal "Stapfia", by numerous entries in the recently published 4862-page "Dictionnaire du Darwinisme et de l'Evolution" (edited by TORT 1996), and by the continued use and frequent citation still today of various of his works, controversial or otherwise, a full century after their initial appearance. A man of great enthusiasm, conviction, and self-confidence, his missionary zeal was well known. For example, as the "T. H. HUXLEY of the European continent," HAECKEL displayed such a vehemence in his uncompromising support and defense of Darwinism that it was said that some of his outbursts astounded – even worried – DARWIN himself!

The present paper is limited primarily to consideration of HAECKEL's novel concept of the Protista as a third major kingdom of organisms and to brief discussion of subsequent, including current, ideas about the evolution and systematics of the diverse "lower" eukaryotic assemblages now widely embraced under the broad and very general term of "the protists". A few words of background information must be given first.

2
Brief Historical Background

With respect to the classification sensu lato of living organisms, the notion that the biotic (including sometimes the abiotic as well!) world contains more groups than just the easily recognized macroscopic plant and animal species extends far back into time. We are indebted to RAGAN (1997) for his recent scholarly discourse on this often largely philosophical subject of a more or less elusive third kingdom for objects or organisms not fitting comfortably into the established animal/plant categories. Nevertheless, although certain protists (but not so-called) were described with a degree of accuracy by scientists of the 16th and 17th (and perhaps even earlier) centuries, it remained for astute microscopists of the late 1700s (e. g., O. F. MÜLLER 1786) and early 1800s (e. g., J. B. P. A. LAMARCK 1815; C. A. AGARDH 1824; C. G. EHRENBERG 1838; F. DUJARDIN 1841; F. T. KÜTZING 1844; L. RABENHORST 1844-1847; C. T. von SIEBOLD 1845, 1848; C. W. von NÄGELI 1847) to offer accounts clearly noting major (mostly morphological) differences between micro- and macroorganisms. [These workers (and their major followers in subsequent generations through mid-20th century) have been deservedly, although all too briefly, saluted in several historical works by the author: see especially CORLISS (1978-1979) and CORLISS (1992).]

Despite the precise observations of such titans of old as those mentioned above, the widely followed **downward** system of taxonomic classification of the times typically left the protists (comprised principally of algae and protozoa) assigned to either one or the other of the two dominant/dominating kingdoms, the Plantae and the Animalia, until arrival of the second half of the 19th century.

During the very busy period 1858 to 1866 (as ROTHSCHILD 1989, has chronicled in a most thorough way; see also RAGAN's 1997, 1998, analyses), half a dozen papers were published that essentially set up formal kingdoms, using four to six separate labels, for organisms many of which – but certainly not all! – are generally subsumed today under the "protist" umbrella. The names of these specified "third kingdoms" and their creators were Protozoa/Acrita (OWEN 1858, 1860, 1861), Primigenum/Protoctista (HOGG 1860), Primalia (WILSON & CASSIN 1864), and Protista (HAECKEL 1866). But remember that various algal and protozoan groups had been recognized for scores of preceding years as quite distinct from most other organisms; most often, however, such groups were rather arbitrarily placed within one and/or the other of the long existing pair of established kingdoms, as indicated above.

ROTHSCHILD (1989) and RAGAN (1997) have offered admirable discussions of the

values and fates of the contributions by OWEN, HOGG, and WILSON & CASSIN, to which the reader is thus referred. These two workers are also in agreement over the principal reasons for the (relative) superiority of HAECKEL's propositions, rife though the latter were with weaknesses and with subsequent revisions (e. g., see HAECKEL 1868, 1874a,b, 1878, 1892, 1894). Therefore, here I shall concentrate solely on the views of HAECKEL, among those five late 19th-century third-kingdom creators, primarily because his proposals were clearly the first to truly embrace an evolutionary (phylogenetic/genealogical) outlook and because their author was a bonafide "working protistologist" himself. It is also essentially only HAECKEL's ideas that ultimately resurfaced, albeit in modified form, in subsequent 20th-century taxonomic treatments of the protists.

3
Pros and Cons of HAECKEL's Heuristic Proposals

Certainly influenced by DARWIN (1859), HAECKEL (1866) is presumed to be the first biologist to present a "phylogenetic tree of life" (reproduced here as Fig. 1). For HAECKEL, especially in his later papers, one important role of some single-celled organisms was to serve as the direct evolutionary origin of the long accepted kingdoms of plants and animals, while his new (third) kingdom specifically contained many additional unicellular groups considered by him not to be immediate ancestors of organisms comprising the other major branches of his tree. As RAGAN (1997) has cogently pointed out, nature at last no longer needed to be represented by a single linear chain (the "scala naturae" of philosophers and theologians through past centuries); rather, a ramified tree provided a far more accurate (albeit also far more complicated!) picture of group interrelationships. HAECKEL stressed the evolutionary approach of his classification to the exclusion of any alternative explanation, despite the far from widespread acceptance of Darwinism (natural selection, etc.) at the time of his own daring speculations.

A second main reason for favoring HAECKEL's Protista over other suggestions of the time is related to the fields of research of the proposers. Only the man from Jena, as I have implied above, was a person qualified to appreciate the merits of the "lower organisms" as progenitors of and/or as separable from the visibly dominating forms of life. HAECKEL had studied in Berlin under Johannes MÜLLER, a man hailed as the founder of the great dynasty of German zoologists and comparative anatomists (see GOLDSCHMIDT 1956) and establisher of the Radiolaria among the protozoa

