TOWARDS A MANAGEMENT HIERARCHY (CLASSIFICATION) FOR THE CATALOGUE OF LIFE

Draft Discussion Document

Rationale

The Catalogue of Life partnership, comprising Species 2000 and ITIS (Integrated Taxonomic Information System), has the goal of achieving a comprehensive catalogue of all known species on Earth by the year 2011. The actual number of described species (after correction for synonyms) is not presently known but estimates suggest about 1.8 million species.

The collaborative teams behind the Catalogue of Life need an agreed standard classification for these 1.8 million species, i.e. a working hierarchy for management purposes. This discussion document is intended to highlight some of the issues that need clarifying in order to achieve this goal beyond what we presently have.

Concerning Classification

Life's diversity is classified into a hierarchy of categories. The best-known of these is the Kingdom. When Carl Linnaeus introduced his new "system of nature" in the 1750s — *Systema Naturae per Regna tria naturae, secundum Classes*, *Ordines, Genera, Species …*) — he recognised three kingdoms, viz Plantae, Animalia, and a third kingdom for minerals that has long since been abandoned. As is evident from the title of his work, he introduced lower-level taxonomic categories, each successively nested in the other, named Class, Order, Genus, and Species. The most useful and innovative aspect of his *system* (which gave rise to the scientific discipline of Systematics) was the use of the binominal, comprising genus and species, that uniquely identified each species of organism.

Linnaeus's system has proven to be robust for some 250 years. The starting point for botanical names is his *Species Plantarum*, published in 1753, and that for zoological names is the tenth edition of the *Systema Naturae* published in 1758. Since that time the expansion of knowledge and increase in the number of described species has required the expansion of the number of hierarchical levels within the system. The ranks of Family and Phylum were introduced in the early 1800s and many super- and sub-categories have been added since then. The kingdom itself is today nested in a category called Domain, although Superkingdom is a better name.

There is currently no consensus among the world's taxonomists concerning which of the many classification schemes to use for the hierarchy of life, in part because of the confusion resulting from Hennig's (1966) redefinition of existing terminology of classification and the separate goals of cladification and classification (Mayr & Bock (2002).

Purposes of a classification

At this point, it is probably useful to consider what is most needed in a classification, which is a system of ordering information. In recent years much has been written about biological classification and some viewpoints have been heatedly expressed. Linnaeus's utilitarian system has itself come under attack (see for example Ereshefshy 2001; Moore 2002), with a number of critics demanding an end to the use of ranks. "Ranks are irrelevant to phylogenetic insights and, being a source of confusion, are excluded" (Patterson 1993), but this viewpoint has been justifiably criticised (e.g. Benton 2000; Dyke 2002). Given the plethora of clade and taxon names in use, ranks at least relativise unfamiliar taxa and convey information about where in a tree they occur.

It is not the purpose here to summarise the various viewpoints but a need to consider what we want from a classification is inescapable. Cavalier-Smith (1998) has given a useful discussion. One bone of contention in recent decades has been whether or not to allow the use of paraphyletic taxa in classification. A paraphyletic taxon is a monophyletic group that does not contain all the descendents (derivatives) of that group. One of the best-known examples is that of Reptilia, nominally a class of Chordata. Since it is agreed that birds (nominally class Aves) have a reptilian ancestor, and Reptilia by convention does not include Aves, then Reptilia is a paraphyletic group. But paraphyletic groups potentially abound at all levels of the taxonomic hierarchy. Indeed, there are many thousands of taxa where it is not yet known if they are paraphyletic (including some of the descendants) or holophyletic (including all of the descendants). Cavalier-Smith's classical understanding of monophyly is pragmatic, including both paraphyletic and holophyletic groups. On this understanding, Reptilia + Aves [+ Mammalia] is holophyletic whereas Reptilia alone is merely paraphyletic; either way, both are monophyletic.

He writes: "Theoretically, the Hennigian attempt to restrict taxa to clades, and forbid paraphyletic groups is incompatible with the basic purpose of phylogenetic classification, even though it misleadingly masquerades under that name. What a biological classification aims to do is to arrange organisms in a hierarchical series of nested taxa, in which each more-inclusive higher-level taxon is subdivided comprehensively into less-inclusive taxa at the next level below. … Cladists have long accepted that the inability to classify ancestral and many fossil taxa is the Achilles heel of Hennigian classificatory principles, and refer to it as a problem; it is not a problem at all for systematics, but merely a defect in the Hennigian ideas on classification. Obviously, if you assert that you must not make paraphyletic groups then you cannot properly classify ancestral species excluded from a particular clade. No comprehensive phylogenetic classification is even theoretically possible unless one accepts paraphyletic as well as holophyletic taxa. The dogma against paraphyletic taxa is logically incompatible with the … goal of taxonomy as the creation of a comprehensive classification of all organisms, both extant and extinct."

An example of a modern classification that attempts to meld cladification with classification is that of birds (treated as infraclass Aves), but in which some sequentially paraphyletic taxa are allowed (Livezey & Zusi 2007). By nesting birds in Reptilia, unnecessary in a traditional Darwinian classification in the view of Mayr and Bock (2002), and in order to reflect the number of branching points to arrive at Neornithes, the new classification introduces a plethora of subcategories. It remains to be seen how successful (widely accepted) this classification will be.

"The purpose of a classification is to provide a simplified reference system that is biologically sound and widely useful. It should be compatible with the phylogeny, but it cannot serve its central simplifying purpose unless it leaves out some of the fine detail about relationships that are essential for some phylogenetic purposes. One can use a phylogeny as a basis for making a classification, but one cannot logically deduce a fully detailed phylogeny from a classification. Nor is a phylogeny sufficient to give a classification. A phylogeny and a classification must be congruent (i.e. not contradictory) but they are different ways of abstracting from and representing biological relationships" (Cavalier-Smith 1998).

Some years ago, Cavalier-Smith (1987) introduced the name Opisthokonta for the monophyletic clade that includes choanoflagellates, fungi, and animals. Molecular phylogeny has since confirmed the validity of this clade (Baldauf et al. 2000), but Cavalier-Smith deliberately did not create a formal taxon Opisthokonta even though at least one cladist urged him to establish a kingdom-level taxon with this name. Cavalier-Smith (1998) rightly argues, "A kingdom Opisthokonta would be much less useful than the existing kingdoms Animalia, Fungi and Protozoa as a way of subdividing the living world into manageable groups of similar organisms, i.e. a classification as opposed to a phylogeny." [The Protozoa (a kingdom in the 1998 scheme of

Cavalier-Smith) could be further divided into three or several kingdoms. Several are indicated in the molecular analysis of eukaryotes by Baldauf et al. (2000), for example; see also the review by Lane and Archibald 2008. In time this may be appropriate (but see below) but the circumscription and relative ranking of these additional groups is still unclear. In any case, Protozoa is arguably monophyletic (Cavalier-Smith 2002b).]

