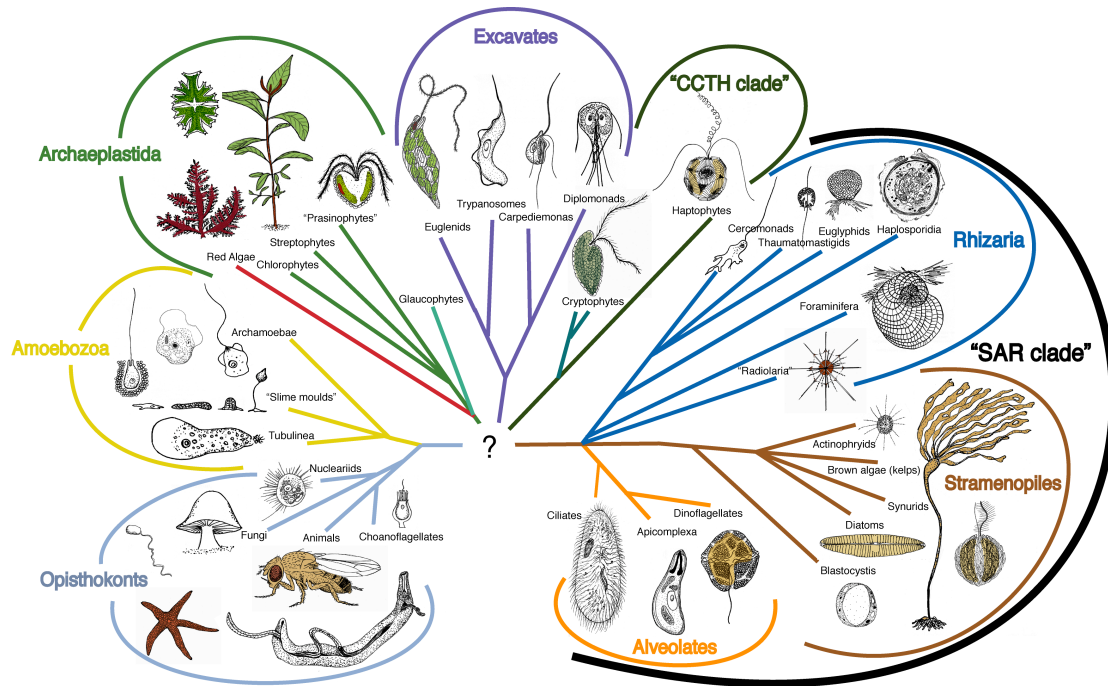


THE EUKARYOTES IN 2011

The groups, their defining features, and the literature

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INTRODUCTION

The following pages provide a primer on the eukaryotic groups: their defining features, and a reading-list for each (an introduction to the detailed, often-forgotten, research literature). We have deliberately used informal names for groups, and provided an indented hierarchy rather than a formal taxonomy, after the style of Patterson (Patterson 1994, 1999). The groups included are those for which strong, uncontroversial evidence exists in the current literature – giving a structure where an extremely large, well-studied group (*e.g.* ciliates) might sit at the same level of the hierarchy as a recently-discovered single species (*e.g.* *Chromera velia*). The appropriate interpretation of this structure is that the large group and the single species are currently sister taxa, possibly pending further systematic investigations; rather than that any inference should be made about genetic “distinctiveness”, or that any impulse toward taxonomic inflation of the single species should necessarily be indulged. The defining features listed here are not necessarily synapomorphies – where they are, this is indicated: protistology is still extremely rich in areas of potential systematic and taxonomic research. Defining features are derived from the published studies cited at the end of each group.

We are attempting to promote stability, but this comes at the expense of excluding some emerging taxonomic and systematic insights. Our non-adoption of formal taxonomy is intended to promote knowledge of “what goes where” over “what is it called”, because eukaryotic systematics is currently changing very rapidly. The general (supergroup) location of any group is unlikely to change, but the fine detail within supergroups – and thus, alpha-level taxonomy, and higher-level names and ranks - is likely to change rapidly in the next few years. Ambiregnality – the valid naming of taxa under both the ICZN and the ICBN – still has the potential to cause confusion in eukaryotic systematics (Patterson and Larsen 1991a). A conventional formal taxonomy, covering many (but not all) of the groups here, can be found in Adl *et al.* (Adl *et al.* 2005).

OPISTHOKONTS

Animals, fungi and their protistan relatives; with the most defined species of any eukaryotic supergroup. Most flagellated taxa have one posteriorly-inserting, posteriorly-directed flagellum, with a barren second basal body; pseudopodia where present are narrow. Mitochondrial cristae are flattened in most taxa. Collagens are present in the animal extracellular matrix and fungal fimbriae, and are not known from other eukaryotes. Chitin occurs elsewhere in the eukaryotes but is known in ecdysozoan animals, in all fungal groups, in *Ichthyophonus* in the ichthyosporids, and in the lorica of the choanoflagellate *Salpingoeca*. There is a conserved gene fusion of dihydrofolate reductase and thymidylate synthase, and a synapomorphic insertion in the EF1-alpha gene; in addition, many taxa utilise an unusual mitochondrial translation code, wherein the UGA (canonical stop) codon encodes tryptophan. No chloroplast-containing lineages are present, although several species have symbiotic or kleptoplastid relationships with algae.