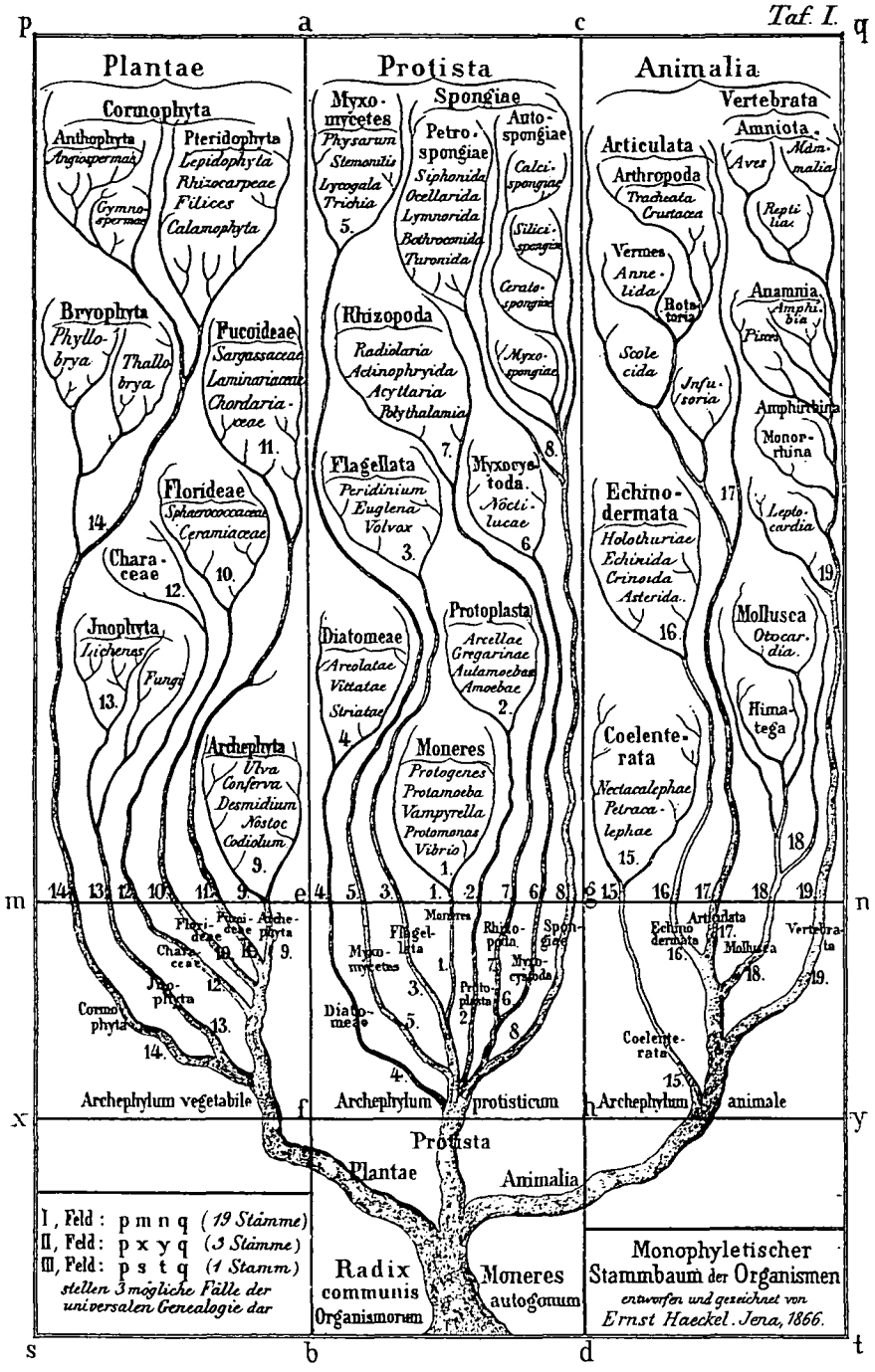

Fig. 1:
Reproduction of HAECKEL's phylogenetic tree of life (from HAECKEL 1866, Plate I).

(MÜLLER 1858). HAECKEL, a magnificent teacher himself, had many followers. His most outstanding protozoological student was surely Richard HERTWIG who, in turn, seemed to have rivaled even the great Otto BÜTSCHLI as an inspiring professor in those decades of German dominance in all scientific fields. HAECKEL produced tremendously detailed and beautifully illustrated monographs on the taxonomy of the Radiolaria (e. g., HAECKEL 1862, 1887a, b, 1888) and of allegedly related groups such as the Heliozoa and Acantharia (both of which he named), while rocking the biological world with his treatises on animal evolution (among the many aphorisms he coined, recall the celebrated one of his Recapitulation Theory, "ontogeny briefly recapitulates phylogeny"). He also studied certain amoebae and ciliates (e. g., HAECKEL 1870, 1873a, b), as well as some diverse "lower" invertebrate groups. He was among the first paleoprotistologists since C. G. EHRENBERG, whose works earlier in the century have generally gone unnoticed (CORLISS 1996).

HAECKEL is thus certainly deserving of the title "Father of Protistology", even though our modern understandings of what taxa of organisms should be studied today under the banner of "protistology" may be quite different from his. As samples of his magnificent illustrations of diverse protists, see Figures 2-4, reproductions of three plates from his popular atlas of the turn of the century (HAECKEL 1904), a work passing through several editions. I return to the matter of his art work shortly (**vide infra**).

HAECKEL's ideas concerning the composition of his kingdom Protista were not immutable: this may be considered as another point in his favor, in my opinion. In 1866, he included such major groups as the Bacteria (his Moneres), naked and some testaceous rhizopod amoebae, slime molds, the radiolarians, foraminiferans, gregarine sporozoa, various flagellates **sensu lato** (*Dinobryon*, *Euglena*, *Volvox*, *Peridinium*, *Noctiluca*, etc.), diatoms, and sponges. In 1878, he added the ciliates and suctoria (designated as animals in 1866) and excluded the sponges. Still later, HAECKEL (1892) acknowledged that his taxonomic kingdoms might not be monophyletic but that they nevertheless represented a "natural" (i.e., evolutionary) classification, which could be improved upon as more was learned about (micro)organisms many of which were yet to be discovered. Two years later (HAECKEL 1894), he wrote of four major groups of organisms (beyond the bacteria and other protists of his "Protista Neutralia"): the Protophyta, Protozoa, Metaphyta, and Metazoa, with the first two – also in his kingdom Protista – considered ancestral to the latter two (plants and animals), respectively. In all of his schemes, he did exclude from the Protista (most of) the blue-green algae (cyanobacteria, as we know them today), the macrophytic green, brown, and red algae, and the fungi, placing all such groups among the plants. While including the majority of the bacteria (his Monera, but today the prokaryotic microorganisms: **vide infra**) as protists, HAECKEL (1866, 1868, 1869, 1870, 1878, 1894; and see Fig. 1) always treated them as a taxon quite distinct from his other protistan groups.

On the negative side of the argument concerning the value of HAECKEL's proposals, two major points may be made. Probably of first importance, from a historical view, was the fact that several of his early critics were very influential figures in protozoological systematics: for example, Otto BÜTSCHLI (1880-1889) of Germany, and W. Saville KENT (1880-1882) and E. A. MINCHIN (1912) of England. Their lack of endorsement of the new Haeckelian kingdom nearly spelled its doom forever. In fact, because of HAECKEL's self-assured bombastic style, poetic imagination, fondness for creating authoritative-sounding aphorisms, and rather brash extension of his revolutionary evolutionary ideas into all fields of human endeavor (e. g., see HAECKEL 1868, 1892, 1899), the great man has literally alienated both outstanding biologists and historians of science – not to mention theologians! – well into recent times (e. g., see COLE 1926; NORDENSKIÖLD 1928; GOLDSCHMIDT 1956; SINGER 1959; MAYR 1982).

A second criticism, more legitimate and one often, admittedly, used by many of his opponents (including the early three cited above), stemmed from the fact that HAECKEL's kingdom, even in its later versions, did indeed embrace a rather motley mixture of microorganisms concerning which phylogenetic

interrelationships were poorly known and taxonomic boundaries were vague. If the categories of Vegetabilia/Plantae and Animalia were already rather arbitrary, his contemporaries (and later systematists as well) asked, what was the advantage of adding a third arbitrary assemblage to our view of the biotic world? If most of the protistan groups could be assigned without too much difficulty to the existing duo of kingdoms, why create a special place for organisms unitable solely, it seemed, on the basis of their (sometimes assumed) unicellularity and their (generally) microscopic size? These are points well made, and such criticisms plague protistologists still today (see subsequent sections of this paper, below).

Interestingly enough, however, despite widespread anti-HAECKEL and anti-Protista feelings, SCHAUDINN and HARTMANN unhesitatingly used the Haeckelian-derived name in the title of their influential new journal (the „Archiv für Protistenkunde"), established in Germany in 1902. And the ever-critical English parasitologist/protozoologist DOBELL (1911) published in that journal a landmark paper entitled, "On the Principles of Protistology". Turning to more recent times, French biologists, in 1965, named a new journal „Protistologica" (replaced, in 1987, by the „European Journal of Protistology"); and the old German „Archiv" has now, in 1998, been rejuvenated under the new title „Protist" (see details in CORLISS 1998a).

Textbook writers of the first three-quarters of the 20th century, with exceedingly rare exception (e. g., JAHN & JAHN 1949: **vide infra**), shunned use of HAECKEL's concept and name with respect to the protozoa (e. g., DOFLEIN 1901, and later editions; CALKINS 1901, and later; MINCHIN 1912; WENYON 1926; HARTMANN 1928, and earlier; KUDO 1931, and see 1966; HYMAN 1940; HALL 1953; and later authors and followers), largely influenced by the men and criticisms given above. Endorsement by botany apparently did not even occur to phycologists, most of whom persistently classified groups of microscopic algal species as "(mini-)plants" along with the macrophytic greens, reds, and browns (which HAECKEL himself had also excluded from his new kingdom). Even today, not many algologists, while separating the algae from the "higher" plants, have embraced the "protist perspective" (CORLISS 1986) when treating the overall systematics of their organisms (CORLISS 1998b), preferring a "phycological perspective" (RAGAN 1998). But R. A. ANDERSEN (1992), a phycologist with an admirable protistological outlook, has pointed out that the algae overall represent at least seven major lineages phylogenetically and that to place them together taxonomically (whether as plants or otherwise) would result in a highly polyphyletic assemblage.

