Biodiversity: molecular biological domains, symbiosis and kingdom origins

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The number of extant species of organisms is estimated to be from fewer than 3 to more than 30×10^6 (May, 1992). Molecular biology, comparative genetics and ultrastructural analyses provide new insights into evolutionary relationships between these species, including increasingly precise ideas of how species and higher taxa have evolved from common ancestors. Accumulation of random mutations and large macromolecular sequence change in all organisms since the Proterozoic Eon has been importantly supplemented by acquisition of inherited genomes ('symbiogenesis'). Karyotypic alterations (polyploidization and karyotypic fissioning) have been added to these other mechanisms of species origin in plants and animals during the Phanerozoic Eon. The new evolution concepts (coupled with current rapid rates of species extinction and ignorance of the extent of biodiversity) prompted this analysis of the field of systematic biology and its role in the reorganization of extant species into higher taxa. Two superkingdoms (= Domains: Prokaryotae and Eukaryotae) and five kingdoms (Monera = Procaryotae or Bacteria; Protoctista: algae, amoebae, ciliates, foraminifera, oomycetes, slime molds, etc.; Mychota: 'true' fungi; Plantae: one phylum (division) of bryophytes and nine phyla of tracheophytes; and Animalia) are recognized. Two subkingdoms comprise the monera: the great diverse lineages are Archaebacteria and Eubacteria. The criteria for classification using molecular, ultrastructural and genetic data for this scheme are mentioned. For the first time since the nineteenth century, logical, technical definitions for each group are given with their time of appearance as inferred from the fossil record in the primary scientific literature. This classification scheme, which most closely reflects the evolutionary history, molecular biology, genetics and ultrastructure of extant life, requires changes in social organization of biologists, many of whom as botanists and zoologists, still behave as if there were only two important kingdoms (plants and animals).

Keywords: Archaebacteria; Evolution; Mychota; Protoctista; Symbiogenesis; Systematics.

The goal of the field of 'systematics' is identification, naming and classifying of all life forms and the organization of this information about the diversity of life on Earth in the context of its evolutionary history. The most common method of depicting the results of evolutionary studies is the 'phylogenetic tree' or 'dendrogram'. Partial phylogenies, by definition, are those that use one key characteristic (e.g., morphology, 5S rRNA nucleotide sequence data, cytochrome *c* amino acid sequence data) upon which the phylogenetic diagram is built.

Total or 'systematic phylogenies' attempt to evaluate the entire suite of genetic, biochemical, ultrastructural, morphological, metabolic and behavioral aspects of the organisms in forming the 'tree.' Because of the comprehensive goals of systematic biology that field of science would seem to have the highest priority in the life sciences. Any scientific pronouncements about biological species diversity and its loss emanate directly from systematics. Yet, in a social sense systematic science is undervalued. The relative obscurity of systematists and their current funding sources reflects the vagaries of history, politics and human social organization.

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Specialists, biologists who are taxonomists, describe and name species in the many journals of the primary literature. Species are grouped and classified into a smaller number of genera; the genera are grouped into progressively fewer taxa each with a larger number of species. The highest taxa (called subkingdoms or phyla in zoology, 'divisions' in botany and 'divisions' or 'domains' in bacteriology) are erected to represent the most significant evolutionary differences between the organisms in question. The explicit goals of taxonomy such as naming, identifying and classifying, were developed by Linnaeus (the Swede Carolus von Linné) in the 18th Century. Linnaeus, who believed in the fixity of species given man by God, was certainly not an evolutionist. In his monumental contribution he classified fewer than 10 000 organisms. His activities were greatly supplemented by subsequent workers most notably the 19th

Table 1. Five-kingdom classification of life.