The name Opisthokonta was previously used for chytrids but the usage adopted here has gained currency and is now widespread. Unrooted phylogenomic studies robustly support a close relationship between Opisthokonta and Amoebozoa. These taxa have historically been grouped as “unikonta”. However, recent studies have suggested that the biflagellate Apusozoa may group with Opisthokonta to the exclusion of Amoebozoa; the nomenclature, rank, and synapomorphies defining this clade have not been agreed. (Amaral-Zettler 2001; Baldauf 1999; Baldauf and Palmer 1993; Burki *et al.* 2008; Cavalier-Smith and Chao 2010; Cavalier-Smith and Chao 2003c; Celerin and Day 1998; Celerin *et al.* 1996; Hackett *et al.* 2007; Hampl *et al.* 2009; Kim *et al.* 2006; King and Carroll 2001; Lang *et al.* 2002; Lee and Young 2009; Liu *et al.* 2009; Medina *et al.* 2003; Mülisch 1993; Patterson *et al.* 1999; Reeb *et al.* 2009; Shalchian-Tabrizi *et al.* 2008; Stechmann and Cavalier-Smith 2002, 2003; Steenkamp *et al.* 2005; Wainright *et al.* 1993)

HOLOZOA

An assembly of the animals, choanoflagellates, and several small protist phyla (*Capsaspora*, *Ministeria*, and ichthyosporids); the paraphyletic assembly of choanoflagellates and other protists is also referred to as “Choanozoa”. All taxa (with the exception of ichthyosporids) are known to contain members with unbranched, non-tapering tentacles; in choanoflagellates and numerous kinds of animal cell (sponge choanocytes or protonephridial cells) these are arranged as a funnel-shaped collar of microvilli supported by actin filaments, surrounding the emergent flagellum, which beats water away from the cell body so that food (or waste) particles are swept between the microvilli and can be ingested. There is a conserved gene fusion of ubiquitin and rps30, and recent metagenomic studies have identified a range of signaling proteins- including notch-domain receptors, focal adhesion kinase 1, and palmitoylated and disc large homologue guanylate kinases- that may constitute discrete molecular synapomorphies. Molecular analyses largely support the monophyly of Holozoa, and a basal divergence from Holomycetes, although paraphyletic relationships have been recovered in some studies. (Baldauf 1999; Brooke and Holland 2003; Cantell *et al.* 1982; de Mendoza *et al.* 2010; Degnan *et al.* 2009; King 2004; Leadbeater 1977; Leadbeater and Manton 1974; Leadbeater and Morton 1974; Liu *et al.* 2009; Maldonado 2004; Medina *et al.* 2003; Nielsen 1987; Nielsen 2001; Ruppert and Smith 1988; Shalchian-Tabrizi *et al.* 2008; Steenkamp *et al.* 2005)

Metazoa (Animals)

An extremely diverse and speciose major group of multicellular, usually motile organisms with a high degree of division of labour (differentiation) between cells; diploid except for eggs and sperm, with meiosis preceding sexual reproduction, and a blastula developing from the fertilised zygote.

There are occluding junctions between cells (septate junctions in invertebrates, tight junctions in chordates and some arthropods), and spot or belt desmosomes for cell-cell adhesion. A number of gene families are uniquely associated with the metazoa, including PRD and ANTP class homeobox and ETS transcription factors; in addition, there is evidence for extensive domain shuffling in several more broadly conserved gene families during early metazoan evolution.

The basal state for sperm is with an ovoid head filled with nucleus, with an anterior acrosome, and a posterior area filled with mitochondria, and a posterior flagellum. The basic metazoan flagellar apparatus (except in adult sponges) consists of a standard 9+2 flagellum with a distal transitional plate, giving rise to two striated rootlets of differing periodicity; a non-flagellar basal body perpendicular to and below the first, giving rise to a microtubular root. Collagen proteins form fibrillar or network structures.