Regarding HAECKEL's remarkable drawings (not limited to protists), a number of which he brought together in the 100 plates of his well known volume „Kunstformen der Natur" (HAECKEL 1904; and see "HAECKEL 1974", a conveniently available reproduction of those very plates, without text and with abbreviated English legends, released by Dover Publications), some biologists have noted that their accuracy often may have been altered by their creator's keen desire to demonstrate symmetry and/or artistic beauty in general in them. In this connection, GOLDSCHMIDT (1956: 33) stated critically, "HAECKEL's radiolaria were too perfect all over. One had the impression that he first made a sketch from nature and then drew an ideal picture as he saw it in his mind". But I believe that most biologists today would conclude that no harm has been done, no deliberate falsification of actual structures has been perpetrated in order to fit a preconceived notion of the biology of the organisms portrayed. [See Figs. 2-4, reproductions of three of HAECKEL's (1904) plates, showing aesthetically pleasing radiolarians, dinoflagellates, and ciliates, protozoan groups perhaps more appropriately referred to here as radioprotists, dinoprotists, and cilioprotists, using suffixes originally suggested in, or derivable from, proposals independently published by MARGULIS (in MARGULIS & SAGAN 1985) and ROTHSCHILD (in HEYWOOD & ROTHSCHILD 1987; and ROTHSCHILD & HEYWOOD 1987, 1988).] HAECKEL apparently loved beauty simply for beauty's sake, and he found it abundantly in the morphology of all creatures, large and small. Bravo!

Finally, a brief note might be inserted here concerning HAECKEL's tremendous outpouring of papers, monographs, and books. Reference

is made to only 17 of these in the present essay, ones most pertinent from the point of view of the subject being treated. But HAECKEL produced many more during his full lifetime. Yet it should also be kept in mind that lists of works often cited in Haeckelian biographies and bibliographies include revised editions (sometimes numerous) of his earlier productions and even other-language translations. Still, a mighty impressive publication record!

Subsequent (mid-20th century and to date) praises and criticisms of the Haeckelian kingdom are treated in following sections of this review.

4
Influence of H. F. COPELAND

A man who heroically resurrected HAECKEL's concept of a kingdom Protista (but who also, in his two later works, rejected HAECKEL's taxonomic name in favor of HOGG's curious Protoctista) was the botanist Herbert F. COPELAND (1938, 1947, 1956). Along with introduction of his own several improvements, COPELAND, vindicating most of HAECKEL's taxonomic motives and methods, firmly disagreed with the objections of numerous past writers (**vide supra**). He strongly believed that the (his own) resulting four-kingdom treatment of all organisms could easily be justified, and that the non-plant and non-animal groups could be characterized without difficulty and thus deserved high-level separation from the long-entrenched major two kingdoms. In 1938, COPELAND recognized as kingdoms Monera HAECKEL, Protista HAECKEL, Plantae LINNAEUS, and Animalia LINNAEUS. He assigned the Fungi to a place among the protists. The macrophytic algae were also transferred to the Protista, except for the green algae (all of which remained in his plant kingdom). Elevation of the bacteria to a kingdom of their own was a particularly overdue taxonomic decision (it had first been suggested by E. B. COPELAND, his father, as early as the year 1927), and he unhesitantly included the "blue-green algae" there. Yet we find that, as late as the 1960s and even 1970s, some authors were (still) treating the prokaryotes as members of the Protista, as "lower protists" (e. g., see JENNINGS & ACKER 1970; POINDEXTER 1971; RAGAN & CHAPMAN 1978; WEINMAN & RISTIC 1968).

Later, COPELAND (1947, and see especially his compact compendium of 1956) insisted on renaming his two kingdoms of "lower organisms" as the Mychota and the Protoctista. Neither of the two replacement names was necessary (his interpretation of the rules of proper nomenclature were too rigid; the Codes in force certainly did not oblige him to take such stringent actions). It is especially unfortunate that he dropped the highly acceptable, sensible, and euphonious name Protista, a decision with long-reaching effects (**vide infra**). "Mychota" was taken from a little-known work of about 25 years earlier (ENDERLEIN 1925). "Protoctista" was taken from HOGG (1860), chosen principally because COPELAND (mistakenly) felt that on grounds of priority Protista HAECKEL 1866, had to be abandoned. In any case, he should then have selected OWEN's Protozoa or HOGG's Primigenum, as ROTHSCHILD (1989) has pointed out. Rather similarly, a number of his strange/unfamiliar phyletic and class names need not be – and, in general, have not been – followed by subsequent authors on the systematics of bacteria, algae, protozoa, and fungi.

Incidentally, while COPELAND was working on his taxonomic treatise, JAHN & JAHN (1949; see also the second edition of this handy little textbook: JAHN et al. 1979) had a brief word on the problem of kingdoms with respect to unicellular organisms. To my knowledge (and as noted by LIPSCOMB 1991), the JAHNS became the first modern biologists to suggest a separate kingdom level for the Fungi. They also created a kingdom for the viruses. And they placed all green, red, and brown algal taxa plus the protozoa in their kingdom Protista. In their books, supposedly limited to treatment of solely protozoan taxa, they included keys to various chrysophytic **sensu lato**, cryptophytic, and chlorophytic algal protists; but many species of the latter groups had, and have long been, claimed taxonomically by both zoologists/protozoologists and botanists/phycologists.

COPELAND's detailed work set the stage for subsequent special treatment of the protists

and their close relatives. It might have had sooner and greater effect were it not for the realization of a truly major split of all organisms, evolutionarily as well as taxonomically, which occurred some five years after appearance of COPELAND's (1956) seminal culminating publication (**vide infra**).

5
Impact of Prokaryotic-Eukaryotic Division of Biotic World

The revolutionary realization that all forms of life must be viewed **evolutionarily** as falling into two great assemblages, clearly distinct one from the other, has been widely acknowledged as one of the greatest biological concepts of the 20th century [although now – e. g., see WOESE (1994) and WOESE et al. (1990) – this is disputed by some modern microbiologists, who claim that recognition of three great divisions or domains, the "Archaea" (archaebacteria), the "Bacteria" (eubacteria), and the "Eucarya" (eukaryotes), first realized two full decades ago (WOESE & FOX 1977), was/is the most significant advance of all].

The prokaryotes (the bacteria **sensu lato**) and the eukaryotes (all other organisms, micro- and macroscopic in size), represent separate assemblages named for their well known nuclear differences (i.e., no discrete nucleus in the former, and a true nucleus, membrane-bound, etc., in the latter); but the groups also possess many other differentiating characteristics (beyond discussion in this paper). This discovery of such a great dichotomy among all known organisms was destined, understandably, to overshadow and postpone serious consideration of the protists as a separate kingdom. Two grand superkingdoms were enough to stimulate and rejuvenate research at the cellular level around the world, and for a period of time protozoa and algae became (mere) representatives of the eukaryotic half of life on Earth.

Details of the recognition of the instantly popular prokaryotic/eukaryotic split have been chronicled elsewhere, by others and in papers by the author (e. g., see CORLISS 1986, 1987). Very briefly, we may recall that the discovery was well publicized and formalized by Roger STANIER and colleagues (e. g., see STANIER & VAN NIEL 1962; STANIER et al. 1963; STANIER 1970). But it is worthy of special note that the brilliant French marine protistologist Edouard CHATTON (1925), in a long-overlooked work concerned principally with a curious parasitic amoeba, was the first biologist to use the terms "procaryote" and "eucaryote" and to realize that such a division existed in the biotic world.