Taxon	Description and estimated number[1] of species
Superkingdom Prokaryota ≡ (Domain PROKARYOTAE)	Bacterial cell organization (chromonema, small ribosomes, continuous DNA synthesis; rotary motor flagella[2]).
KINGDOM MONERA	Single homologous genomes. All modes of metabolism represented[3].
Eubacteria	Eubacterial 16S rRNA and lipids; peptidyl-glycan cell walls (examples: enterobacteria; cyanobacteria and other phototrophs; mitochondria and plastids; spirochetes and other Gram-negative bacteria; Gram-positive bacteria). (10 000)[1].
Archaebacteria	Archaebacterial ribosomes and 16S rRNA; ether-linked lipids (examples: methanogenic, thermacidophilic and halophilic bacteria). (500).
Superkingdom Eukaryota ≡ (Domain EUKARYOTA)	Nucleated cell organization with chromatin (histones, nucleosomes, nuclear pore complexes); mitotic karyokinesis; actin-based cytokinesis; microtubule-based, intracellular motility systems; intermittent DNA synthesis. Proteinaceous, etc. walls. Two modes of metabolism[3].
KINGDOM PROTOCTISTA	Microorganisms and their larger descendants composed of multiple heterologous genomes. Variations on mitosis and meiosis; many have undulipodiated[4] cells. (Examples: algae, chytrids, slime molds, ciliates). (250 000).
KINGDOM MYCHOTA[5]	Fungi. Haploid or dikaryotic, osmotrophic heterotrophs that develop from fungal spores and display zygotic meiosis (examples: yeasts, mushrooms, lichens); chitinous walls; no undulipodiated cells. (70 000).
KINGDOM PLANTAE	Embryophytes. Gametophytes develop from haploid spores; fertilization of eggs by undulipodiated sperm or male nuclei produces sporophyte embryos that are retained in maternal tissue (examples: bryophytes, tracheophytes). Plasmodesmata between cells; cellulosic walls. (400 000).
KINGDOM ANIMALIA	Diploids develop from products of anisogamous (sperm/egg) fertilization into blastula embryos (examples: porifera, mollusks, chordates). Ingestive nutrition, complex cell connections (e.g., desmosomes, septate junctions), muscle tissue; no cell walls. (30 000 000).

[1]Upper estimates, May 1991; Margulis et al., 1990.

[2]Extracellular flagella composed of flagellin proteins powered by rotary motors.

[3]Chemo-organoheterotrophy to photolithoautotrophy, all modes represented in prokaryotes. Chemo/photo refers to source of energy; organo/litho refers to source of electrons; hetero/auto refers to source of carbon. Chemo-organoheterotrophy and photolithoautotrophy are are the two modes of metabolism associated with eukaryotes. For the bacterial alternatives, see Table I-2 in Margulis et al., 1990.

[4]Intracellular undulipodia (underlain by kinetosome/centrioles) powered by microtubule-associated proteins in [9 (2) + 0] arrays.

[5]Preferred formal name of kingdom (Melvin Fuller, pers. commun.).

Fig. 1. Orgins of life and time of appearance of members of the five kingdoms in the fossil record.

century naturalists (Henry Walter Bates, Alfred Russel Wallace, L. Walter Rothschild, Charles Darwin, etc.). Only since the work of Darwin — and later G.G. Simpson, E. Mayr and others — have taxonomies been explicitly 'systematic', i.e., attempts made to unite concepts of Darwinian evolution with practices of classification (Mayr, 1982).

Although newly discovered species and genera require names approved by one of the three codes (International Code of Zoological Nomenclature, London; International Code of Botanical Nomenclature, Norway; International Code of Nomenclature of Bacteria, Washington, DC; Lapage et al., 1975), the code practices differ greatly and, in the case of the phototrophic motile protoctists, they are frankly contradictory (Bold et al., 1978). The lack of consensus concerning the highest taxa and their evolutionary history has led to such confusion that most modern biologists and their grant officers, tend to disdain systematics (except for the use of species names of course) and ignore the results of taxonomic work. Limited to dead material and using far more costly biochemical methods, most experimental scientists believe they replace 'traditional taxonomy' with more 'objective' schemes by providing molecular sequence data. However the names of the taxa used to designate organisms (e.g., 'protozoa') may be so ill-defined or obsolete that the otherwise valuable data is rendered meaningless. My goal here is to define higher taxa (Table 1; Fig. 1) based on information from molecular and cell biology in conjunction with morphology and to advocate use of the best aspects of the historical documentation practices of the organized 'systematic societies': zoological, bacteriological and botanical codes and their international congresses.