Animals can be divided into Porifera (sponges; with organic, calcite or siliceous spicules; with asexual reproduction by gemmules, or hermaphroditic sexual reproduction releasing gametes at different times, zygotes forming ciliated blastula-like larvae; adults sessile with totipotent cell differentiation into choanocytes, amoeboid cells, and secretory cells; with an extracellular matrix, but lacking desmosomes, nervous system, localised gonads and digestive glandular cells), Placozoa (flat disc-like animals that walk on their flagella; with two layers of flagellated epithelia surrounding a middle layer containing undifferentiated cells, syncytial contractile cells, eggs, sperm, and digestive glandular cells; lacking an extracellular matrix, basement membrane, and nervous system; asexual reproduction by binary division of body; includes *Trichoplax*), Mesozoa (osmotrophic endoparasites, multicellular with ciliated epithelium; with gap, septate and adhaerens junctions between cells; lacking gastrulation, basement membrane, extracellular matrix, digestive tissues), and Eumetazoa (reproduction via egg and sperm forming a zygote, which divides to become a blastula; cells migrate through gastrulation, with differentiation into ectoderm, endoderm, mesoderm and neuroderm, which differentiate into organs; with basement membrane, elaborate cell junctions; with a nervous system and digestive glandular cells; containing radially symmetrical cnidarians and ctenophores, and bilaterian acoels, protostomes (lophotrochozoa + ecdysozoa) and deuterostomes (chordates + hemichordates + echinoderms)). Porifera are believed to diverge basally within the metazoa; however, the precise branching relationships, and particularly whether Porifera and Eumetazoa are monophyletic or paraphyletic assemblies, are debated. A wide range of parasitic taxa are known, ranging from myxozoa (highly reduced cnidarian parasites of fish, formerly thought to be related to microsporidia) to platyhelminthes, nematodes, arthropods, and even some chordates (e.g. candiru, lampreys). Several species (e.g. the sea slug *Elysia chlorotica*) are known to acquire chloroplasts by kleptoplastidy from algae. Complete genome sequences are available for a wide range of species, including model Porifera (e.g. *Geodia neptuni* and *Tethya actinia*; both mitochondrial only), Placozoa (*Trichoplax adhaerens*) and Eumetazoa (*Homo sapiens*, *Drosophila melanogaster*, the cnidarian *Nematostella vectensis*, and the phytoparasitic nematode *Meloidogyne*

incognita). A close relationship to choanoflagellates is robustly supported by morphological and molecular evidence, although one single-gene study has robustly supported an immediate sister-group relationship with *Ministeria* to the exclusion of choanoflagellates. (Abad *et al.* 2008; Aleshin *et al.* 2007; Anderson 1998; Anderson *et al.* 1998; Boute *et al.* 1996; Degnan *et al.* 2009; Ender and Schierwater 2003; Exposito *et al.* 1993; Franzén 1987; Green and Dove 1984; Hejnol *et al.* 2009; Larroux *et al.* 2007; Lavrov *et al.* 2005; Lom and Dyková 1997; Nielsen 1987, 1998; Nielsen *et al.* 2001; Peterson and Eernisse 2001; Philippe *et al.* 2009; Putnam *et al.* 2007; Ruiz-Trillo *et al.* 2008; Ruthmann *et al.* 1986; Schierwater *et al.* 2002; Schwartz *et al.* 2010; Shalchian-Tabrizi *et al.* 2008; Steenkamp *et al.* 2005; Zrzavý *et al.* 1998)

Choanoflagellates

Small spherical or ovoid, unicellular and colonial “collar-flagellates”, with a single anterior flagellum inside a funnel collar of pseudopodial extensions supported by actin filaments. The flagellar apparatus (*e.g.* in *Monosiga* and *Codosiga*) can include rings of fibrillar material around the flagellar basal body, from which emerge radiating microtubules, either singly or in blocks. The microtubules extend to the bundles of actin filaments that support the collar. The cell exterior may be covered with a variety of structures ranging from organic sheaths to complex siliceous cages; these have taxonomic value.

Species have been identified from freshwater, marine benthic and pelagic habitats; no parasitic taxa are known. The group is divided into Monosigidae (naked taxa), Salpingoecidae (taxa with a cellulose theca), and Acanthoecidae (taxa with a lorica of siliceous strips). A genome has been completed for *Monosiga brevicollis*; preliminary analysis reveals similar gene content, but surprisingly different genome organisation from metazoa, with three unique classes of retrotransposons, a highly diversified array of tyrosine kinases, and differences in subtelomeric gene content. Meiotic genes have been identified, suggesting that choanoflagellates are sexual, and three genes of the glutamate synthase pathway appear to have been laterally acquired from algal donors. There is longstanding molecular support for a close relationship between choanoflagellates and metazoa; recent multigene studies have, however, failed to recover consistent branching relationships between the Metazoa, choanoflagellates and other Holozoan taxa. (Carr *et al.* 2010; Carr *et al.* 2008a; Carr *et al.* 2008b; Hibberd 1975; Karpov 1999; Karpov and Leadbeater 1997; King *et al.* 2008; Lara *et al.* 2009; Leadbeater 1977; Leadbeater and Manton 1974; Leadbeater and Morton 1974; Manning *et al.* 2008; Robertson 2009; Ruiz-Trillo *et al.* 2008; Shalchian-Tabrizi *et al.* 2008; Steenkamp *et al.* 2005).

Capsaspora owczarzaki

A species of amoeba with long filose pseudopodia up to 3 times the diameter of the cell. One of the pseudopodia can be used as a “feeding peduncle” and is extended towards prey cells and used for saprotrophic ingestion of the prey’s cytoplasm (which distinguishes this species from the nucleariids). It is ecologically distinctive, being a symbiont in the haemolymph of the snail *Biomphalaria glabrata* and therein a parasite of the trematode *Schistosoma mansoni*. It undergoes asexual fission to produce separate but identical daughter cells (which distinguishes it from members of the Ichthyosporids). *Capsaspora* contains genes encoding membrane-associated guanylate kinases, a protein family otherwise unique to choanoflagellates and metazoa, and implicated in the evolution of

multicellularity in animals. Originally classified as a nucleariid, phylogenomic analyses variously suggest sister-group relationships to ichthyosporids and to *Ministeria*, and close relationships with metazoa and choanoflagellates. (Amaral-Zettler 2001; de Mendoza *et al.* 2010; Hertel *et al.* 2002; Liu *et al.* 2009; Ruiz-Trillo *et al.* 2006; Ruiz-Trillo *et al.* 2008; Shalchian-Tabrizi *et al.* 2008; Stibbs *et al.* 1979).