In due time, the value of using unicellular algae and protozoa in research on (eukaryotic) cells, so different from the prokaryotic cells of

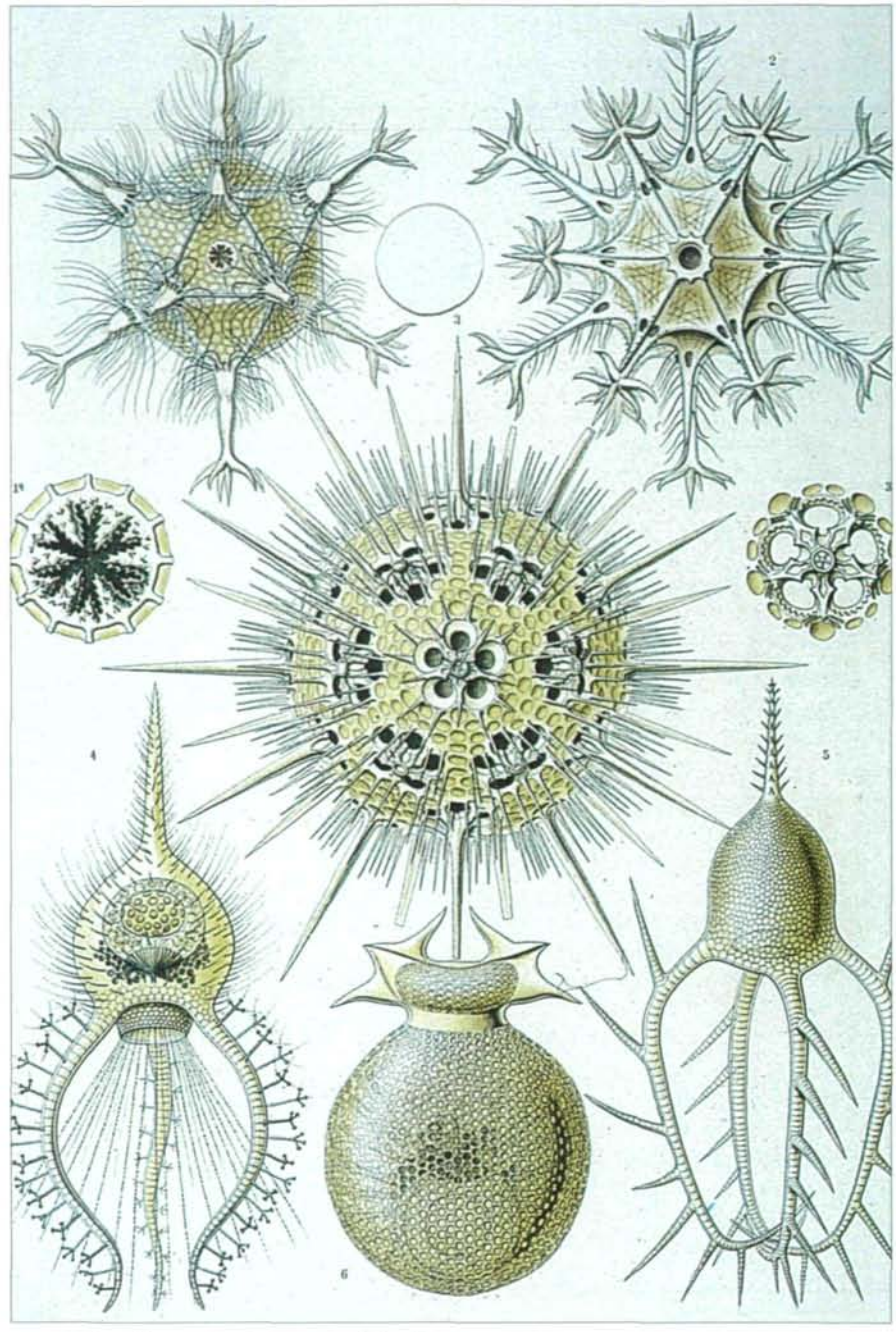

Fig. 2:
Reproduction of HAECKEL's drawings of several species of radiolarian protozoa (radioprotists) (from HAECKEL 1904, Plate I).

bacteria, became appreciated. And these protists were somewhat like bacteria in not being parts of tissues, being mostly microscopic in size, and often being culturable under refined laboratory conditions. The emerging field of eukaryogenesis came to recognize protists as serving as the "missing link" between bacterial origins of life and the rise of multicellular, multitissued organisms of both plant and animal nature (CORLISS 1989).

6
Contributions of R. H. WHITTAKER

The ecologist Robert H. WHITTAKER, noted for his work in ecosystems analysis, was the first major worker to refocus evolutionary and taxonomic attention on unicellular eukaryotes (but see ROTHSCHILD 1989, and LIPSCOMB 1991, for discussion of the fine contributions of some other biologists, not mentioned in the present brief account, who published in the period roughly between COPELAND and WHITTAKER and into the early 1970s). Disagreeing with COPELAND's kingdom set-up, WHITTAKER (1957, 1959, 1969, 1977; WHITTAKER & MARGULIS 1978) suggested that overall nutritional modes, as well as level of structural organization, should play a significant role in recognition of separate kingdoms of organisms. His own papers over time presented slight alternative rearrangements, but his most cited one (WHITTAKER 1969) deserves our special attention because there he clearly recognized and defended five major assemblages, named Monera, Protista, Plantae, Fungi, and Animalia. Nomenclaturally, this decision of his was an improvement over COPELAND (1956) in restoring the label "Monera" for the bacteria and the name "Protista" for the combined group of protozoa and essentially unicellular algae (although exclusive of the "lower chlorophytes").

Taxonomically, WHITTAKER's separation of the Fungi from COPELAND's diverse Protoctista represented another welcome refinement (but recall that JAHN & JAHN 1949, had already promoted this idea, although on a different basis: see LIPSCOMB 1991). The macrophytic algal groups, taking with them the microscopic greens, were all assigned by WHITTAKER to the plant kingdom, a retrograde step with respect to the brown algal line, as I view it, since the browns have proven to be closely related to (other) heterokontic algal protists, including numerous unicellular (and microscopic) groups (see CORLISS 1984, 1994, and many pertinent references therein, especially CAVALIER-SMITH 1986, 1989, and PATTERSON 1989).

WHITTAKER's (1969) well publicized paper had tremendous influence on practicing biologists and textbook writers of the time, and the concept of a five-kingdom system of classification for all organisms acceptably satisfied – indeed fired – the imagination of even the non-scientifically trained public. It brought species of protists back into the limelight, as pointed out above, and heralded the emergence of a bonafide interdisciplinary research field distinctly identifiable as "protistology" (CORLISS 1986).

7
NeoHaeckelian Kingdom Protista

The time was thus right for reacceptance of Ernst HAECKEL's "tree of life" concept and of his proposed third major kingdom, the Protista, with refinements necessitated by the greatly increased knowledge amassed during the decades following his insightful promulgations. But, in fact, some of the same uncertainties that had bothered early critics (**vide supra**) remained in force in the case of WHITTAKER's five-kingdom idea: how (or whether!) to keep all algal groups together in one kingdom; and what to do, in general, about the probable polyphyletic nature of the Protista, convenient though it was to treat the assemblage as if it were monophyletic.

A new champion was needed at this crucial historical point, and Lynn MARGULIS enthusiastically rose to meet the challenge. HAECKEL's kingdom (unfortunately with its name once again reverting – à la COPELAND 1956, and mostly for the same mistaken reason – to Protoctista) survived well for nearly two decades (although not without its critics) and, indeed, is still an acceptable concept today in some circles (**vide infra**).

Numerous, stimulating, and rapidly forth-

coming were papers, chapters, and books by MARGULIS and colleagues during the exciting period from 1970 until (and including) the present. For our purposes here (mainly discussing protistan systematics), the following references may specifically be cited: MARGULIS (1974), MARGULIS & SCHWARTZ (1982, 1988, 1998), MARGULIS et al. (1990); more can be found in the bibliographies of those works (also see listings in CORLISS 1984, 1986, 1994, 1998b). But further, at least brief mention should be made of MARGULIS's highly heuristic influence, through her writings and oral presentations, in popularizing research into the significance of symbiosis in the evolution of all present-day forms of life (e. g., see MARGULIS 1970, 1976, 1981, 1993, 1996).

The five kingdoms of MARGULIS have changed but little, either in name or with respect to included lower taxa, over the years. In fact, in her popular and widely dispersed book (written with Karlene V. SCHWARTZ), four of the kingdoms have always been called the Protoctista, the Fungi, the Plantae, and the Animalia. The fifth (actually, the first) has been labeled the Monera in the first edition of the volume (MARGULIS & SCHWARTZ 1982), the Prokaryotae (Monera) in the second (MARGULIS & SCHWARTZ 1988), and the Bacteria (Prokaryotae, Procaryotae, Monera) in the third (MARGULIS & SCHWARTZ 1998). Such consistency has been valuable from the pedagogical point of view and has lent a welcome stability. Whether or not it is fully supported by recent studies is a topic to which we return below.