In this context, the excellent review of classification and ordering systems by Mayr and Bock (2002) is a "must-read". Their philosophy, which is in accord with that of Cavalier-Smith, should arguably form the basis of any over-arching classification that is adopted by the Catalogue of Life. Our goal is arguably a traditional "Darwinian classification", in their terminology. Such a classification is based on "a balanced consideration of both genealogical branching (cladogenesis) and similarity (amount of phyletic evolutionary change = anagenesis)." "A Darwinian classification is as genealogical as a cladification, only it is a genealogy of groups (classes) and not of clades." These authors usefully consider the impact of ecological shifts on classification, giving as examples "(1) the entry of archosaurian reptiles into the arboreal/aerial environment and thereby evolving into birds, (2) the shift of artiodactyl ungulates to water and giving rise to the Cetacea (whales), and (3) the adoption of a parasitic lifestyle by some lineages of turbellarians which gave rise to trematodes and cestodes … in each case, the parental group is not affected by the evolution of these buds. … As the parental taxon (Reptilia) from which the Mammalia originated has not changed, its categorical rank is not affected. … Perhaps the greatest advantage of a Darwinian classification is that it calls attention to the ecological significance of the shift in adaptive anagenesis. … Not only is a Darwinian classification phylogenetic, it is also more inclusive than an ordering system based only on branching points because it also considers *the amount of evolutionary change after the branching points*." These authors noted: "The most disturbing finding of our survey is that in biosystematics there are now two widely supported and competing ordering systems, Darwinian classification and Hennigian cladification." This is one of the factors that may confound our arriving at a comprehensive management hierarchy for the Catalogue of Life.

Major kingdom-level classifications

Margulis and Schwartz (1998) have given a useful summary of the history of classification. Their popular textbook *Five Kingdoms* (in three editions) is based on Whittaker's (1959) five-kingdom scheme (bacteria, protoctists, plants, animals, fungi), itself a development of Copeland's (1956) four-kingdom scheme (in which Fungi is not a kingdom). Cavalier-Smith (1981) argued that the minimum number of kingdoms suitable for general purposes was six. In that year he introduced the Chromista, defined then as now on both ultrastructural and molecular grounds. This kingdom is now widely accepted, including by the Catalogue of Life, although the scope and content of the Chromista are still being refined. Cavalier-Smith (1987) circumscribed and raised a putatively basal protozoan group, Archaezoa, to kingdom rank, at the same time raising both Eubacteria and Archaebacteria to kingdom rank, effectively creating an eight-kingdom scheme. Subsequently it was discovered that the "Archaezoa" were not, as thought, primitively amitochondriate, their condition being derived, and this kingdom was abandoned. Cavalier-Smith currently treats Bacteria as a single prokaryote kingdom and his system remains at six kingdoms (Cavalier-Smith 2004a).

Cavalier-Smith (1998, 2002a, 2006) rejects the three-domains scheme (Archaea, Bacteria, Eucarya) of Woese et al. (1990), as do Margulis and Schwartz (1998). Instead these authors argue the case for two superkingdoms, the one prokaryote (synonymous with Bacteria), the other eukaryote. Archaebacteria (Archaea) is treated as a subkingdom by Margulis and Schwarz (1998) and as a phylum by Cavalier-Smith (1998, 2002a). Mayr and Bock (2002) commented: "Ignoring degree of difference and relying totally on branching points has led in recent years to many rather absurd classifications. For instance, it induced an author to give the Archaebacteria a rank as high as the total of the eukaryotes."

Viruses are not considered in the above-mentioned popular-level accounts. Cavalier-Smith (1998) regards viruses as “laterally transmissible parasitic genetic elements”, not living organisms.

Criteria for a Management Classification

What does the Catalogue of Life require of a management classification? In the booklet accompanying the 2008 Annual checklist (Bisby et al. 2008), it is mentioned that a GSD aspires to “have an explicit mechanism for seeking at least one responsible/consensus taxonomy, and for applying it consistently.” It further states that the classification employed in the checklist “has been agreed by Species 2000 and ITIS as a practical management tool to provide access to the Catalogue, the Catalogue of Life Taxonomic Classification Edition 1. This top level classification has remained unchanged in 2005–2008.”

The high-level classification currently in use is clearly evolving. In part it reflects traditional concepts; in part, certain groups like prokaryotes and Fungi reflect consensus views among an authoritative body of experts; in the case of ITIS the classification of invertebrates partly reflects one or more textbooks that have been influential (and remain so) in the North American context (e.g. Brusca & Brusca 2003).

To serve the needs of the Catalogue of Life and its broad user community, a case can be made for re-evaluating the existing high-level classification. Arguably, we need a fairly robust classification scheme that (a) reflects current expert opinion in such a way that it is neither geographically not personality-biased, (b) is likely to be stable for the next five years, and (c) is neither so new that it is untested nor so out of date as to be misleading or unhelpful. As per the preamble above, it should also be a “Darwinian classification”. What follows is a discussion of selected taxa that either advances an opinion or leaves the question open for consideration. An expert panel could be asked to vote in order to achieve a decision that can be adopted by the Catalogue of Life.

A Discussion of Selected Taxa

1. VIRUSES

Regardless of whether or not these important biological entities are life forms, their inclusion in the Catalogue of Life is pragmatic and utilitarian. Classification is based on a consensus of the International Committee on Taxonomy of Viruses (ICTV). If viruses are not considered life forms, however, they cannot technically be considered a kingdom of life.

Recommendation: Continue with the status quo.

2. PROKARYOTA

The objections of Cavalier-Smith (1998, 2002a) and Mayr and Bock (2002) (see also Rivera and Lake 2004) to the concept of three domains, two of which are prokaryotes, have not been widely accepted by bacteriologists and the Catalogue of Life probably has no alternative but to follow the consensus of the majority even if the question is still open. Currently the Catalogue uses the BIOS system developed by a team based at the National Institute for Environmental Studies (Japan) and is part of a collaborative effort that includes contributions by J. Euzéby and B. Tindall. The taxonomy is based on Release 7.4 of the nomenclatural taxonomy of G.M. Garrity, T.G. Lilburn and J.R. Cole.

Recommendation: Continue with the status quo.

3. PROTOZOA

With the segregation of a kingdom Chromista (see below) from the "Protista" or "Protoctista" (see Margulis & Schwartz 1998), Protozoa is the most appropriate name for the balance of organisms remaining (Cavalier-Smith 1998). The most comprehensive illustrated treatments of protozoan taxa are those published as the *Illustrated Guide to the Protozoa*, but whereas the first (single-volume) edition of this compendium (Lee et al. 1985) was accompanied by a full classification, the recent two-volume edition (Lee et al. 2000) is less definitive. An introductory essay on changing views of protistan systematics (Patterson 2000) lists five hierarchical systems in abbreviated form to phylum or class level, including that of Cavalier-Smith (1998) before settling on a rankless alphabetical list of 72 taxon names/vernacular names (genus and higher). The first taxonomic chapter in volume one deals with "Order Choanoflagellida", which is not listed as such among the 72 names; it is hiding in the list among the "Opisthokonts (chytrids, fungi, collar flagellates, metazoa)".