Ministeria

Small spherical marine organisms with radiating, equally spaced, very fine smooth arms up to several times the diameter of the body in length, which are grown and used raptorially to catch bacteria that have stuck to the cell surface. The ability to grow fine arms as a fast response suggests that they may be supported by actin microfilaments, similar to the arms making the collar of choanoflagellates. One species has a fine stalk containing microtubule doublets, and can vibrate, suggesting the presence of a (hitherto uncharacterised) flagellum. Multigene phylogenies variously suggest sister-group relationships with metazoa, metazoa + choanoflagellates, and *Capsaspora*. (Cavalier-Smith and Chao 2003c; Patterson *et al.* 1993a; Shalchian-Tabrizi *et al.* 2008; Steenkamp *et al.* 2005; Tong *et al.* 1997).

Ichthyosporids

Also called Mesomycetozoa: a clade of osmotrophic opisthokonts, with spherical or ovoid cells, containing a large central vacuole and thick cell walls. Cell walls may contain chitin; nuclei and chromatin are prominent, and many species may utilise a multinucleate stage. Mitochondrial cristae are predominantly flattened, although tubular cristae have been observed in one species. The plasma membrane of *Creolimax fragrantissima* has been observed to separate into branching tubules, and subplasmalemmal vesicles have been observed in other taxa; it is not known yet whether this organisation constitutes a genuine synapomorphy. There is genetic evidence for sexuality, although only asexual reproduction has been observed. Ichthyosporids include the dermocystid pathogens of vertebrates (which produce uniflagellated zoospores) and the ichthyophonid parasites of marine invertebrate digestive tracts (which produce amoeba-like dispersive cells, and may form aggregated cell clusters). Historically classified as fungi, molecular phylogenies robustly recover a close relationship with metazoa and choanozoa, and associated protist lineages, but variously suggest immediate sister-group relationships with *Capsaspora*, *Corallochytrium*, and a position basal to all other choanozoa. (Fredricks *et al.* 2000; Lang *et al.* 2002; Liu *et al.* 2009; Lohr *et al.* 2010; Marshall and Berbee 2010; Marshall *et al.* 2008; Medina *et al.* 2003; Mendoza *et al.* 2002; Mort-Bontemps *et al.* 1997; Mülisch 1993; Ragan *et al.* 1998; Ruiz-Trillo *et al.* 2004; Ruiz-Trillo *et al.* 2008; Shalchian-Tabrizi *et al.* 2008; Spanggaard *et al.* 1996; Steenkamp *et al.* 2005; Ustinova *et al.* 2000)

HOLOMYCETES

A diverse clade, consisting of fungi, and two protist (nucleariids and fonticulids) groups. Individuals may be flagellated, amoeboid, filamentous, or have complex body organisation. Pseudopodia, where present, are tapering and may be branched. Mitochondrial genomes may be rich in introns, although this is not always true (e.g. the chytrid *Harpochytrium*). Molecular phylogenies robustly support a basal

divergence of Holomycetes from Holozoa. (Bullerwell *et al.* 2003; Bullerwell and Lang 2005; Lang *et al.* 2002; Lara *et al.* 2009; Liu *et al.* 2009)

Nucleariids

Aflagellated, predominantly spherical amoebae with radiating fine, non-branching, non-granular, non-axopodial pseudopodia, which consume whole prey cells. Some species are naked, while others are covered with siliceous scales, plates or spherical “perles” (*Pompholyxophrys* species), or spines, or a test, which is hollow and has a meshwork structure, or there may be a filamentous extracellular matrix (*Nuclearia* species); the pseudopodia emerge through these structures. When flattened, cells have filose pseudopodia emerging from the anterior edge. The pseudopodia are not supported by microtubules, and microtubule-organising centres such as centrospheres appear to be absent: this distinguishes them from superficially similar centrohelids or radiozoa. Mitochondrial cristae are flattened. One species, *N. pattersonii*, has been isolated from roach gills and contains a bacterial endosymbiont. A mitochondrial genome has been completed for *N. simplex*, and reveals multiple introns, and the use of a canonical translation table. Molecular studies place nucleariids as basal to fungi, and as the immediate sister-group of fonticulids. (Amaral-Zettler 2001; Brown *et al.* 2009; Cavalier-Smith and Chao 2003c; Dyková 2003; Lara *et al.* 2010; Liu *et al.* 2009; Medina *et al.* 2003; Mikrjukov 1999; Mikrjukov 2000b; Nicholls and Durrschmidt 1985; Patterson 1985a; Patterson *et al.* 1987; Ruiz-Trillo *et al.* 2004; Steenkamp *et al.* 2005; Surek and Melkonian 1980; Thomsen 1978; Wujek and O’Kelly 1991; Yoshida *et al.* 2009)

Fonticulids

Coprophilic “cellular” slime moulds, where the trophic stage is amoebae with filose pseudopodia. Amoebae aggregate to form a pyramidal sorocarp. Mitochondrial cristae are discoidal. Multigene studies robustly support a sister-group relationship to the nucleariids. (Brown *et al.* 2009; Deasey 1981; Deasey 1982; Page and Blanton 1985; Worley *et al.* 1979).