Whereas one of WHITTAKER's (see especially 1969) central aims, with rare exception, was to accept only groups of **uni**cellular and **micro**scopic organisms in his protistan/protoctistan kingdom, MARGULIS (e. g., 1974, 1976, and later works) placed her emphasis in the other direction, on requirements for membership in the "higher" kingdoms. That is, she strove to make certain that solely **multi**cellular and multitissued **macro**scopic organisms appeared in her kingdoms of plants, animals, and fungi. As a result, her protoctistan assemblage became much larger (in numbers of contained phyla) embracing, as it did, the red, the brown **sensu lato**, and all the green algae (including charophytes), the chytrids, and all the slime molds (and other "lower" fungal taxa). But MARGULIS agreed with WHITTAKER in his several improvements over COPELAND's (1956) scheme; for example, in ridding the protistan melange of the earlier worker's "higher" fungal groups and the sponges.

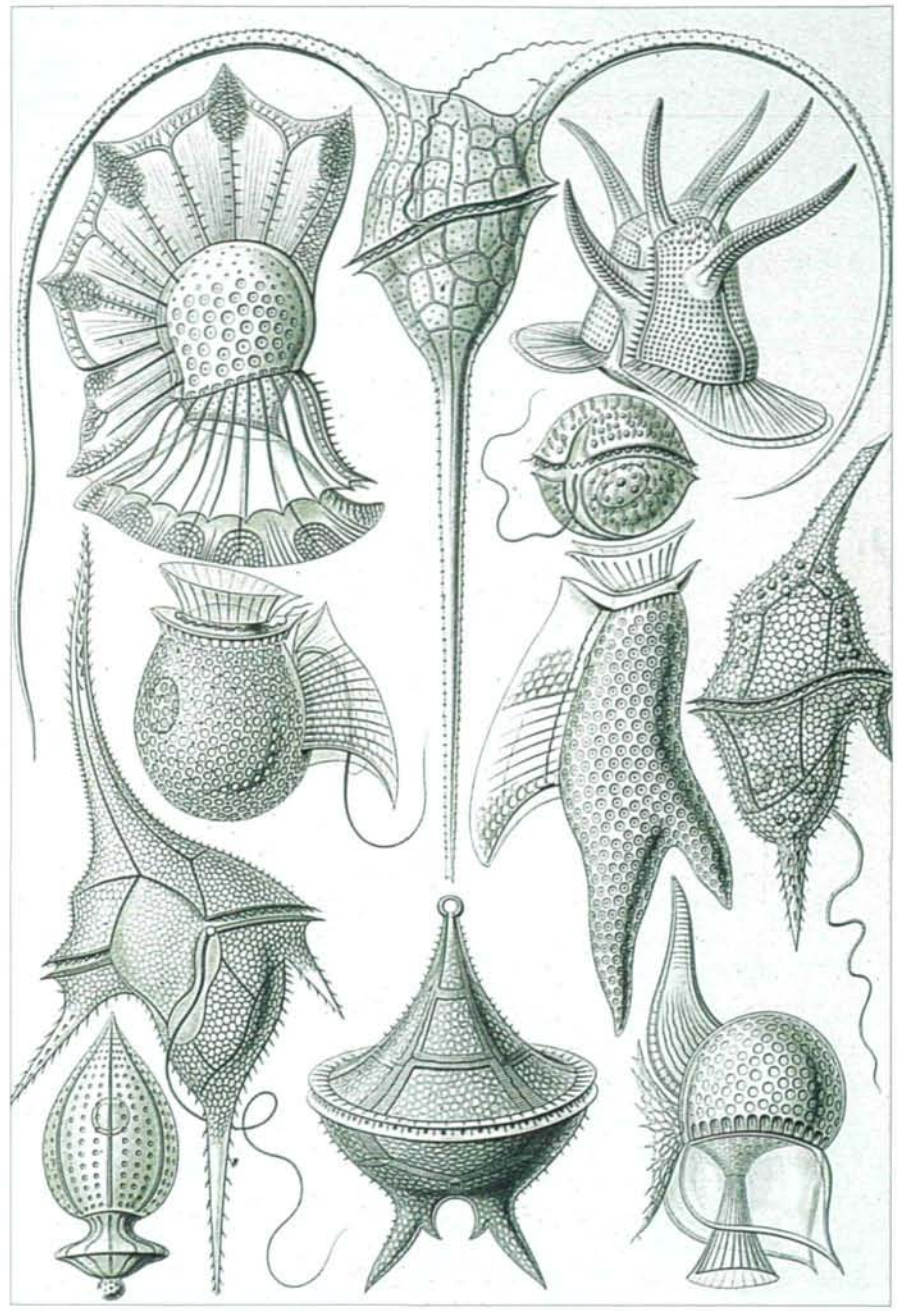

Fig. 3:
Reproduction of HAECKEL's drawings of several species of dinoflagellates (dinoprotists) (from HAECKEL 1904, Plate XIV).

Perhaps a further word needs to be said concerning the controversy, not entirely a semantic one, over the choice of a kingdom name, that is, between "Protista" and "Protoctista." For MARGULIS and her most faithful followers, the protists are the unicellular members of the kingdom; the protoctists overall, on the other hand, are said to embrace **also**

the major multicellular macrophytic algal lineages included there. It is true that HAECKEL placed the latter groups outside his more restricted third kingdom (his Protista **sensu stricto**). But, for the majority of working protistologists today, body size and even simple multicellularity (which surely has arisen more than once in protistan evolution) are not held to be significant bases for separation. Indeed, COPELAND (1956) himself, whose taxonomic work was/is much admired by MARGULIS, included most of the macrophytic algal groups (and the multicellular fungi as well!) within **his** Protoctista (but recall that he used this name merely as a preferred **synonym** of Protista: *vide supra*).

During the years in which numerous workers (the writer among them: e. g., see CORLISS 1984, 1986, 1987, 1989) wholeheartedly supported the five-kingdom hypothesis, many of us preferred simply to use the Haeckelian name Protista for what could be construed to be the practically identical kingdom persistently called Protoctista by MARGULIS. TAYLOR (1978) cautiously used only the vernacular term "lower eukaryotes" to describe his protistan assemblage (plus the fungi and all algal lines).

No matter slight nomenclatural differences/changes, independence of the fungi and the prokaryotes, some algal lines in and/or out, and the like: the consideration of the protists as comprising a single distinct high-level taxonomic group, relatively primitive, and serving as the evolutionary proving ground for the "higher" eukaryotes, was first clearly postulated by Ernst HAECKEL well over a century ago. The Margulisian concept and scheme, while considerably expanded and much more refined, may still appropriately be thought of today – and not disparagingly – as basically Haeckelian in nature.

8
Current Ideas Concerning High-level Systematics of Protists

Even during the peak of research excitement over the protists and their possible roles in the phylogeny and evolution of other eukaryotic organisms, some biologists did not share the Margulisian or neoHaeckelian view that protists displayed integrity as a taxonomic group. LEEDALE (1974) was an early dissenter, stressing the possibilities that the algae and protozoa might well be considered to represent (merely) a structural level or grade of (cellular) organization, on the one hand, or a multitude of separate kingdoms, too diverse to be amalgamated into one taxon, Protista, on the other hand. The overall classification scheme of MÖHN (1984) represented a fairly extreme example of the latter view: some 11 separately named kingdoms were deemed necessary to contain protistan groups. CAVALIER-SMITH (e. g., 1981, 1983) also distributed protists through several eukaryotic kingdoms (five or six in later papers: **vide infra**). CORLISS (1986; Table 1) may be consulted for detailed information on the varying numbers of eukaryotic kingdoms found in the literature of the years 1969 through 1985; and see the comprehensive treatment by LIPSCOMB (1991). Nevertheless, a "protistological perspective" (CORLISS 1986, 1998b) did – and does – hold sway in a significant number of research papers, often interdisciplinary in nature, that are concerned with the evolution and phylogeny of major groups of algae, protozoa, and "lower" fungi. The unique effort by ROTHSCHILD & HEYWOOD (1987; and see discussion in ROTHSCHILD 1989) to reconcile taxonomy and phylogeny, using a "from the bottom up" rather than a "top down" approach and identifying monophyletic groupings (which were then assigned vernacular names, all with "-protista" as suffix), deserves special mention but is beyond further consideration here.