This isn't very helpful. Cavalier-Smith is acknowledged by Patterson (2000) as "one of the major architects of contemporary schemes of classification and is influential on the constructs of others" but is criticised on the grounds that "Unlike most contemporary workers, Cavalier-Smith endorses the inclusion of polyphyletic [he doesn't — Heliozoa is cited as an example but Cavalier-Smith uses only the name not the traditional content — see below under Chromista] and paraphyletic groups of organisms. … This makes it unpalatable to the mainstream of taxonomic philosophy". As an example of the problem of ranks, Patterson (2000) cites that of a kingdom (Animalia) having been derived from within a group of lower rank, in this case the order Choanoflagellida (Phylum Choanozoa), but as mentioned above this is not a problem for systematics (Mayr & Bock 2002).

Cavalier-Smith has been studying cellular ultrastructure since the late 1970s and has a long history of publication integrating the results of molecular sequencing with ultrastructure to achieve an evolving classification scheme. Critics object to the many new taxon names introduced by Cavalier-Smith during the past quarter-century and the fact that his classification is constantly being modified, but this is only to be expected as it is refined by new information. In fact, a consensus phylogeny has emerged from the corpus of work carried out by the "protozoologist" community and a large number of protozoan group names invented by Cavalier-Smith (clades and taxa) are in common use (e.g. Amoebozoa (including Eumycetozoa), Rhizaria, Retaria, Cercozoa, Excavata, Alveolata, Euglenozoa, etc.) as a search of literature and the internet will reveal. Cavalier-Smith (2002b, 2003a) published a definitive classification of Protozoa that has been refined as more detailed work has been carried out on different clades and taxa within the kingdom, e.g. the Cercozoa (Cavalier-Smith & Chao 2003a), Choanozoa and Apusozoa (Cavalier-Smith & Chao 2003b), Metamonada and Loukozoa (Cavalier-Smith 2003b), Phaeodaria (Radiozoa) (Polet et al. 2004), Myzozoa (Dinozoa and Apicomplexa) (Cavalier-Smith & Chao 2004), Euglenozoa (von der Heyden et al. 2004), and Rhizaria (Bass et al. 2005). We have the choice of using the synthesis classification resulting from this body of work (I have a copy) or assigning rank names to the rankless categories made available by David Patterson to Mike Ruggiero. [I understand from Mike that this is what he is doing but this could be problematic.]

Recommendations: 1) That we choose a ranked classification scheme for a paraphyletic kingdom Protozoa. 2) That we choose a synthesis derived from that developed by Cavalier-Smith and his research partners. 3) That we submit this to peer review among selected "protozoologists" including David Patterson. At present, the classification scheme in the 2008 Annual Checklist is an uncritical mix of taxon names, some of which can be attributed to Cavalier-Smith; a large number are unplaced.

4. CHROMISTA

The most recent detailed classifications of this kingdom, by Cavalier-Smith (2003, 2004b), Cavalier-Smith and Chao (2006), and Cavalier-Smith and von der Heyden (2007), include six phyla in two subkingdoms. Subkingdom Cryptista includes the photosynthetic cryptophytes and the colourless kathablepharids. As an example of the differences in treatment of these constituent groups, whereas Cavalier-Smith (2004b) has three cryptistan classes (Cryptophyceae and Goniomonadea in subphylum Cryptomonada and Leucocryptea in subphylum Leucocrypta), the compendious *The Illustrated Guide to the Protozoa*, published by the Society of Protozoologists (Lee et al. 2000), has an entry for order Cryptomonadida (containing both *Cryptomonas* and *Goniomonas*, with neither assigned to family) (Kugrens et al. 2000) and, widely separated in the same volume under the heading "Residual free-living and heterotrophic flagellates", a family Kathablepharidae that contains, inter alia, the genus *Leucocryptos* (Patterson et al. 2000). In the 2008 annual Checklist, the "algal" taxa seem to have been covered thanks to AlgaeBase, but not the non-photosynthetic forms. A benefit of Cavalier-Smith's taxonomy is that he accounts for all of these forms in a cohesive scheme whereas most other treatments leave some of the putative constituent groups hanging.

Recommendation: Consult Mike Guiry, David Patterson, and Tom Cavalier-Smith concerning the taxonomic scope of cryptistan chromists and make a decision accordingly.

Cavalier-Smith and Chao (2006) recognise only three heterokont (stramenopile) phyla — the predominantly photosynthetic Ochrophyta (containing a number of algal classes), the non-photosynthetic Pseudofungi, and the Bigyra (now comprising subphyla Opalozoa, Bicoecia, and Sagenista). In some schemes, all three phyla are lumped together as phylum Heterokontophyta (e.g. Cavalier-Smith 1995a; Hoek et al. 1995). Cavalier-Smith (1986) first introduced the taxon Heterokonta. It has been widely accepted and it seems logical that his current use of the taxon (an infrakingdom that includes subordinate phyla) should prevail. The 2008 Annual Checklist has a curious treatment (see below).

Cavalier-Smith and Chao (2006)	CoL Annual Checklist 2008
Phylum Ochrophyta	Phylum Ochrophyta
Phylum Pseudofungi	
Class Bigyromonadea (*Developopayella*)	
Class Hyphochytrea (*Hyphochytrium*)	Phylum Hyphochytriomycota
Class Oomycetes (*Saprolegnia*)	Phylum Oomycota
Phylum Bigyra	
Subphylum Opalozoa	
Class Nucleohelea (*Actinophrys*)	
Class Proteromonadea (*Proteromonas*)	
Class Opalinea (*Opalina*)	
Class Blastocystea (*Blastocystis*)	
Subphylum Bicoecia	Phylum Sagenista
Class Bisoecea (*Bicosoeca*)	Class Bicosoecophyceae
Subphylum Sagenista	
Class Labyrinthulea (*Labyrinthula*)	Phylum Labyrinthulomycota

Sagenista is another Cavalier-Smith taxon (Cavalier-Smith 1995b), first introduced as a heterokont phylum but recently (Cavalier-Smith and Chao 2006) reduced to a subphylum of Bigyra. From the outset it has always contained the slime nets with their sagenosomes (*Labyrinthula*) and the thraustochytrids. [It originally also included the bicosoecids, which Cavalier-Smith and Chao (2006) since elevated to a class.] The Annual Checklist is illogical in accepting the name Sagenista and then removing the labyrinthulas and related forms from it. The Annual Checklist also has an entry "Not assigned to a phylum" that includes class Schizocladiophyceae. Cavalier-Smith (2004b) and Cavalier-Smith and Chao (2006) include *Schizocladia* (order Schizocladiales) in the ochrophyte class Phaeophyceae (brown algae). If accepted as a full class it should still be placed in the Ochrophyta.

Concerning Ochrophyta — the 2008 Annual Checklist has some major problems concerning the diatoms (an ochrophyte class). I haven't checked in detail but it appears that two classification systems are in simultaneous use (one from AlgaeBase and one from ITIS?). Two diatom classes Coscinodisciophyceae and Fragilariophyceae, are listed under phylum Ochrophyta in kingdom Chromista, whereas class Bacillariophyceae is listed as a phylum-rank entry under kingdom Plantae. Without detailed checking, it is not clear how much overlap there is; certainly order Rhizosoleniales occurs twice in the 2008 Checklist, in both the Chromista and the Plantae.

Recommendation: Consult Mike Guiry, Paul Kirk, Tom Cavalier-Smith, and other chromistan specialists concerning an appropriate classification for heterokont diversity, including the numbers and scope of the classes of Ochrophyta, which differ significantly among authors.