Fungi

A large clade of osmotrophic mycelial organisms that form hyphae (threads) and reproduce using spores; and their phagotrophic unicellular relatives. Hyphae grow apically, and may or may not be divided into cells by septa. Cell walls contain chitin and beta-glucans; fungal fimbriae contain non-fibrillar collagen. Nutrition is osmotrophic via the mycelium; the storage product is glycogen. Lysine synthesis occurs via the α -amino adipate pathway. Uniquely among studied eukaryotes, fungi produce nonribosomal peptide synthetases, which catalyse the biosynthesis of small peptides via a thiotemplate mechanism. There is widespread evidence for sexuality within the fungi, which may occur via a variety of mechanisms, ranging from permanent sexual dimorphism to mating between and even within two or more interchangeable mating-types. Molecular phylogenies strongly suggest a sister-taxon relationship to Nucleariids. (Adl *et al.* 2005; Bowman *et al.* 1992; Bushley and Turgeon 2010; Celerin and Day 1998; Celerin *et al.* 1996; Hibbett *et al.* 2007; Lara *et al.* 2009; Lee *et al.* 2010; Lin *et al.* 2005; Lutzoni *et al.* 2004; Steenkamp *et al.* 2005)

Ascomycetes

“Sac” fungi, accounting for about 75% of all fungi, including *Penicillium chrysogenum*, source of penicillin and *Saccharomyces cerevisiae*, baker’s yeast; with mycelial habit and no flagellated stages. The defining feature is the sac-like ascus, a cell where karyogamy, meiosis and (nuclear or plasma) membrane division occur to produce *ca.* 8 ascospores which develop in the cell; the ascus often develops in a sterile fruiting body (the ascoma), either from ascogenous hyphae, from a crozier or from a single cell. There is a dikaryotic (functionally diploid) mycelium stage in the life cycle, though the dikaryotic mycelium can co-occur with the differentiated haploid ascoma. The hyphae have chitin and glucan walls; septa may have plasmodesmata, or be uniperforate or multiperforate, according to the life cycle stage; the septal pore structure can be used to differentiate groups within the ascomycetes.

The Ascomycetes is the largest group of fungi, and includes most of the lichen-forming species as well as insect symbionts, and endophytic and mycorrhizal symbionts of plants. There are a large number of known parasitic and pathogenic ascomycetes, including *Magnaporthe grisea* (rice blast fungus, which is believed to be the most destructive and economically significant rice pathogen), the human pathogens *Pneumocystis carinii* and *Candida albicans*, and several other parasites of animals, plants, and even other ascomycetes. The Ascomycetes may be divided into: *Neolecta* (mycelial and multinucleate, ascomata stalked and fleshy, lacking interascal tissue; cylindrical asci formed from binucleate cells, producing ellipsoidal ascospores with thin walls), *Taphrinomycotina* (mycelium present or absent, asci formed from binucleate cells, no interascal tissue or croziers; including *Schizosaccharomyces*, fission yeast, and *Pneumocystis*, human pathogen), *Saccharomycetes* (mycelium reduced or absent, with septate hyphae with multiple pores; most vegetative cells proliferate by budding or fission, cell walls lack chitin; ascomata absent; asci produced by mitosis, with interascal tissue; includes *Candida* and *Saccharomyces*), and *Pezizomycotina* (Mycelium with filamentous hyphae with septate walls with single pores, haploid life cycle with dikaryotic stage immediately prior to sexual reproduction, differentiated male antheridium and female ascogonium; ascogenous hyphae and croziers producing asci; extremely diverse and speciose). Genome sequences are available for a number of species, including *S. cerevisiae*, *Schizosaccharomyces pombe*, *Neurospora crassa*, *M. grisea*, *P. carinii* and *C. albicans*, and genomic deletion maps have been assembled for *S. cerevisiae* and *S. pombe*; comparative analysis of ascomycete genomes reveals evidence for extensive segment and genome duplication and gene loss in different lineages. Phylogenetic studies concur with the suite of morphological features in suggesting that this group is monophyletic and sister taxon to the Basidiomycetes. (Adl *et al.* 2005; Bruns *et al.* 1992; Dean *et al.* 2005; Dujon *et al.* 2004; Fitzpatrick *et al.* 2006; Galagan *et al.* 2003; Gargas *et al.* 1995; Giaever *et al.* 2002; Hibbett *et al.* 2007; Humber 2008; Jones *et al.* 2004; Kimbrough 1994; Kuramae *et al.* 2006; Lutzoni *et al.* 2004; Nishida 1994; Odds 1987; Reichle 1965; Rodriguez *et al.* 2009; Ruiz-Trillo *et al.* 2008; Schaffer 1975; Shalchian-Tabrizi *et al.* 2008; Slaven *et al.* 2006; Spirek *et al.* 2010; Steenkamp *et al.* 2005; Wang *et al.* 2009; Wetmore 1973; Wood *et al.* 2002; Yuan *et al.* 2010)

Basidiomycetes

“Club” fungi, mostly with a dikaryotic, mycelial habit and no flagellated stages. Hyphae are septate (with plasmodesmata, multi-pore or uni-pore structures joining cells) and may have clamp connections: outgrowths from dividing hyphal cells which retain the dikaryotic condition. The basidium is the defining structure: a cell, produced from the mycelium, in which karyogamy and meiosis occur to produce 2-4 haploid basidiospores, which are released and develop exogenously into hyphae. Ballistospores may occur, spores which are discharged into the air with force, and can be produced by one of several life cycle stages (depending on species).