The molecular data for all species (combined with the other sorts of data on morphology, life cycle, genetics and development) have the potential to revitalize the field of systematic biology such that phylogenetic diagrams encompassing life on Earth and reflecting its single evolutionary past can be constructed. Modern phylogenetic diagrams (i.e., total phylogenies that take into account all of the information about a group of organisms) can be drawn that depend closely on the data derived from molecular phylogenies. Yet, despite the details (amount of sequence data and methods of alignment), molecular phylogenies are intrinsically limited; they use only one or two of the 5 – 10 000 types of macromolecules present in any organism. Thus, at best, any molecular phylogeny can be only a 'partial phylogeny.' Even beyond the low level of representation of any single macromolecular type, the concepts of phylogenetic systematics (Hennig, 1966), are in principle, flawed. Phylogenetic diagrams are inadequate because the branches (representing the lineages of organisms) are allowed only to end (by extinction) or bifurcate (to form new species). Since we know that new species form by unification and integration of symbionts in which different lineages combine and recombine (i.e., the process of symbiogenesis, Khakhina, in press), the consistent failure to include anastomosis of branches continues to perpetrate errors of omission in nearly all evolutionary representations.

That modern insights into the mechanisms of speciation have not yet been incorporated into formal systematic science is apparent by three measures: (1) the failure of phylogenetic systematists to draw anastomozing branches on dendrograms as required by unification of stable hereditary symbionts derived from different lineages, (2) the absence of consistent naming practices** when a membrane or integument bounded 'individual' is clearly the product of the integration of symbionts and (3) the relative ignorance of biologists (botanists, zoologists) of microbiology and vice versa.

The number of species alive today is unknown*. This is especially true of the smaller animals and all the microorganisms (May, 1992). Macromolecular sequence analysis, in these cases especially, provides powerful new insights into evolutionary relationships between species,

*30 × 10^6 is the preferred value. Since fewer than 300 000 or more than 3 billion species are highly unlikely, one concludes that the number of extant species is unknown to probably a factor of 100. **(See Mindell p. 53 of this volume).

Table 2. Phyla of the five kingdoms.

Prokaryotae (PROKARYA). Single homologous genomes.

KINGDOM MONERA
Subkingdom Archaebacteria[1] (**Division Mendosicutes**)
Phyla:
1. Methanocreatices (methanogens)
2. Halophilic bacteria
3. Thermoacidophilic bacteria

Subkingdom Eubacteria
Phyla (16), distributed in three divisions:
I. Aphragmabacteria (**Division Tenericutes**)
II. Gram-negative bacteria (**Division Gracilicutes**)
III. Gram-positive bacteria (**Division Firmicutes**)

Eukaryotae (EUKARYA). Multiple heterologous genomes.

KINGDOM PROTOCTISTA
Phyla, distributed in four divisions:
I. Lack undulipodia; lack complex sexual cycles
1. Rhizopoda (amoebae[2])
2. Haplosporidia (animal parasites)
3. Paramyxea (animal parasites)
4. Myxozoa (animal parasites)
5. Myxospora (animal parasites)
6. Ellobiopsida (animal parasites)

II. Lack undulipodia; complex sexual cycles present
7. Acrasea (cellular slime molds)
8. Dictyostelida (cellular slime molds)
9. Rhodophyta (red algae)
10. Conjugaphyta (conjugating green algae, desmids)

III. Undulipodia; lack complex sexual cycles
11. Xenophyophora
12. Cryptophyta (cryptomonads)
13. Glaucocystophyta
14. Karyoblastea (giant amoebae)
15. Zoomastigina
   (amoebomastigotes, bicosoecids, choanomastigotes, diplomonads, pseudociliates, kinetoplastids, opalinids, protero-monads, parabasalids, retortamonads, pyrsonymphids)[3]
16. Ebridians
17. Euglenida (euglenids)
18. Chlorarachnida (green amoebae)
19. Prymnesiophyta (haptomonads, coccolithophorids)
20. Raphidophyta (motile algae)
21. Eustigmatophyta (motile algae)

IV. Undulipodia; complex sexual cycles present
22. Actinopoda (polycystine and phaeodarian 'radiolarians,' heliozoans, acantharians)
23. Hyphochytriomycota (hyphochytrids)
24. Labyrinthulomycota (slime nets)
25. Plasmodiophoromycota (plant parasites)
26. Dinomastigota (dinoflagellates, mastigote algae)