There are two classes of Haptophyta — Pavlovophyceae and Prymnesiophyceae — both of which have been accepted by Andersen (2004). The 2008 Annual Checklist, however, includes the Pavlovales in the Prymnesiophyceae.

Recommendation: Consult Mike Guiry concerning appropriate placement of *Pavlova*. There are four unplaced genera nested under Haptophyta in the 2008 Annual Checklist. These need resolving; they may already have a place in Cavalier-Smith's schema.

The traditional Heliozoa (sun protists) has long been recognised to be polyphyletic (Patterson 1993). Recent work (Cavalier-Smith & Chao 2003, 2006) has shown that some, like the well-known genus *Actinophrys*, are related to opalozoans in the phylum Bigyra; others belong among the protozoan phylum Cercozoa (Nikolaev et al. 2004). The core remaining group that now defines phylum Heliozoa comprises only the order Centrohelida, within which two new suborders have been recognised (Cavalier-Smith & von der Heyden, 2007). Owing to a weak grouping of centrohelids with haptophytes on 18S rRNA trees, the Heliozoa is provisionally considered to be chromistan not protozoan.

Recommendation: That the Cavalier-Smith and von der Heyden (2007) classification of phylum Heliozoa be accepted.

A new chromistan phylum, Telonemia (Shalchian-Tabrizi et al. 2006, 2007) was recently established for two named species of *Telonema*, a marine heterotrophic flagellate, and some unidentified forms. A protozoan class Telonemea was first recognised by Cavalier-Smith (1993). Initially allied with the then protozoan phylum Opalozoa, Telonemea was subsequently transferred to the phylum Apusozoa (Cavalier-Smith 2003a). Its present placement among the chromalveolates seems secure but it is likely to require its own chromistan subkingdom (Shalchian-Tabrizi et al. 2006).

Recommendation: That the phylum Telonemia be included in the 2009 Checklist.

5. PLANTAE

As with the other kingdoms, Plantae is classified in a variety of ways. Fundamentally, there are algal phyla (red and green) and embryophytes (land plants). The ancestral embryophyte is thought to be among the Charales (stoneworts) or Coleochaetales. Bremer (1985), a cladist, erected a phylum Streptophyta to include the ancestral algal embryophyte and all descendent groups (bryophytes, pteridophytes, and seed plants). At the other extreme, each of the main bryophyte, pteridophyte, and spermatophyte subdivisions has been accorded phylum (or Division) status. This latter treatment is exemplified in the 2008 Annual Checklist, which lists three bryophyte phyla, four pteridophyte phyla, and five seed-plant phyla. This treatment is terribly anachronistic and must be abandoned. [On what grounds can one possibly justify a separate phylum for *Gingko*, or for gnetophytes (which appear to be nested among the Pinales according to the latest molecular studies)?] A sensible middle approach, found in Cavalier-Smith (1998) but not restricted to him, is to recognise just two embryophyte phyla — Bryophyta (comprising liverworts, hornworts, and mosses) and Tracheophyta, all species of which are characterised by a diploid phase that has xylem and phloem. The treatment of Plantae adopted for the "Species 2000 New Zealand project" and accepted by all authors additionally comprises four algal phyla — Glaucophyta, Cyanidiophyta, Rhodophyta, and Chlorophyta. [Cyanidiophyta is not in Cavalier-Smith (1998) but work since then has shown that cyanidiophytes have the smallest known genomes of any phototrophic eukaryotes (Muravenko *et al*. 2001); additional studies of cytomorphology, biochemistry, and molecular-sequence data (e.g. Pinto *et al.* 2003) support the segregation of the Cyanidiophyta from the Rhodophyta at the level of phylum. Indeed, Cyanidiophyta is in the 2008 Annual Checklist.]

Recommendation: That the Catalogue of Life adopts a pragmatic plant classification similar to or modified after that in Cavalier-Smith (1998) at the phylum level.

6. ANIMALIA

Animalia in the 2008 Annual Checklist comprises 31 phyla. The number of phyla in Brusca and Brusca (2003), presumably favoured by ITIS, is 34. The differences are accounted for as follows: (1) Monoblastozoa (in Brusca & Brusca) — comprises a single poorly known taxon, *Salina salve*, found only once in a saline culture (Frenzel 1892). Not in Checklist but may as well be included. (2) Rhombozoa and Orthonectida (in Brusca & Brusca) — combined as Mesozoa in the Checklist. (3) Kinorhyncha, Loricifera, and Priapul(id)a (in Brusca & Brusca) — combined as Cephalorhyncha in Checklist. (4) Myxozoa (in Checklist) is not a phylum in Brusca and Brusca. Today there is a great deal of consensus concerning the phyla of Animalia but some questions remain. These are discussed below, alphabetically, under the phylum names presently used in the Checklist.

(i) Phyla Acanthocephala, Gnathostomulida, Rotifera

Each of these is commonly treated by biologists as a separate phylum (e.g. Ruppert & Barnes 1994; Margulis & Schwartz 1998; Brusca & Brusca 2003). However, some molecular data (e.g. Garey et al. 1996; Garcia-Varela & Nadler 2006) and morphological features suggest that Acanthocephala is nested in Rotifera. A syncytial epidermis links rotifers, *Seison* (a marine rotifer-like organism found on nebaliid crustaceans), and Acanthocephala, moving Ahlrichs (1995, 1997) to propose the name Syndermata for this grouping. As revealed by transmission (Rieger & Tyler 1995) and scanning electron microscopy (Sørensen 2003), the jaw apparatus of gnathostomulids and rotifers is remarkably similar. That of *Seison* is less obviously homologous (Segers & Malone 1998), and the Seisonidea may have diverged from rotifers at an early stage of their evolution. On the other hand, *Seison* has similar sperm to acanthocephalans and the epidermis of both groups contains bundles of filaments. For those who wish to treat these major groups as phyla, the cat among the pigeons was the discovery of *Limnognathia maerski*, representing a new class of organism (Micrognathozoa) from cold fresh waters in Greenland and the Crozet Islands (Kristensen & Funch 2000; De Smet 2002). It has a remarkable jaw apparatus (the most complicated known among invertebrates) that has clear homologies, in both the jaw elements and the musculature, with both the trophi in Rotifera and the jaws in Gnathostomulida. [The jaw apparatus appears to have significance for these groups as the radula does for Mollusca.] Accordingly, these three groups have been considered to be closely related and were united by Kristensen and Funch (2000) in the Gnathifera, a phylum first introduced by Alrichs in 1995. A morphological cladistic analysis supports this association (Jenner 2006). It is still an open question whether the Rotifera is paraphyletic. Nielsen (1995) considers it a sister taxon of Acanthocephala. A solution used in the Sp2000NZ project and advocated here is to treat Acanthocephala as a class of Gnathifera and not a subclass of Rotifera. Accordingly, we have a phylum Gnathifera that includes classes Gnathostomulida, Micrognathozoa, Rotifera, and Acanthocephala. Within class Acanthocephala, the classification of Monks (2001) is recommended. After email discussion last year, Nicolas Bailly suggested the following classification:

Phylum Gnathifera
  Subphylum Gnathostomulida
    Class Gnathostomulida
  Subphylum Micrognathozoa
    Class Micrognathozoa
  Subphylum Syndermata
    Class Rotifera
      Subclass Eurotatoria
      Subclass Seisonida (as Pararotatoria in 2008 Checklist)
    Class Acanthocephala

Nicolas noted: As we don't store the subphyla and subclasses, there is no confusion between subphyla and class names. On the other hand, what we could provide also is a full hierarchy for advanced users, or the full hierarchy in a flat text file. Note that all abandoned names should nevertheless be traceable through a thesaurus.