Basidiomycetes include several animal and plant endosymbiont and epibiont lineages, of which some are parasitic and of economic (including *Armillaria gallica*, a forest pathogen which can cover very large areas of soil; *Uromyces*, “rust fungus” and *Ustilago*, “smut fungus”- plant crop pathogens) or medical importance (the human pathogen *Cryptococcus neoformans*). Three major groups are recognised: the Uredinales (“rust fungi”, with very complex life cycles, mycelial or yeast habit; xylose in cell walls, layered centrosomes, septal pores with plug but no cap); the Ustilaginales (“smut fungi”, mycelial parasites, many with saprobic yeast or ballisticonidial stages, xylose absent, globose unlayered centrosomes, septal pores without plugs or caps), and the large assemblage Hymenomycetes, including mushrooms and yeasts in the tremellomycetes. A number of genomes have been sequenced, including saprotrophic (*Phanerochaete chrysosporium*), ectomycorrhizal (*Laccaria bicolor*) and parasitic species (*Ustilago maydis*). Molecular studies robustly support basidiomycete monophyly and an immediate sister-group relationship with the Ascomycetes. (Adl *et al.* 2005; Bauer *et al.* 2001; Bruns *et al.* 1992; Doublés and McLaughlin 1991; Fell *et al.* 2001; Fitzpatrick *et al.* 2006; Hibbett and Thorn 2001; Kamper *et al.* 2006; Kuramae *et al.* 2006; Lutzoni *et al.* 2004; Martin *et al.* 2008; Martinez *et al.* 2004; McLaughlin *et al.* 1985; Money 1998; Rodriguez *et al.* 2009; Ruiz-Trillo *et al.* 2008; Schaffer 1975; Shalchian-Tabrizi *et al.* 2008; Smith and Sale 1992; Steenkamp *et al.* 2005; Swann *et al.* 2001; Wang and Qiu 2006; Wang *et al.* 2009; Yuan *et al.* 2010)

Zygomycetes

Fungi with a mycelial habit, and no flagellated stages. Hyphae are long, haploid and multinucleate; many are coenocytic. Sexual reproduction occurs via the fusion of gametangia on the hyphae, to produce diploid zygospores which then undergo meiosis to generate a spore sac; spores germinate and become hyphae. Some species are used as fermenting agents in East Asian cuisine (*e.g.* *Rhizopus oligosporus* in tempeh production). Many species are parasitic, including several potentially lethal human pathogens (*e.g.* *Rhizopus oryzae*, a causative agent of mucormycosis, and *Mortierella verticillata*, a causative agent of zygomycosis); some parasitic species may themselves contain bacterial endobionts, which may increase the virulence and pathogenicity of the host.

Zygomycetes are currently divided into five lineages, although the underlying systematics is uncertain and the taxonomy is likely to change: Mucoromycetes (saprotrophic, ectomycorrhizal, or mycoparasitic filamentous fungi, with septa present only in older hyphae and with plasmodesmata at septal pores; asexual reproduction by merosporangia and sexual reproduction by globose

zygospores); Entomophthorales (predominantly arthropod parasites with filamentous aseptate thalli, which may fragment to form multinucleate hyphal bodies; asexual reproduction by conidia and sexual reproduction by thick-walled zygospores); Kickxellomycetes (saprotrophic, symbiotic, or mycoparasitic fungi, hyphae with regular septa, each containing a lenticular cavity and plugs; asexual reproduction by merosporangia or trichospores, and sexual reproduction by sometimes ornamented zygospores), Zoopagomycetes (parasites of other fungi and of microanimals, with a filamentous coenocytic or septate thallus; asexual reproduction by merosporangia and sexual reproduction by nearly globose zygospores), and Basidiolobus (soil fungi, with a filamentous septate thallus and uninucleate cells; sporophores with a subsporangial vesicle; asexual reproduction by conidia and sexual reproduction by zygospores with a centriole-like organelle). A complete genome sequence is available for the mucoromycete *R. oryzae*, and mitochondrial genomes for the mucoromycete *M. verticillata* and the kickxellomycete *Smittium culisetae*; preliminary data from *R. oryzae* reveals evidence for a recent whole-genome duplication event. Recent molecular analyses have suggested that the zygomycetes are paraphyletic, with mucoromycetes branching as one or more immediate sister-taxa to the ascomycetes and basidiomycetes, and all remaining zygomycete taxa branching as a well-supported sister-clade to these lineages; the resultant changes to the taxonomy, nomenclature and rank of this phylum remain under debate. (Adl *et al.* 2005; Barr 1981; Fuller and Reichle 1968; Hawker *et al.* 1966; Hibbett 2006; James *et al.* 2000; Jeffries and Young 1979; Keeling 1998, 2003; Kito *et al.* 2009; Liu *et al.* 2009; Lutzoni *et al.* 2004; Ma *et al.* 2009; Moss and Young 1978; Nagahama *et al.* 1995; Olson 1973; Paquin *et al.* 1997; Schüssler *et al.* 2001; Seif *et al.* 2005; Steenkamp *et al.* 2005; Tanabe *et al.* 2000; Tanabe *et al.* 2004; Tehler *et al.* 2003; Validiviva and Heitman 2007; White *et al.* 2006).