27. Chrysophyta (golden yellow algae)
28. Chytridiomycota (chytrids, water molds)
29. Plasmodial slime molds (myxomycotes, protostelids)
30. Ciliophora (ciliates)
31. Granuloreticulosa (reticulomyxids, foraminifera)
32. Apicomplexa (animal parasites)
33. Bacillariophyta (diatoms)
34. Chlorophyta (green algae)
35. Oomycota (water molds, plant and insect parasites)
36. Xanthophyta (yellow green algae)
37. Phaeophyta (brown algae)

KINGDOM MYCHOTA
Phyla:
1. Zygomycota (conjugating molds)
2. Ascomycota (molds, yeasts)
3. Basidiomycota (mushrooms, rusts, smuts, puffballs)
4. Deuteromycota (molds)
5. Mycophycophyta (lichens)

KINGDOM ANIMALIA
Phyla:
1. Placozoa (*Trichoplax*)
2. Porifera (sponges)
3. Cnidaria (coelenterates)
4. Ctenophora (comb jellies)
5. Mesozoa (parasitic worms)
6. Platyhelminthes (flatworms)
7. Nemertina (worms)
8. Gnathostomulida (worms)
9. Gastrotricha (worms)
10. Rotifera (wheel animals)
11. Kinorhyncha (worms)
12. Loricifera
13. Acanthocephala (worms)
14. Entoprocta (worms)
15. Nematoda (roundworms)
16. Nematomorpha (worms)
17. Ectoprocta (worms)
18. Phoronida (worms)
19. Brachiopoda (lampshells)
20. Mollusca (snails, clams)
21. Priapulida (worms)
22. Sipuncula (worms)
23. Echiura (worms)
24. Annelida (segmented worms)
25. Tardigrada (water bears)
26. Pentastoma (parasites)
27. Onychophora (velvet worms)
28. Arthropoda (ticks, insects, crustaceans)
29. Pogonophora (tubeworms)
30. Echinodermata (starfish, sea urchins)

31. Chaetognatha (worms)
32. Hemichordata (worms)
33. Chordata (sea squirts, fish, mammals)

KINGDOM PLANTAE
    Phyla:
      1. Bryophyta (mosses, liverworts)
      2. Psilophyta
      3. Lycopodophyta (clubmosses)
      4. Sphenophyta (Equisetophyta; horsetails)
      5. Filicinophyta (Pteridophyta; ferns)
      6. Cycadophyta (cycads)
      7. Ginkgophyta (maidenhair trees)
      8. Coniferophyta (pines, firs)
      9. Gnetophyta
     10. Angiospermophyta (Magnoliophyta; flowering plants)

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[1]Preferred spelling 'Archaeobacteria' in Bergey's Manual (Holt, 1983–1992).
[2]Common names where available.
[3]Probably more phyla will be constructed.
The evolution of the multiple-genomic eukaryotes from their single-genomic prokaryotic ancestors is plotted against time in Fig. 2. Nucleocytoplasm derived symbiogenetically from integration of archaebacteria (probably *Thermoplasma*) and motile eubacteria (probably spirochetes). Mitochondria evolved from integrated oxygen-respiring eubacteria (proteobacteria) whereas plastids of algae and plants came from still other symbiogenetically integrated eubacteria (cyanobacteria).

even for organisms that can not be grown in the laboratory (Giovannoni et al., 1990). The new techniques, coupled with results of electron microscopical analyses have yielded realistic concepts of how members of these species have evolved from common ancestors. The higher taxa — families, phyla (Table 2) and kingdoms — probably evolved in the same way as did species (Bermudes and Margulis, 1987). Accumulation of random mutation once considered the only important way species evolve, is supplemented by origin of new species and higher taxa by 'macromutation' including the inheritance of acquired genomes of various sizes (e.g., 'symbiogenesis' (Khakhina, 1979; Nardon et al., 1990; Margulis and Fester, 1991), by karyotypic fissioning (Todd, 1992) and by polyploidy (Mayr, 1982). Our sense of urgency toward documenting and classifying extant organisms is generated by our increasing awareness of rapid rates of anthropogenic extinction, on the one hand and by serious deficiencies in our

knowledge of the extent of biological diversity on the other. But diversity can not be adequately documented unless the classification scheme that permits organization of extant species and other groups into higher taxa actually reflects, as well as possible, the history of the organisms in question. The systematic organization of the extant biota presented here is based on the work of hundreds of individual scientists. As R.M. Hutchins said about the University of Chicago, 'it may not be good but it is the best we have.'