Recommendation: That we consider the use of phylum Gnathifera in the Catalogue of Life and treat Acanthocephala etc. as classes. This is something we could put to a vote after canvassing invertebrate specialists including Reinhardt Kristensen and Wolfgang Sterrer.

(ii) Phylum Arthropoda

As a general comment, most GSDs will be accompanied by a standard classification that is favoured by the GSD author and his/her colleagues, hence the Catalogue of Life management teams don't have to decide what hierarchy to use for that GSD. Often, however, a GSD will comprise just part of a phylum and not be accompanied by a comprehensive phylum-level classification. The Arthropoda is a case in point, and arriving at such a classification will be a challenge, particularly as so many internal relationships are constantly being clarified. For the Crustacea, however, a good start was made by Martin and Davis (2001). This comprehensive classification covers the entire subphylum. It is widely used, though not universally insofar as specialists of various crustacean groups modify or adapt parts of it according to their preference and/or new knowledge. Boxshall (2007) has highlighted the ongoing controversies and unresolved taxonomic problems within Crustacea.

Recommendation: That we seek a synthesis for the Arthropoda by amalgamation of the most highly regarded schemes for each of the constituent subphyla and classes.

(iii) Phylum Cephalorhyncha

Adrianov and Malakhov (1995) erected this phylum for Kinorhyncha, Loricifera, Priapulida, and Nematomorpha so it is inconsistent for the 2008 Annual Checklist to list Nematomorpha separately if Cephalorhyncha is chosen. On the other hand, the first three of these phyla have in common an eversible snout (introvert) with scalid-spines and inner and outer retractor muscles, a similar excretory filter (protonephridium), and similar sense organs and there is some justification for uniting them in a single group, the Scalidophora (Lemburg 1995). On the other hand, Kinorhyncha has internal and external body segmentation, lacking in the other groups. Neuhaus and Higgins (2002) have noted that conflicting evidence exists for every one of the possible sister-group relationships among these phyla and prefer to keep them separate in a superphylum Scalidophora (which has priority over Cephalorhyncha).

Recommendation: That the Catalogue of Life abandons Cephalorhyncha and treats each of these phyla separately (as in Brusca & Brusca 2003). However, Priapulida should be spelled thus, not Priapula. This has been thoroughly discussed on http://wwwuser.gwdg.de/~clembur/priapufr.htm, where the author points out that Priapulida has been in use for more than a century, is the name favoured by all experts of the group, is abundantly found in a Google search (compared to Priapula), and that the latter is used mainly only in a few textbooks and by some molecular workers.

(iv) Cnidaria, Myxozoa
Recently, a classification of Cnidaria was published (Daly et al. 2007) that provides a way of checking the completeness of the existing arrangement in the 2008 Annual Checklist (an amalgam of the Hexacorallia GSD and the balance of taxa contributed by ITIS). The family Tetraplatiidae, unplaced in the 2008 Checklist, is included in the Narcomedusae. Interestingly, this new classification makes no mention of the Myxozoa, conclusively demonstrated last July to be cnidarian (Jiménez-Guri et al. 2007). The Myxozoa are treated as a cnidarian class in the Sp2000NZ project.

Recommendations: That the existing 2008 Checklist be compared with the new classification published by Daly et al. (2007) and that the Myxozoa be subsumed in Cnidaria.

(v) Echinodermata
The 2008 Checklist has a class-level taxon Somasteroidea, a group that is somewhat anachronistic in the recent context (dating from Fell 1962). In fact it has no living species and the included genus *Platasterias* is nowadays classified as an asteroid.

Recommendation: That Chris Mah be approached to check the asteroid classification.

(vi) Ectoprocta and Entoprocta
The earliest available name for these unrelated creatures was Polyzoa, introduced in 1830, followed by Bryozoa one year later. Polyzoa was popular in Britain and Australasia, Bryozoa in Europe and North America. Ectoprocta and Entoprocta were introduced as subphyla of Bryozoa in 1869. Libbie Hyman raised the subphylum names to phylum in the 1950s, in her magisterial series on the invertebrates, and since then they have been popularised in North American textbooks on invertebrates. This is unfortunate. No publishing member of the International Bryozoology Association, established in 1965, uses Ectoprocta, and the opinion of this body should prevail. Kamptozoa (coined as a phylum name in 1929) is increasingly used in contradistinction to Entoprocta.

Recommendation: That Ectoprocta and Entoprocta be abandoned in favour of Bryozoa and Kamptozoa, respectively.

(vii) Mesozoa
Pawlowski et al. (1996) and Hanelt et al. (1996), respectively using 18S ribosomal RNA and DNA sequences, inferred that the Rhombozoa and Orthonectida are not each other's closest relatives. Ribosomal DNA and *Hox* gene sequences indicate that rhombozoans may be lophotrochozoans that have secondarily lost many morphological characters (Katayama et al. 1995; Kobayashi et al. 1999). The presence of cuticle and muscle fibres in orthonectids is in marked contrast to dicyemids, in which they are absent (Slyusarev 2000, 2003).

Recommendation: That the annual Checklist abandon Mesozoa in favour of the phylum names Rhombozoa (or Dicyemida) and Orthonectida, as in Margulis and Schwartz (1998) and Brusca and Brusca (2003). [Note that specialist F.G. Hochberg (Santa Barbara Museum of Natural History) advocates the use of Dicyemida over Rhombozoa. Dicyemida is used in the Sp2000NZ project.]

(viii) Nemata
Why is this spelling used instead of Nematoda, which is standard in most sources? A classification of Nematoda is provided by Hodda (2007) in which there are five classes (compared to two in the 2008 Checklist).

Recommendation: That the spelling and classification of Nematoda be checked with current experts.

(ix) Platyhelminthes
The classification scheme used in the 2008 Annual Checklist would be considered conservative by some, not reflecting the results of recent research. Many textbooks retain the economically important parasitic flukes (Digenea and Monogenea) and tapeworms (Cestoda) as classes parallel to Turbellaria, mostly for practical reasons, and the view of Mayr and Bock (2002) would be that this is appropriate. Ehlers (1986) has shown there are three distinct groups within Platyhelminthes (which may itself be monophyletic), viz Acoelomorpha (Acoela and Nemertodermatida), Catenulida, and Rhabditophora. In some molecular treatments (e.g. Wallberg et al 2007) the two acoelomorph orders come out as separate groups of basal Bilateria. Tyler (2004), on the other hand, has pointed out the morphological characters that unite acoelomorphs with the balance of Platyhelminthes. Following Tyler (2004), the Sp2000NZ project treats each of the three major groups discerned by Ehlers as subphyla. Thus Rhabditophora contains two classes — Archoophora and Neoophora. Archoophora includes, inter alia, the turbellarian orders Macrostomorpha, Polycladida, and Lecithoepitheliata; Neoophora contains not only the balance of turbellarian orders but also the parasitic flukes and tapeworms as subinfraclasses under infraclass Neodermata. This treatment loses the traditional class ranks of flukes and cestodes but retains the orders. The classification of Lockyer et al. (2003) is helpful in reflecting these relationships but, as indicated in the introductory material, there are problems inherent in trying to translate, too far, a cladogram into a classification.