Currently, the high-level classification of the protists is "in a state of flux" (CORLISS 1994, 1998b), although some workers in the recent past have rather pessimistically considered the situation to be closer to chaotic (leading one to wonder if "Regnum Chaoticum LINNAEUS 1767" – see RAGAN 1998 – might yet aptly be called back into service?!?). Because of our growing knowledge of protistan diversity (through increasingly refined studies and realization of the complexities of symbiotic origin of many contemporary forms), I believe that we are obliged to acknowledge the inevitability of inflated taxonomic

schemes for proper reflection of group relationships, lamentable though this conclusion is from a didactic point of view.

We continue to have options with respect to systematic arrangements of "lower" (indeed, of all) eukaryotes (and prokaryotes as well, but this great assemblage – or two great assemblages à la WOESE – is beyond the scope of the present review), and four of these are considered below. In addition to applying modern evolutionary/phylogenetic concepts and methodologies, we still would do well to reflect on the ultimate uses or purposes to which classification systems are put and on the universally agreed general dictum that one should choose simplicity over complexity whenever appropriately possible (OCCHAM's Razor, in effect): see relevant comments and advice in BARDELE (1997), CORLISS (1972, 1976, 1983, 1990, 1994, 1998b), LIPSCOMB (1991), MAYR & ASHLOCK (1991), RAGAN (1998), ROTHSCHILD (1989), SILVA (1984, 1993), and VICKERMAN (1992). Here, we shall leave aside a possible fifth option, one that might be said to be based on a separation/classification of all microorganisms into functional groups (e. g., see PRATT & CAIRNS 1985; SIEBURTH & ESTEP 1985; and comments in CORLISS 1998b).

8.1 Protists as Evolutionary Grade

The protists can be thought of as representing simply an evolutionary grade or a level of cellular organization, with perhaps some of them serving a role as phylogenetic way-stations enroute to emergence of so-called "higher" eukaryotic forms. Very likely, they (i.e., ancestors of present-day forms) served as a bridge between the kingdom(s) of prokaryotes and the presently dominating (although perhaps only body size-wise!) groups of "higher" eukaryotes. And many of them might be considered evolutionary experiments in eukaryogenesis (CORLISS 1987).

This option sidesteps a number of taxonomic problems, all the way up to whether or not all protistan groups can be considered, together, to represent a unified single kingdom. It essentially ignores the probable fact that numerous assemblages of protists are not in an evolutionary line leading to any "succeeding" groups (beyond themselves), as HAECKEL (1866, 1878) appreciated long ago. Identification of subgroupings is still required, and our curiosities still need to be satisfied regarding their possible phylogenetic relationships, one to another (and also to the other "real?!?" groups of organisms).

Nevertheless, from a pedagogical point of view, biologists may find it helpful to present representative unicellular protists as examples of an abiding type of biological (cellular) organization, irrespective of their place in the taxonomic hierarchy of life forms (BARDELE 1997).

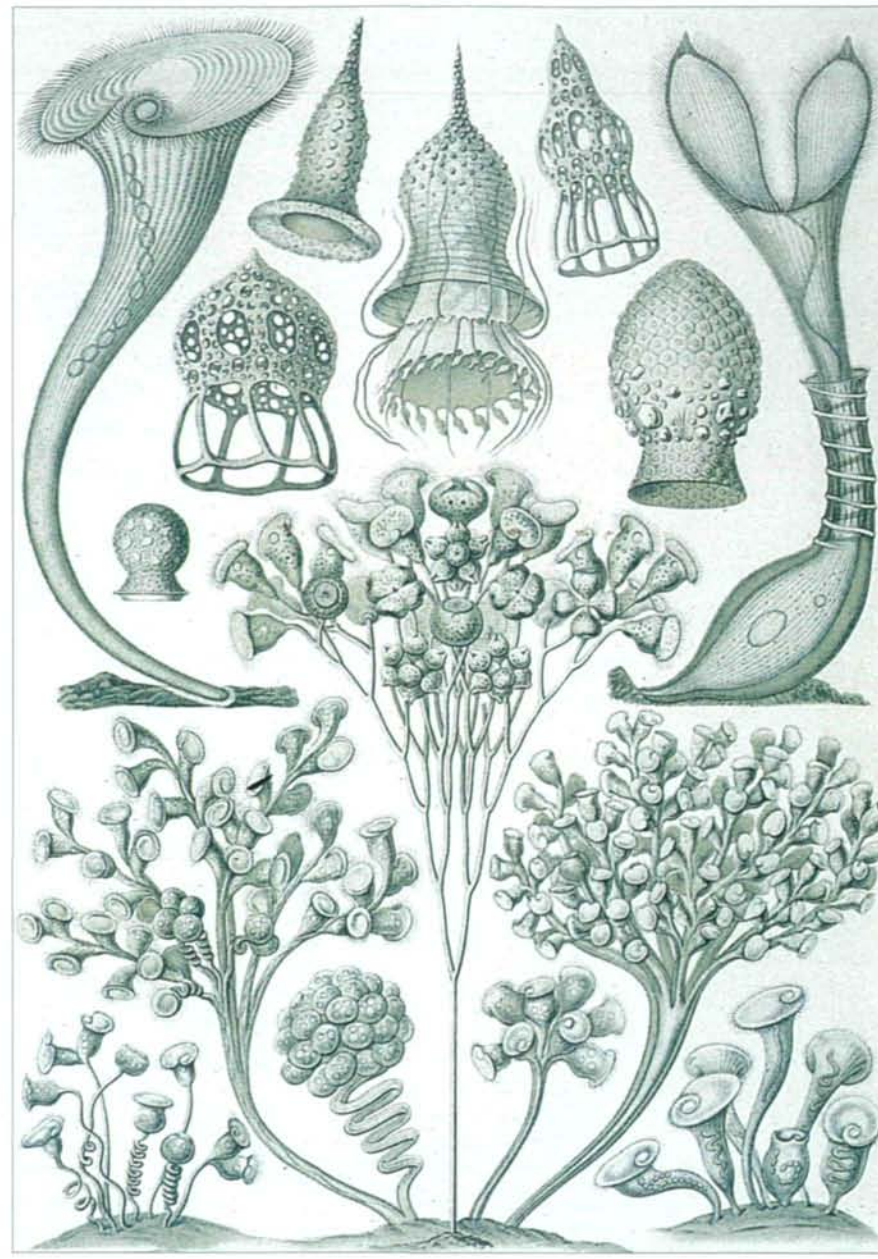

Fig. 4:
Reproduction of HAECKEL's drawings of several species of ciliates (ciliopro-tists) (from HAECKEL 1904, Plate III).

8.2 Protists as Phylogenetic Clades

From another point of view, groups of protistan species may be considered to represent (remnants of) evolutionary lines or lineages often without yet-known clear-cut taxonomic relationships to each other. All such clades, in theory, can be recognized by strict application of the rule of monophyly (HENNIG 1950, 1966; WILEY 1981; LIPSCOMB 1984; and today there are many additional books and papers of relevance available on this popular subject), a methodology greatly aided by the advent of precise ways to sequence ribosomal RNAs, for example. CAVALIER-SMITH (1995a) discussed the impact of such overall molecular researches on the development of protistology in its second decade as a rejuvenated field of biological inquiry. And PHILIPPE & ADOUTTE (1995) have reminded us of difficulties and pitfalls inherent in studies of the molecular phylogeny of eukaryotes in general.