Criteria for classification are listed here in order of importance. For any given individual organism (recognized by the fact that it is bounded by membrane, integument, skin or other completely intact solid covering) the number of genomic systems (i.e., total genetic material plus associated protein synthetic systems, including 5S, 16S and 23S rRNA or their equivalents) and the relationship between the systems are first noted. For 'individuals' it must be asked: are they composed of multiple

copies of homologous genomic systems — 'homogenomic multicellular' — or are they integrated heterologous genomic systems — 'integrated hereditary symbionts'? Expressed differently, the genomic status of the cells which comprise the organism is first determined. Whether or not the genomic systems are prokaryotic (non-nucleate) or eukaryotic (nucleate) is then evaluated. Two superkingdoms (Prokaryotae and Eukaryotae, Table 1) are easily distinguished since all members of the former are composed of cells that contain single genomic systems in one ('single-celled' or monad) or many copies of the same genomic system ('multicellular': thalloid, filamentous, colonial, etc., or polymonad). (The term 'superkingdom' for the highest, most inclusive, taxon is used in the same way as 'Domain' by Woese et al., 1990 and is equivalent to it. (See Taylor, 1974, for the monad/polymonad dyad/polydyad concept.) Given this overall division of life into bacteria and other organisms, five kingdoms are recognizable. The first is the Monera, or all bacteria which are unicellular and multicellular organisms composed of prokaryotic cells. They are formally called 'Procaryotae' by bacteriologists, Holt, 1992; Balows et al., 1992, or 'Prokarya' by Woese et al., 1990). The four kingdoms of organisms composed of multiheterogenomic chromatin-containing nucleated cells all contain multicellular members (polydyads, polytriads, polytetrads, etc.). The earliest of these to evolve are the dyad and triad eukaryotic microorganisms and their larger descendants exclusive of the animals, plants and fungi sensu stricto. All algae including chlorophytes, diatoms, rhodophytes and phaeophytes (but of course excluding 'cyanophytes' which are unequivocally bacteria), as well as slime molds, foraminifera, slime nets, ciliates, chytrids, oomycotes and many other groups, belong to this taxon, defined and characterized in Table 1. The current list of phyla of these dyad or triad organisms is in Table 2. The formal name for this enormously diverse and poorly known group of aquatic organisms is Kingdom Protoctista (Margulis et al., 1990). This kingdom includes representatives of the earliest biomineralized or otherwise preserved eukaryotes found in the fossil record.