Recommendation: That a panel of experts advise the Catalogue of Life concerning an appropriate classification for Platyhelminthes.

(x) Xenoturbellida
This phylum is not listed as such in either Brusca and Brusca (2003) or in the 2008 Annual Checklist — not surprising, since it has only recently been recognised. *Xenoturbella*, a flatworm-like genus with only two described marine species (Israelsson 1999), is arguably the most primitive deuterostome (Bourlat et al. 2003, 2006; Stach et al. 2005).

Recommendation: That the phylum Xenoturbellida be included in the next Checklist.

7. FUNGI
This is Paul Kirk’s area. I note that a new tree of life has been developed for the Fungi that will no doubt inform the Index Fungorum (Bruns 2006; James et al. 2006). Inter alia, the Microsporidia is not listed in the 2008 Annual Checklist classification.

References

Adrianov, A.V.; Malakhov, V.V. (1995). The phylogeny and classification of the phylum Cephalorhyncha. *Zoosystematica Rossica 3*: 181–201.

Alrichs, W.H. 1995: Ultrastruktur und Phylogenie von *Seison nebaliae* (Gube 1859) und *Seison annulatus* (Claus 1876) – Hypothesen zu phylogenetischen Verwandtsschaftsverhaltsnissen innerhalb der Bilateria. Dissertation, Georg-August University, Gottingen. Cuvillier-Verlag, Gottingen. 310 p.

Alrichs, W.H. 1997: Epidermal ultrastructure of *Seison nebaliae* and *Seison annulatus* and a comparison of epidermal structures within the Gnathifera. *Zoomorphology 117*: 41–48.

Andersen, R.A. (2004). Biology and systematics of heterokont and haptophyte algae. *American Journal of Botany 91*: 1508–1522.

Baldauf, S.L.; Roger, A.J.; Wenk-Siefert, I.; Doolittle, W.F. (2000). A kingdom-level phylogeny of eukaryotes based on combined protein data. *Science 290*: 972–977.

Bass, D.; Moreira, D.; López-García, P.; Polet, S.; Chao, E.E.; von der Heyden, S.; Pawlowski, J.; Cavalier-Smith, T. (2005). Polyubiquitin insertions and the phylogeny of Cercozoa and Rhizaria. *Protist 156*: 149–161.

Benton, M.J. (2000). Stems, nodes, crown clades, and rank-free lists: is Linnaeus dead? *Biological Reviews 75*: 633–648.

Bisby, F.; Roskov, Y.R.; Orrell, T.;M.; Nicholson, D.; Paglinawan, L.E.; Bailly, N.; Kirk, P.M.; Bourgoin, van Hertum, J. (Eds) (2008). *Species 2000 and ITIS Catalogue of Life: 2008 Annual Checklist*. CD-ROM. Species 2000, Reading.

Bourlat, S.J.; Juliusdottir, T.; Lowe, C.J. ; Freeman, R. ; Aronowicz, J.; Kirschner, M.; Lander, E.S.; Thorndyke, M.; Nakano, H.; Kohn, A.B.; Heyland, A.; Moroz, L.L.; Copley, R.R.; Telford, M.J. (2006). Deuterostome phylogeny reveals monophyletic chordates and the new phylum Xenoturbellida. *Nature 444*: 85–88.

Bourlat, S.J.; Nielsen, C.; Lockyer, L.E.; Littlewood, D.T.J.; Telford, M. (2003). *Xenoturbella* is a deuterostome that eats molluscs. *Nature 424*: 925–928.

Boxshall, G.A. (2007). Crustacean classification: on-going controversies and unresolved problems. *Zootaxa 1668*: 313–325.

Bremer, K. (1985). Aummary of green plant phylogeny and classification. *Cladistics 1*: 369–385.

Bruns, T. (2006). A kingdom revised. *Nature 443*: 758–759.

Brusca, R.C.; Brusca, G.J. (2003). *Invertebrates*. Second Edn. Sinauer Associates Inc., Sunderland.

Cavalier-Smith, T. (1981). Eukaryote kingdoms, seven or nine? *BioSystems 14*: 461–481.

Cavalier-Smith, T. (1987). The origin of cells, a symbiosis between genes, catalysts and membranes. *Cold Spring harbour Symposium on Quantitative Biology 52*: 805–824.

Cavalier-Smith, T. (1993). The protozoan phylum Opalozoa. *Journal of Eukaryotic Microbiology 40*: 609–615.

Cavalier-Smith, T. (1995a). Cell cycles, diplokaryosis and the archezoan origin of sex. *Archiv für Protistenkunde 145*: 189–207.

Cavalier-Smith, T. (1995b). Zooflagellate phylogeny and classification. *Cytology 37*: 1010–1029.

Cavalier-Smith, T. (1998). A revised six-kingdom system of life. *Biological Reviews 73*: 203–266.

Cavalier-Smith, T. (2002b). The neomuran origin of archaebacteria, the negibacterial root of the universal tree and megabacterial classification. *International Journal of Systematic and Evolutionary Microbiology 52*: 7–76.

Cavalier-Smith, T. (2002a). The phagotrophic origin of eukaryotes and phylogenetic classification of Protozoa. *International Journal of Systematic and Evolutionary Microbiology 52*: 297–354.

Cavalier-Smith (2003a). Protist phylogeny and the high-level classification of Protozoa. *European Journal of Protistology 39*: 338–348.

Cavalier-Smith, T. (2003b). The excavate protozoan phyla Metamonada Grassé emend. (Anaeromonadea, Parabasalia, *Carpediemonas*, Eopharyngia) and Loukozoa emend. (Jakobea, *Malawimonas*): their evolutionary affinities and new higher taxa. *International Journal of Systematic and Evolutionary Microbiology 53*: 1741–1758.

Cavalier-Smith, T. (2004a). Only six kingdoms of life. *Proceedings of the Royal Society of London, B, 271*: 1251–1262.

Cavalier-Smith, T. (2004b). Chromalveolate diversity and cell megaevolution: interplay of membranes, genomes and cytoskeleton. Pp. 75–108 *in* Hirt, R.P.; Horner, D.S. (eds), *Organelles, Genomes and Eukaryote Phylogeny*. CRC Press, London.

Cavalier-Smith, T. (2006). Rooting the tree of life by transition analyses. *Biology Direct 1(19)*: 1–83. doi:10.1186/1745-6150-1-19

Cavalier-Smith, T.; Chao, E.E.-Y. (2003a). Phylogeny and classification of phylum Cercozoa (Protozoa). *Protist 154*: 341–358.

Cavalier-Smith, T.; Chao, E.E.-Y. (2003b). Phylogeny of Choanozoa, Apusozoa, and other Protozoa and early eukaryote evolution. *Journal of Molecular Evolution 56*: 540–563.