Nephridiophagids

Spore-forming parasites of the malpighian tubules of insects. Infection is via the oral uptake of spores; reproduction occurs in the host tubule epithelium or lumen, to produce uninucleate amoeboid cells, which differentiate into multinucleate plasmodia. The plasmodia divide into merozoites or spores. The spore walls contain chitin. Molecular studies support a position within the fungi, as a close relative of the zygomycetes; the exact position is not agreed. (Fabel *et al.* 2000; Ganapati and Narasimhamurti 1960; Lange 1993; Radek and Herth 1999; Radek *et al.* 2002; White *et al.* 2006; Wylezich *et al.* 2004)

Glomeromycetes

A group consisting entirely of obligate arbuscular mycorrhizal symbionts of plants. Although mycorrhizal ascomycetes and basidiomycetes are known, glomeromycetes are the mycorrhizal symbionts of almost all plants that have a fungal root symbiosis. Glomeromycetes have an asexual life cycle, aseptate hyphae, and large, multinucleate spores with layered walls. Spores form singly or in sporocarps outside the host, and make contact with plant roots following germination into hyphae. Inside the roots, they form tree-like structures (arbuscules) with very reduced cell walls which allow transfer of nutrients into the plant root cells, which also have reduced cell walls when arbuscules are present. The glomeromycete *Geosiphon pyriformis* contains endosymbiotic cyanobacteria. A mitochondrial genome has been completed for *Glomus*

intraradices. There is evidence for substantial genomic and transcriptomic variation even within specific arbuscular mycorrhizal isolations. Multigene phylogenies recover a deep-branching position within the fungi, and in one case suggest a sister-group relationship to the zygomycete *Mortierella*. (Adl *et al.* 2005; Aleshin *et al.* 2007; Bécard and Pfeffer 1993; Boon *et al.* 2010; Corradi *et al.* 2004; Corradi and Sanders 2006; Helgason *et al.* 2003; Hibbett *et al.* 2007; Kuhn *et al.* 2001; Lee and Young 2009; Morton 1988; Morton and Benny 1990; Schüssler *et al.* 2001; Wang and Qiu 2006)

Chytrids

Coenocytic fungi that form unwalled flagellated zoospores for reproduction, which then convert into either walled spores or a diploid thallus. Many taxa have a hyphal thallus; the hyphae contain septa with plasmodesmata; there are one or more sporangia. Zoospores have a characteristic arrangement of the flagellar apparatus: in most taxa there is a single posteriorly directed flagellum, with the second flagellum represented only by a very short basal body, parallel to and closely connected to the first by fibrillar material. The flagellar transition zone has a distinctive concentric fibre, and there are “props” between the flagellar apparatus and the cell membrane. Chytrids include a number of parasitic taxa, including the amphibian parasite *Batrachochytrium dendrobatidis*, and several parasites of diatoms, which may play a key role in rendering photosynthetic biomass edible to primary consumers.

Traditional groupings include: Monoblepharidales (flagellar apparatus similar to those in some choanoflagellates, with concentric striated fibrillar rings around the flagellar basal body, and a 270-degree radiating layer of microtubules extending from the rings; with the basal bodies parallel; with a nonfenestrated rumposome), Neocallimastigales (obligate endosymbionts of ruminant and reptilian digestive tracts, with genome-lacking hydrogenosomes instead of mitochondria; with two or many flagella without dormant basal bodies; with a saddle-like structure surrounding the basal body, and a single bundle of microtubules, with or without interconnecting fibrils, extending from the flagellar basal body down to a posterior dome structure; and with an extremely low content of polyunsaturated fatty acids), Spizellomycetales (nucleus attached to basal bodies with closely adpressed or connected by microtubular root; basal bodies at an angle), and the apparently polyphyletic Chytridiales (uniflagellated or with multiple flagella; nucleus not connected to basal bodies; basal bodies connected by fibrillar material, flagellar root extending to the rumposome - lipid globule surrounded by a microbody and laminated fibres). A complete genome is available for *B. dendrobatidis*, and mitochondrial genomes are available for five chytrid genera: *Monoblepharella*, *Harpochytrium* and *Hyaloraphidium* (monoblepharidales), *Spizellomyces* (spizellomycetale) and *Rhizophydium* (chytridiale). Preliminary analysis suggests highly reduced mitochondrial genome content, and in particular few mitochondrial-encoded tRNAs; uniquely amongst fungi, mitochondrial tRNAs may be subject to post-transcriptional editing. Multigene phylogenies strongly support a deep-branching position within the fungi, predominantly as an independent lineage (excluding rozellids), although some studies have suggested a sister-group relationship to blastocladiomycetes and/ or some zygomycetes, and paraphyletic derivations of recognised chytrids. (Adl *et al.* 2005; Barr 1978, 1980, 1981, 1990, 1992; Barr and Désaulmiers 1986, 1988; Barr *et al.* 1987; Barr and Hadland-Hartman