Because so many white, osmotrophic, filamentous, matted eukaryotes superficially resemble the 'true fungi' it has been suggested by Mel Fuller (University of Georgia, pers. commun/, 1991) that the appellation Mychota be reserved for members of the Kingdom Fungi in the strict sense as non-undulipodiated spore-forming haploids that undergo zygotic meiosis. The term 'fungi' would continue to be used informally in an ecological context, i.e., for those organisms with the 'fungal way of life'. (This is entirely comparable to the terms 'algae', 'phytoplankton' or 'photoplankton' which are used informally for all phototrophic protoctists, i.e., aquatic non-embryophytic oxygenic photosynthetic eukaryotes). 'Fungi' then would continue to refer to hyphae-forming chitinous-walled organisms with an osmotrophic, absorptive way of life which are free-living or symbiotrophic, including necrotrophic ('parasitic' and 'pathogenic') forms. Many of these are protoctists (e.g., plasmodiophorans, hyphochytrids, oomycetes, etc., Kendrick, 1992). The term 'Mychota' would be reserved for the 'true' fungi: members of the phyla Zygomycota, Ascomycota, Basidiomycota, or Mycophycophyta (the lichens), which first appear in the record approximately 450 million years ago. The other familiar kingdoms are of course the plants in the strict sense: Kingdom Plantae (haplodiploids that develop from maternally retained embryos), which includes only bryophytes (mosses, liverworts and hornworts) and tracheophytes (vascular plants, primarily land-dwelling organisms). The first plants appeared about 450 million years ago. The animals (Kingdom Animalia, all of whose members develop from sperm-fertilized eggs in which zygotes form blastular embryos) have more than 33 phyla (Margulis and Schwartz, 1988). The first soft-bodied animals appeared with large protoctists about 750 million years ago in the worldwide Ediacaran 'fauna' (McMenamin and McMenamin, 1990). They must have fed on phototrophic bacteria and protoctists since no plants
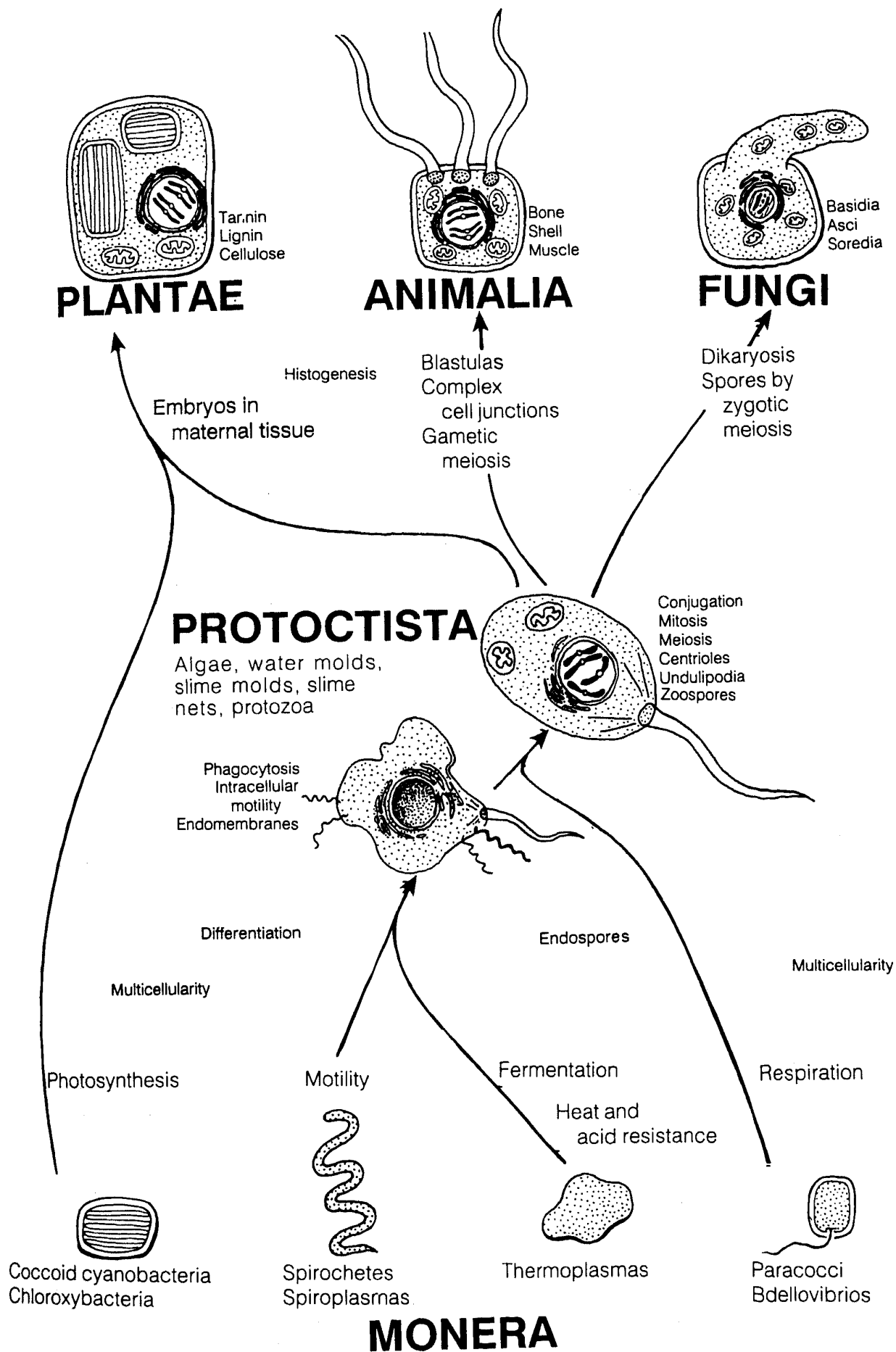
Fig. 2. Anastomozing phylogenies in the origins of all eukaryotic kingdoms from their prokaryotic ancestors. See footnote (p. 45) and accompanying paper by Mindell (BioSystems, 27 (1992) 53–62).