Cavalier-Smith, T.; Chao, E.E. (2004). Protalveolate phylogeny and systematics and the origins of Sporozoa and dinoflagellates (phylum Myzozoa nom. Nov.). *European Journal of Protistology 40*: 185–212.

Cavalier-Smith, T.; Chao, E. E.-Y. (2006). Phylogeny and megasystematics of phagotrophic heterokonts (kingdom Chromista). *Journal of Molecular Evolution 62*: 388–420.

Cavalier-Smith, T.; von der Heyden, S. (2007). Molecular phylogeny, scale evolution and taxonomy of centrohelid Heliozoa. *Molecular Phylogenetics and Evolution 44*: 1186–1203.

Copeland, H.F. (1956). *The Classification of Lower Organisms*. Pacific Books, Palo Alto.

Daly, M.; Brugler, M.R.; Cartwright, P.; Collins, A.G.; Dawson, M.N.; Fautin, D.G.; France, S.C.; McFadden, C.S.; Opresko, D.M.; Rodriguez, E.; Romano, S.L.; Stake, J.L. (2007). The phylum Cnidaria: a review of phylogenetic patterns and diversity 300 years after Linnaeus. *Zootaxa 1668*: 127–182.

De Smet, H. (2002). A new record of *Limnognathia maerski* Kristensen & Funch, 2000 (Micrognathozoa) from the subantarctic Crozet Islands, with redescription of the trophy. *Journal of Zoology 258*: 381–393.

Dyke, G.J. (2002). Should paleontologists use "phylogenetic" nomenclature? *Paleontology 76*: 793–796.

Ehlers, U. (1986). Comments on a phylogenetic system of the Platyhelminthes. *Hydrobiologia 132*: 1–12.

Ereshefsky, M. (2001). *The Poverty of the Linnaean Hierarchy. A Philosophical study of Biological Taxonomy*. Cambridge University Press, Cambridge.

Fell, H.B. (1962). A surviving somasteroid from the eastern Pacific Ocean. *Science 136*: 633–636.

Frenzel, J. (1892). Untersuchungen über die mikroskopische fauna Argentiniens. *Salinella salve* nov. gen. nov. spec. *Archiv für Naturgeschichte 58*: 66–96, pl. 7.

Garcia-Varela, M.; Nadler, S.A. 2006: Phylogenetic relationships among Syndermata inferred from nuclear and mitochondrial gene sequences. *Molecular Phylogenetics and Evolution 40*: 61–72.

Garey, J.R.; Near, T.J.; Nonnemacher, M.R.; Nadler, S.A. 1996: Molecular evidence for Acanthocephala as a subtaxon of Rotifera. Journal of Molecular Evolution 43: 287–292.

Hennig, W. (1966). *Phylogenetic Systematics*. University of Illinois Press, Urbana.

Hodda, M. (2007). Phylum Nematoda. *Zootaxa 1668*: 265–293.

Hoek, C. van den; Mann, D.G.; Jahns, H.M. (1995). *Algae. An Introduction to Phycology*. Cambridge University Press, Cambridge.

Israelsson, O. (1999). New light on the enigmatic *Xenoturbella* (phylum uncertain): ontogeny and phylogeny. *Proceedings of the Royal Society of London, B, 266*: 835–841.

James, T.Y.; Kauff, F.; Schoch, C.L.; Matheny, P.B.; Hofstetter, V.; Cox, C.J.; Celio, G.; Gueidan, C.; Fraker, E.; Miadlikowska, J.; Lumbsch, H.T.; Rauhut, A.; Reeb, V.; Arnold, A.E.; Amtoft, A.; Stajich, J.E.; Hosaka, K; Sung, G.-H.; Johnson, D.; O'Rourke, B.; Crockett, M.; Binder, M.; Curtis, J.M.; Slot, J.C.; Wang, Z.; Wilson, A.W.; Schüßler, A.; Longcore, J.E.; O'Donnell, K.; Mozley-Standridge, S.; Porter, D.; Letcher, P.M.; Powell, M.J.; Taylor, J.W.; White, M.M.; Griffith, G.W.; Davies, D.R.; Humber, R.A.; Morton, J.B.; Sugiyama, J.; Rossman, A.Y.; Rigers, J.D.; Pfister, D.H.; Hewitt, D.; Hansen, K.; Hambleton, S.; Shoemaker, R.A.; Kohlmeyer, J.; Volkmann-Kohlmeyer, B.; Spotts, R.A.; Serdani, M.; Crous, P.W.; Hughes, K.W.; Matsuura, K.; Langer, E.; Langer, G.; Untereiner, W.A.; Lücking, R.; Büdel, B.; Geiser, D.M.; Aptroot, A.; Diederich, P.; Schmitt, I.; Schultz, M.; Yahr, R.; Hibbett, D.S.; Lutzoni, F.; McLaughlin, D.J.; Spatafora, J.W.; Vilgalys, R. (2006). Reconstructing the early evolution of Fungi using a six-gene phylogeny. *Nature 443*: 818–822.

Jenner, R.A. (2004). Towards a phylogeny of the Metazoa: evaluating alternative phylogenetic positions of Platyhelminthes, Nemertea, and Gnathostomulida. *Contributions to Zoology 73*: 3–163.

Jiménez-Guri, E.; Philippe, H.; Okamura, B. ; Holland, P.W.H. (2007). *Buddenbrockia* is a cnidarian worm. *Science 317* : 116–118.

Katayama, T.; Wada, H.; Furuya, H.; Satoh, N.; Yamamoto, M. (1995). Phylogenetic position of the dicyemid Mesozoa inferred from 18S rDNA sequences. *Biological Bulletin 189*: 81–90.

Kobayashi, M.; Furuya, H.; Holland, P.W.H. (1999). Dicyemids are higher animals. *Nature 401*: 762.

Kristensen, R.M.; Funch, P. 2000: Micrognathozoa: a new class with complicated jaws like those of Rotifera and Gnathostomulida. *Journal of Morphology 246*: 1–49.

Kugrens, P.; Lee, R.E. (2000). Order Cryptomonadida Senn, 1900. Pp. 1111–1125 *in*: Lee, J.J.; Leedale, G.F.; Bradbury, P. (eds), *An Illustrated Guide to the Protozoa, Second Edition: Organisms traditionally referred to as Protozoa, or newly discovered groups*. Society of Protozoologists, Lawrence. Vol. 2.

Lane, C.E.; Archibald, J.M. (2008). The eukaryotic tree of life: endosymbiosis takes its TOL. *Trends in Ecology and Evolution 23*: 268–275.

Lee, J.J.; Hutner, S.H.; Bovee, E.C. (Eds) (1985). *An Illustrated Guide to the Protozoa*. Society of Protozoologists, Lawrence.ix + 629 p.

Lee, J.J.; Leedale, G.F.; Bradbury, P. (Eds) (2000). *An Illustrated Guide to the Protozoa, Second Edition: Organisms traditionally referred to as Protozoa, or newly discovered groups*. Society of Protozoologists, Lawrence. 2 vols, v + 1432 p.

Lemburg, C. (1995). Ultrastructure of sense organs and receptor cells of the neck and lorica of the *Halicryptus spinulosus* larva (Priapulida). *Microfauna Marina 10*: 7–30.