The impressive phylogenetic trees or cladograms resulting from many molecular (as well as morphological/ultrastructural) approaches often present nearly insurmountable (to date) challenges to erection of (traditional) hierarchies of ranked taxonomic groups. If the reasoning on this subject by PATTERSON (1994; and see PATTERSON & SOGIN 1993) and others can be sustained as a valid argument – viz., that high-level ranks and hierarchies will be of diminished significance in the future – then cladistic/phylogenetic conclusions could come to replace traditional "megasystematics" (apt term coined by CAVALIER-SMITH) for protists and all other organisms as well. From didactic and other pragmatic points of view, such an outcome seems difficult to accept for many (but a decreasing number?) of us biologists who are perhaps addicted to classical taxonomic arrangements. Maybe some sort of compromise can be reached: is a call for an arbitrator in order? In any case, I am inclined to (have to) agree with RAGAN's (1998) very recent assessment, that "monophyly (holophyly) is our strongest line of defense against rampant arbitrariness."

Furthermore, there is no question of the immense value of robust phylogenetic trees in understanding the evolutionary relationships within given groups of organisms. The modern literature is replete with excellent examples of this (for two quite recent ones, with emphasis on results of rRNA studies, see SOGIN 1994; SOGIN et al. 1996). For a treatment of protists alone, LIPSCOMB (1991), in a comprehensive cladistic study using the "constellation of characters" approach (CORLISS 1976), has postulated that there are a dozen separate, presumably monophyletic lines, involved; but no taxonomic ranks or names are assigned to them by her nor are attempts made to show the possible taxonomic relationships of these clades to each other.

I am indebted to Mark RAGAN (personal communication; and now see RAGAN 1998) for bringing to my attention the fact that BATHER (1927), more than 70 years ago, perceptively foresaw the difficulties of using phylogenetic trees as a highly suitable basis for a hierarchical arrangement of any groups of organisms. For the protozoa, incidentally, later RAABE (1964) voiced the same view, independently but not as eloquently. BATHER, although of course knowing nothing of the molecularly derivable trees/cladograms possible today, suggested three reasons for drawing the conclusion of his stated above: (1) The "more complete the phylogenetic tree, the further it must depart from a classification based originally on different principles." (2) The "more refined our analysis becomes, the greater is the difficulty of representing its results in any classificatory scheme." And (3) A "classification which obscures the qualities of the goods as delivered loses thereby in practical value."

8.3 Protists as Single Discrete Kingdom

As indicated on a preceding page, the neoHaeckelian concept, which retains a single kingdom for protists (now plus three other eukaryotic kingdoms: the popular five-kingdom arrangement if all prokaryotes are assigned to a single additional kingdom), remains a valid choice or option for treatment of the implicated algal, protozoan, and "lower" fungal assemblages. This MARGULIS-favored solution is highly satisfactory from the points of view of convenience and relative

simplicity for information retrieval systems and for the education/edification of high-school and college students, the general public, non-scientific professional people, and non-biological scientists. It could serve – and already is admirably serving – the purposes of such clientele.

Unfortunately, from both evolutionary (including cladistic) and megasystematic stands, the notion of a single Protista/Protoctista kingdom for inclusion of the many diverse taxa of the "lower" eukaryotes is now widely recognizable by most if not all research-oriented protistologists (see comments in CORLISS 1994, 1998b; and **vide infra**) as an unsatisfactory choice. Nevertheless, this particular option, for the utilitarian reasons just noted, could be said to remain equally as viable as the two preceding ones described above.

8.4 Protists throughout Multiple Eukaryotic Kingdoms

Finally, an option which I believe is easily supportable and perhaps the soundest among the choices being discussed briefly in this paper is to assign various of the high-level protistan groups, now known to be widely diverse evolutionarily and taxonomically, to separate eukaryotic kingdoms, at least several and probably ideally many in number (the latter view should find favor with the cladistic/phylogenetic systematists). This is not a new idea, of course, as I have already pointed out on preceding pages. In very recent years, analyses of information accumulated from molecular as well as ultrastructural, biochemical, ecological, and other studies are revealing more than ever before the many clear-cut evolutionary gaps between and among classical algal, fungal, and protozoan phyla. Taxonomic inflation at the top, or at least near-top (phyletic), level seems inevitable, distasteful though it may be (as mentioned above) from the several utilitarian points of view supporting the single neo-Haeckelian kingdom for all protists.

Reaching such a megasystematic conclusion, controversial though it may be, need not be too complicated (see discussions in CAVALIER-SMITH 1993, 1997a, 1998a; CORLISS 1994, 1995, 1998b). In fact, the number of kingdoms involved can be as low as five or six (see Table 1); and all of them (and much of their taxonomic content) have already been named and described or redescribed in the recent literature (primarily in works by CAVALIER-SMITH: see appropriate references in the papers cited above). This multikingdom option solves several long-standing problems and criticisms of both earlier and some contemporary protistan classification schemes, going back as far as HAECKEL's (1866, 1878) original works up through COPELAND (1956), WHITTAKER & MARGULIS (1978), LIPSCOMB (1991), PATTERSON (1994), MARGULIS & SCHWARTZ (1998), and others not given here.

Put succinctly, the matters involved concern placements/locations of the main algal lines, the phylogenetically very primitive amitochondriate protistan groups, the "typical" autotrophic algae contrasted with the "typical" phagotrophic protozoa, and the "true" unicellular fungi and their pseudofungal look-alikes. To this short list one may add the problems caused by the curious phyla Microspora and Myxozoa, taxonomically baffling groups of parasitic microorganisms until very recently always placed, if with reluctance, somewhere among the protozoan protists. Recent careful sequencing work suggests that they should now be assigned to quite different kingdoms: the microsporidians to the kingdom Fungi and the myxosporidians of old to the Animalia, placements which may be said to have been foreseen years ago by the keen protozoologists/parasitologists Elizabeth CANNING (e. g., 1977, and later) and Jiří LOM (1964, and later). Recent researches – with some still in progress – on all such problems are cited and discussed in concurrent papers by CAVALIER-SMITH (1997a, b, 1998a, b) and CORLISS (1998b).

Probably the most striking change or improvement embodied in the recent five or six-kingdom hypothesis is related to the definitive placement of the green algal line **in toto** – and **only** this algal clade – in the kingdom Plantae. But not to be overlooked is the fact that COPELAND (1956) and a few other workers (see ROTHSCHILD 1989; LIPSCOMB 1991; and references therein) had already made this shift, so highly unacceptable to MARGULIS. COPELAND had separated the greens from the

browns and reds, with only the green algae (uni- and multicellular) remaining with the "higher" plants (although the reds may, albeit controversially, belong in the Plantae as well, as CAVALIER-SMITH 1981, 1987, quite long ago, postulated: and see RAGAN & GUTELL 1995). But few workers (botanists, zoologists, or protistologists) have accepted this phylogenetically supported taxonomic decision openly – the splitting up of algal lines and (re)assigning them to different kingdoms – in the 40-odd years since COPELAND's monograph (except principally CAVALIER-SMITH 1981, 1983, and later papers). However, using molecular techniques, workers (e. g., see ANDERSEN 1992; SOGIN 1989, 1991; DAUGBJERG & ANDERSEN 1997; and references cited in such papers) have – for some time – clearly recognized that greens, browns, and reds are not sibling taxa (and see discussion in CAVALIER-SMITH 1995b).

9 Author's Tentatively Proposed Revision

Using standard ranks and hierarchies, we have progressed from HAECKEL's three-kingdom tree, viz., Protista, Plantae, and Animalia, with its mixed bag of phyla/classes (Figure 1), to my here tentatively proposed revised five-kingdom arrangement (Table 1, with all prokaryotic groups purposely excluded), with its kingdoms Protozoa, Chromista, Plantae, Fungi, and Animalia, novel to the extent that every one of them now includes unicellular protistan representatives. Some 35 more or less discrete phyla are required to contain all known species of my protists, the bulk of which are assigned to either the Protozoa or the Chromista, but with also half a dozen to the Plantae; and, in a further attempt to reduce polyphyly and/or paraphyly in general in my groupings, the chytrids and the microsporidians are placed in the Fungi and choanoflagellates and myxozoa in the Animalia. For overall descriptions and characterizations (and included subgroups) of the kingdoms and phyla that I am now recognizing, information well beyond the limited scope of the present essay, the reader is referred especially to CORLISS (1994, 1998b) and, for many details, to CAVALIER-SMITH (1993, 1998a, b, and references therein). The taxonomic disagreements that I may have with the conclusions reached by CAVALIER-SMITH, although not to be disregarded, are for the most part neither major nor extensive: for example, I am now following him in the reduction of the former "kingdom Archezoa" to a subkingdom, or less, ranking within the Protozoa.