existed at that time. The greatest diversity of taxa in the animal kingdom clearly is in the marine environment where unfortunately it is least known. Of the 33 phyla of animals, only two have entirely terrestrial classes (e.g., Arthropods such as Insecta and Chordates such as Aves). Even those two phyla have classes of entirely aquatic, especially marine organisms (e.g., crustaceans, teleost fishes).

Of the many enzymes, co-factors and other macromolecules in all cells, the sequences of only very few (amino acids of universally distributed proteins, nucleotides of long-chain nucleic acids) are useful for establishment of evolutionary relationships between representatives of all life on Earth. Their use is determined by: the prevalence of the molecular sequences with the same function in all organisms that are to be compared, the amount of information stored in the sequence and the availability of methods of analysis. In the absence of complete DNA sequence data of the organism to be placed on any phylogenetic diagram, the use of the genes for the large subunit ribosomal RNA (rRNA) has proved immensely useful in the clarification of the relationships between bacteria (Woese et al., 1990); protoctists (Sogin et al., 1989; Schlegel, 1991) as well as animals, plants and fungi (summarized in Strickberger, 1990). Yet, in all eukaryotes, rRNA molecules are associated with at least two heterologous genomes. Because one (e.g., nucleocytoplasmic rRNA) can not be privileged over the others (e.g., mitochondrial or plastid rRNA) in construction of the phylogeny of the whole, the introduction of three parallel domains (Archaea, Prokarya, Eukarya; Woese et al., 1990) as if they all were single-genomic and therefore comparable is illogical (Margulis and Guerrero, 1991; Woese et al., 1990) and should be unacceptable to all biologists, especially those interested in the relation between evolutionary history and taxonomy, for reasons outlined by Mayr, 1990, 1991.

As Mayr (1990) notes, taxonomic hierarchies and information-retrieval systems and classifications of the living world are not limited to specialists. They must be optimized for general, international use by teachers, agriculturists, fishermen, soil scientists, hospital workers and everyone else who deals with the diversity of life. Woese et al. violate the taxonomic principles: that the best classification scheme is based on as many diagnostic differences as possible (Mayr 1991).

Molecular biological data makes it imperative that two diverse subkingdoms are recognized in the bacteria: the two great lineages are Archaebacteria (Archeobacteria = Archaea, Woese et al., 1990) and Eubacteria, all the other bacteria, including cyanobacteria and eukaryotic organelles (mitochondria and plastids). Inferred from stromatolites and microfossils preserved in cherts, members of these subkingdoms first appeared about 3500 million years ago, far earlier than any eukaryotes (which appear as acritarchs, spherical fossil protoctists, during the Proterozoic Eon about 1500 million years ago, Vidal, 1984.)

This classification scheme, which reflects most closely the evolutionary history, molecular biology, genetics and ultrastructure of extant life, is only slightly modified from the form in which it was first introduced into the literature by Whittaker (1959). The resistance against its acceptance is not scientific, rather it is related to professional social organization (e.g., microbiologists and protozoologists who study necrotrophic microorganisms of interest in the health professions, although they study some yeasts and other fungi, traditionally ignore the phototrophic bacteria, algae and other organisms closely related to those whose necrotrophy interests them). Since identical organisms are described by oceanographers as 'phytoplankton' or 'nanoplankton', by botanists as 'algae,' by zoologists as 'phytomonads,' and by ecologists and the public as 'aquatic plants,' understandably the confusion about the high taxonomic levels is monumental. Serious studies of the extant of genetic, metabolic, physiological and structural (morphological) diversity of the organisms in question require changes in the professional societies of systematic biologists, most of whom, as botanists and zoologists, tend to ignore contradicting terminology, discount the evolutionary role of bacteria and be unaware of the existence of protoctists. Many avoid the