Livezey, B.C.; Zusi, R.L. (2007). Higher-order phylogeny of modern birds (Theropoda), Aves: Neornithes) based on comparative anatomy. II. Analysis and discussion. *Zoological Journal of the Linnean Society 149*: 1–95.

Lockyer, A.E.; Olson, P.D.; Littlewood, D.T.J. (2003). Utility of complete large and small subunit rRNA genes in resolving the phylogeny of the Neodermata (Platyhelminthes): implications and a review of the cercomer theory. *Biological Journal of the Linnean Society 78*: 155–171.

Margulis, L.; Schwartz, K.V. (1998). *Five Kingdoms: An illustrated guide to the phyla of life on Earth*. Third Edn. W.H. Freeman & Co., New York.

Mayr, E.; Bock, W.J. (2002). Classifications and other ordering systems. *Journal of Zoological Systematics and Evolutionary Research 40*: 169–194.

Monks, S. 2001: Phylogeny of the Acanthocephala based on morphological characters. *Systematic Parasitology 48*: 81–116.

Moore, G. (2002). Down with the kingdom (phylum, class, and order too). *Science 297*: 1650–1651.

Muravenko, O.V.; Selyakh, I.O.; Kononenko, N.V; Stadnichuk, I.N. (2001). Chromosome numbers and nuclear DNA contents in the red microalgae *Cyanidium caldarium* and three *Galdieria* species. *European Journal of Phycology 36*: 227–232.

Neuhaus, B.; Higgins, R.P. (2002). Ultrastructure, biology, and phylogenetic relationships of Kinorhyncha. *Integrative and Comparative Biology 42*: 619–632.

Nielsen, C. (1995). *Animal Evolution. Interrelationships of the living phyla*. Oxford University Press, Oxford.

Nikolaev, S.; Berney, C.; Fahrni, J.; Bolivar, I.; Polet, S.; Mylnikov, A.P.; Aleshin, V.V.; Petrov, N.B.; Pawlovski, J. (2004). The twilight of Heliozoa and rise of Rhizaria, an emerging supergroup of amoeboid eukaryotes. *Proceedings of the National Academy of Sciences, U.S.A. 101*: 8066–8071.

Patterson, D.J. (1993). Protozoa: evolution and systematics. Pp. 1–14 *in*: Hausmann, K.; Hülsmann, N. (eds), *Progress in Protozoology*. Gustav Fischer Verlag, Stuttgart.

Patterson, D.J. (2000). Changing views of protistan systematics: the taxonomy of Protozoa – an overview. Pp. 2–9 *in*: *An Illustrated Guide to the Protozoa, Second Edition: Organisms traditionally referred to as Protozoa, or newly discovered groups*. Society of Protozoologists, Lawrence. Vol. 1.

Patterson, D.J.; Vørs, N.; Simpson, A.G.B.; O'Kelly, C. (2000). Residual free-living and predatory heterotrophic flagellates. Pp. 1302–1328 *in*: Lee, J.J.; Leedale, G.F.; Bradbury, P. (eds), *An Illustrated Guide to the Protozoa, Second Edition: Organisms traditionally referred to as Protozoa, or newly discovered groups*. Society of Protozoologists, Lawrence. Vol. 2.

Pinto, G.; Albertano, P.; Ciniglia, C.; Cozzolino, S.; Pollio, A.; Yoon, H.S.; Bhattacharya, D. (2003). Comparative approaches to the taxonomy of the genus *Galdieria* Merola (Cyanidales, Rhodophyta). *Cryptogamie Algologie 24*: 13–32.

Polet, S.; Berney, C.; Fahrni, J.; Pawlovski, J. (2004). Small-subunit ribosomal RNA gene sequences of Phaeodaria challenge the monophyly of Haeckel's Radiolaria. *Protist 155*: 53–63.

Rieger, R.M.; Tyler, S. 1995: Sister-group relationship of Gnathostomulida and Rotifera-Acanthocephala. *Invertebrate Biology 114*: 186–188.

Rivera, M.C.; Lake, J.A. (2004). The ring of life provides evidence for a genome fusion origin of eukaryotes. *Nature 431*: 152–155.

Ruppert, E.E.; Barnes, R.D. (1994). *Invertebrate Zoology*. Sixth Edn. Saunders College Publishing. Orlando.

Segers, H.; Melone, G. 2002: A comparative study of trophi morphology in Seisonidea (Rotifera). *Journal of Zoology 244*: 201–207.

Shalchian-Tabrizi, K.; Eikrem, W.; Klaveness, D.; Vaulot, D.; Minge, M.A.; Le Gall, F.; Romari, K.; Throndsen, J.; Botnen, A.; Massana, R,; Thomsen, H.A.; Jakobsen, K.S. (2006). Telonemia, a new protist phylum with affinity to chromist lineages. *Proceedings of the Royal Society of London, B, 273*: 1833–1842.

Shalchian-Tabrizi, K.; Kauserud, H.; Massana, R.; Klaveness, D.; Jakobsen, K.S. (2007). Analysis of environmental 18S ribosomal RNA sequences reveals unknown diversity of the cosmopolitan phylum Telonemia. *Protist 158*: 173–180.

Slyusarev, G.S. (2000). Fine structure and development of the cuticle of *Intoshia variabili* (Orthonectida). *Acta Zoologica 81*: 1–8.

Slyusarev, G.S. (2003). The fine structure of the muscle system in the female of the orthonectid *Intoshia variabili* (Orthonectida). *Acta Zoologica 84*: 107–111.

Sørensen, M.V. 2003: Further structures in the jaw apparatus of *Limnognathia maerski* (Micrognathozoa), with notes on the phylogeny of the Gnathifera. *Journal of Morphology 255*: 131–145.

Stach, T.; Dupont, S.; Israelsson, O.; Fauville, G.; Nakano, H.; Kånneby, T.; Thorndyke, M. (2005). Nerve cells of *Xenoturbella bocki* (phylum uncertain) and *Harrimannia kupferi* (Enteropneusta) are positively immunoreactive to antibodies raised against echinoderm neuropeptides. *Journal of the Marine Biological ssociation of the United Kingdom 85*: 1519–1524.

Tyler, S. (2004). Platyhelminthes – the nature of a controversial phylum. http://www.umesci.maine.edu/biology/labs/platyhelm.htm.

von der Heyden, S.; Chao, E.E.; Vickerman, K.; Cavalier-Smith, T. (2004). Ribosomal RNA phylogeny of bodonid and diplonemid flagellates and the evolution of Euglenozoa. *Journal of Eukaryotic Microbiology 51*: 402–416.

Wallberg, A.; Curini-Galletti, M.; Ahmadzadeh, A.; Jondelius, U. (2007). Dismissal of Acoelomorpha: Acoela and Nermertodermatida are separate early bilaterian clades. *Zoological Scripta 36*: 509–523.

Whittaker, R.H. (1959). On the broad classification of organisms. *Quarterly Review of Biology 34*: 210–226.

Woese, C.R.; Kandler, O.; Wheelis, M.L. (1990). Towards a natural system of organisms: proposal for the domains Archaea, Bacteria, and Eucarya. *Proceedings of the National Academy of Sciences U.S.A. 87*: 4576–4579.