My classification may still fall short of some colleagues' expectations, in several respects (e. g., seemingly endorsing polyphyly in several instances). And I am well aware of the revisory impact that startling new data may cause. Incidentally, only phyla that I consider to be composed solely of **protists**, be they uni- or multicellular in nature (although all included species are essentially without multiple tissues), are listed in Table 1. That is, I am concerned here with the kingdom-level taxonomic location of only the "lower" eukaryotic assemblages of organisms, groups that I have uniformly identified and treated as protistan phyla. Names of the **other** phyla belonging to the three so-called "higher" kingdoms (i.e., Plantae, Fungi, Animalia) are purposely omitted from Table 1.

I may have too many separate phyla, especially from a pedagogical viewpoint. But the major significance of the arrangement offered here (a slight revision over those found in CORLISS 1994, 1995, 1998b: e. g., Microspora is placed within the Fungi; Choanozoa and Myxozoa are moved from Protozoa to Animalia; Opalozoa is moved from Protozoa to Chromista, essentially as Opalinata; and one or two additional phyla are recognized within Protozoa and Chromista) is my discarding of the notion that the Protista have to be – or even can be – confined to or maintained as a **single** kingdom. Surely, as others (most insistently and persistently, CAVALIER-SMITH) have also pointed out in past years, a more natural and evolutionarily and phylogenetically more proper arrangement requires wider dispersal or separation of high-level groups showing such diversity in their genetic and phenotypic characteristics. In my opinion, we must also abandon the long-attractive idea (since dates of dropping of the still earlier conventional Plantae/Animalia dichotomy: see especially

the Margulisian system discussed on preceding pages) that the "higher" kingdoms cannot, simply by arbitrary declaration, contain any unicellular members.

As mentioned on preceding pages, cladograms derived from molecular and/or morphological (usually ultrastructural) data support the general concept of assignment of protistan forms to multiple kingdoms (or, at least, to separate high-level taxonomic or cladistic groupings). However, many modern phylogeneticists highly eschew speculation and "educated guesses", strategies sometimes apparent in the classification schemes of workers such as CAVALIER-SMITH and the present writer. To what extent can such arbitrariness or liberty be taken (and forgiven) in the name of continuity, convenience, utility, and/or stimulation to further research? With respect to predictions based on scanty proof, perhaps today's systematic protistologists could be said to be in good company... with HAECKEL himself!?! E. C. DOUGHERTY (in DOUGHERTY & ALLEN 1960) once made an observation that may be of relevance and thus worthy of repetition here. He wrote, that it is "better to have a working hypothesis, even if based on fragile evidence, than to shrug aside a question of phylogeny as prematurely posed."

Table 1
Protistan phyla assigned to eukaryotic kingdoms (phyletic names arranged alphabetically).

Kingdoms	Included Protistan Phyla
PROTOZOA	Apicomplexa, Archamoebae, Ciliophora, Dinozoa, Euglenozoa, Foraminifera, Heliozoa, Metamonada, Mycetozoa, Neomonada, Parabasala, Percolozoa, Radiozoa, Rhizopoda
CHROMISTA	Bicosoecae, Chrysophyta, Cryptomonada, Diatomae, Dictyochae, Haptomonada, Labyrinthomorpha, Opalinata, Phaeophyta, Pseudofungi, Raphidophyta
PLANTAE	Charophyta, Chlorophyta, Glaucophyta, Prasinophyta, Rhodophyta, Ulvophyta
FUNGI	Chytridiomycota, Microspora
ANIMALIA	Choanozoa, Myxozoa

10 Concluding Thoughts

One hopes that the future will bring an abundance of new data and fresh interpretations, and improved concepts, all of which may result in some widely satisfying way of appreciating the diversity of the protists, on the one hand, and their expanded overall taxonomy, on the other hand.

As I have recently stated elsewhere (CORLISS 1998b), the interdisciplinary protist perspective is a healthy one, despite the multiple problems briefly exposed in this essay. It would be ideal to have the megasystematics of these numerous (some 120,000 described species: CORLISS 1984; but perhaps 200,000 is a more accurate estimate: CORLISS 1990, 1994) and fascinating organisms resolved by the beginning (or early years) of the 21st century. As everyone agrees, however, much more research work in protistology **sensu lato** needs to be carried out before such a goal can be fully realized.

Through it all, our debt to the initial vision and courage of the great German biologist Ernst HAECKEL, Father of Protistology, will remain a tremendous one.

11 Acknowledgments

It is a pleasure to acknowledge counsel requested and received (although not always followed) during preparation of this essay from protistological colleagues Tom CAVALIER-SMITH, Mark RAGAN, and Lynn ROTHSCHILD. I am also grateful to Dr. Erna AESCHT for translating the abstract into German and kindly providing the materials used in my Figures 1-4.

12 Zusammenfassung

HAECKELS Reich Protista und moderne Konzepte in der systematischen Protistologie.

Ernst HAECKEL, einer der ganz Großen unter den Biologen der zweiten Hälfte des 19. Jahrhunderts, errichtete kühn ein neues drittes Organismenreich Protista für weitgehend mikroskopisch kleine und einzellige Lebewesen, die seiner Ansicht nach nicht länger zu den beiden traditionellen Reichen der makroskopischen und vielzelligen Pflanzen und Tiere gestellt werden sollten. Dieses systematische Konzept auf evolutionärer Grundlage, vorgeschlagen 1866, verfeinert 1878 (und in den folgenden Jahren), war von Anfang an umstritten und ist es heute noch. Wie auch immer, die Idee war – und ist – von großem Wert, wenn auch nur, um die Aufmerksamkeit auf die phylogenetischen Komponenten der Taxonomie zu lenken und auf die sonst vielfach ignorierten überaus diversen Gruppen der hauptsächlich mikroskopischen eukaryotischen Lebewesen, die nun weithin als „die Protisten" bekannt sind (bestehend aus den konventionellen Algen, Protozoen und „niederen" Pilzen). Dieser Beitrag diskutiert, nach einem kurzen geschichtlichen Abriß, Versuche im 20. Jahrhundert, die systematische Behandlung der höheren Kategorien aller Protisten zu verbessern. Die vorgestellten gegenwärtigen Meinungen, eine davon kann als besonders neo-Haeckelianisch betrachtet werden, sollen zeigen, daß die Megasystematik der Protisten in ständiger Veränderung bleiben wird, bis mehr relevante Daten für detaillierte Analysen zur Verfügung stehen. In Anbetracht der sich wandelnden Verwendungen oder Zielrichtungen, denen solche Megasysteme letztendlich unterliegen können, ist es eine der bedeutendsten Herausforderungen, der sich Bearbeiter dieses Gebietes heutzutage gegenüber sehen, Wege zu finden wie man die Information von phylogenetischen Kladogrammen in die Rangfolge hierarchisch gegliederter Klassifikationsschematas bringt (falls die Beibehaltung letzterer in Zukunft wünschenswert erscheint). In einer Tabelle präsentiert der Autor kurz seine gerüstartige Ordnung der höheren Protistentaxa, die einen Fortschritt gegenüber jenen in der rezenten Literatur bringen möchte, indem sie folgenden Gedanken besonders betonen: Die Vielfalt der Protisten ist zu groß, um auf ein einziges Reich beschränkt zu bleiben, und daher müssen die Species auf alle verschiedenen Reiche der eukaryotischen Lebewelt, die heute zunehmend anerkannt sind, verteilt werden.

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