results of molecular-evolutionary studies even when these greatly complement other sources of information. All this work unambiguously shows the greatest biological diversity to be in the microcosm. Still behaving as if all life can be dichotomously grouped into only two kingdoms (plant and animal) the social organization and funding strategies of these scientists and their grant officers limit understanding. To alleviate this problem new scientific societies must develop means to deal with problems of naming, storing, classifying and documenting 'type specimens' of organisms that are neither animal nor plant (Corliss, 1990). International co-operation is essential and systematics, as a science, must return to its position as central to all of evolutionary biology, including evolution of microorganisms. The extent to which culture collections, herbaria, video micrographic documentation, museum specimens or other means of storing information about the eukaryotic micro-organisms and their descendants must be assessed.

The naming issue becomes especially acute for eukaryotic organisms since all of them are products of hereditary intracellular symbioses and therefore all potentially carry more than a single name. The usual practice, however inchoate, is simply to recognize the larger member in any symbiotic association and ignore the microscopic. Lichens generally are named after their fungal component and, in documenting species of cattle, the entodiniomorphid ciliates that digest the cellulose of grass are ignored. In symbionts in which the partners are more nearly equal in size or equally conspicuous, however, the naming procedures are overtly confused. Glaucocystophytes like the motile protists *Cyanophora*, for example, are named and grouped by their internal cyanobacterial photobionts and their less colorful heterotrophic hosts are ignored (Kies and Kremer, 1990). By contrast, the internal photobiont (*Chlorella vulgaris*) is not considered in the naming of green motile protists such as *Paramecium bursaria*, which is named for its host and classified in the Phylum Ciliophora (ciliates). Consortia bacteria (e.g., *Pelochromatium rubrum*), on the other hand, are named for the symbiotic com-

plex. Each of the individuals (phototrophic and motile bacteria) comprising the association are differently named and separately classified. Biological nomenclatural practices are entirely analogous to the recognition of 'form-taxa' by geologists who name reefs, stromatolites, worm burrows and mammal tracks by their structure knowing all the while that these are community structures or traces and not the remains of single individual bodies of organisms. The irony is that all members of the superkingdom Eukaryota are community structures in the same sense, i.e., heterologous genomic composites of more than single homologous genomes. Composed of hereditary symbionts and therefore more than a single biont, all eukaryotes are co-evolved microbial communities so tightly integrated that new levels of individuality have emerged. Given this fact, it is clear that biologists, in naming and classifying eukaryotes, traditionally confer appellations on composites as if they were individuals. Hence, unlike geologists (and the possible exception of lichenologists), who are explicit about the 'form-taxon' designation, biologists apply form-taxa names to co-evolved symbiotic complexes recognizable as individuals without awareness of this lapse in logic. These gross inconsistencies can only be exacerbated by the absence of international agreement among the journals and organizations charged with the enhancement of scientific knowledge about the eukaryotic microorganisms and their non-animal and non-plant descendants: *The European Journal of Protistology, Journal of Phycology, Journal of Protozoology*, to name but a few. Until issues raised by Corliss (1990) are openly debated in an arena involving all relevant botanical, microbiological and zoological organizations no possible resolution of the naming, classifying, storage and accessibility to knowledge and handling of new type specimens can proceed. Nomenclatural confusion (which is rampant in all of the subfields of biology) must be discussed openly and formally as intrinsic to the effort to stop the destruction of the Earth's biodiversity.

In a series of computer model experiments Lovelock (in press) has strengthened earlier claims that the mathematics of biodiversity is

enhanced by simultaneous consideration of the physical environment in which the organisms evolved. Diversity in species (i.e., the 'diversity index') is demonstrated to be greatest when the environment is least stressed. Diversity is least under extreme environmental conditions; the total number of different species present at one time is less important then the potential of the ecosystem to provide different species with change of conditions (Lovelock, in press). If we are to ever understand the relation of species diversity to environmental stability, past and present, we must improve our methods of estimating species diversity and its change through time (evolution). These considerations make appropriate description of the Earth's life and past life mandatory. Like any overall taxonomic scheme of the Earth's entire biota, Tables 1, 2 and Fig. 1 are meant only as guides to the beginning of such an inevitably international and panscientific discussion.

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