1978; Berger *et al.* 1998; Bowman *et al.* 1992; Bullerwell *et al.* 2003; Bullerwell and Lang 2005; Comlekcioglu *et al.* 2010; Fuller and Calhoun 1968; James *et al.* 2000; Kagami *et al.* 2007; Li *et al.* 1993; Liggenstoffer *et al.* 2010; Longcore 1993, 1995; Lutzoni *et al.* 2004; Mollicone and Longcore 1994; Nagpal *et al.* 2007; Philippe *et al.* 2009; Powell and Gillette 1987; Rosenblum *et al.* 2008; Ruiz-Trillo *et al.* 2008; Shalchian-Tabrizi *et al.* 2008; Steenkamp *et al.* 2005; Tanabe *et al.* 2005; Taylor and Fuller 1980; Wang *et al.* 2009)

Blastocladiomycetes

Fungi with a filamentous stage containing hyphae with multiperforate septa, and with a uniflagellate zoospore stage. The microtubules of the flagellar apparatus originate from a fibrillar sleeve surrounding the flagellar basal body, and extend in 9 groups of 3 to surround the nucleus, which is proximal to the flagellum. The nucleus is conical, and covered with a distinctive cap of ribosomes, surrounding the abflagellar side of the nucleus and visible by light microscopy; mitosis is closed. Cells contain a “side-body complex” of lipid globules and membrane cisternae, similar to chytrids. Species may be saprotrophs or parasites of plants, green algae, invertebrates, and other fungi. Mitochondrial genomes have been completed for *Blastocladiella emersonii* and *Allomyces macrogynus*; in addition, EST libraries have been collated for *B. emersonii* under a variety of different environmental stress conditions. Suggested from SSU rDNA phylogenies to be a basal member of the zygomycetes, recent phylogenomic analyses have suggested that blastocladiomycetes constitute a deep branch or paraphyletic array within the fungi, either at the base of the zygomycetes, ascomycetes and basidiomycetes, at the base of the chytrids, or basal to all other fungi other than microsporidia and rozellids. (Aleshin *et al.* 2007; Barr 1981; Borkhardt *et al.* 1988; Borkhardt and Olson 1986; Georg and Gomes 2007; Gutman *et al.* 2009; James *et al.* 2006; James *et al.* 2000; Lara *et al.* 2009; Lutzoni *et al.* 2004; Moss and Young 1978; Nagahama *et al.* 1995; Philippe *et al.* 2009; Ruiz-Trillo *et al.* 2008; Shalchian-Tabrizi *et al.* 2008; Steenkamp *et al.* 2005; Tambor *et al.* 2008; Tanabe *et al.* 2004; Tehler *et al.* 2003; White *et al.* 2006)

Microsporidia

Amitochondriate, aflagellated, obligate intracellular parasites of ciliates and animals, including the bee parasite *Nosema apis* and *Nosema bombycis*, the agent of pébrine (silkworm pepper disease), and several human parasites (*e.g.* *Encephalitozoon cuniculi*) that can have severe effects on immunosuppressed individuals. Microsporidia are only free-living as spores, which have a coiled extrusion apparatus which is an invagination of the cell membrane. The cell membrane encloses a lamellate and vesicular polaroplast, posterior vacuole, and a coiled polar filament which attaches to the anterior end of the cell by an umbrella-shaped anchoring disk, and posteriorly contacts the posterior vacuole. The polar filament is everted to penetrate host cell walls, and empty the contents of the spore (amoeboid sporoplasm) into the host cell. Spore walls contain chitin and glucan. There is a mitosome (reduced mitochondrion) in some taxa. The cytoplasm is enriched with ribosomes, and most taxa have diplokaryotic (paired, closely adpressed, synchronously dividing) nuclei in some or all stages. The genomes of *E. cuniculi* and *E. intestinalis* have been completed, and are the most compact of all studied eukaryotes, with evidence for extensive intron loss.

Unlike all other studied “fungi”, there is no evidence for the presence of nonribosomal peptide synthetases, or of components of the α -amino adipate lysine biosynthesis pathway; however, there is genetic evidence for sexuality. The presence of 70S ribosomes, with 16S/23S subunits, simple ultrastructure, apparent lack of mitochondria, and highly derived SSU rRNA and EF1 alpha sequences originally suggested a basal placement in the eukaryotes; but analyses of protein sequences with a correction for rate heterogeneity, and the presence of chitin in the spore walls, all indicate a fungal origin; some more recent analyses have suggested an origin within or at the base of the zygomycetes, or basal to all osmotrophic fungi. (Adl *et al.* 2005; Bushley and Turgeon 2010; Fischer and Palmer 2005; Hibbett *et al.* 2007; Hirt *et al.* 1999; Inagaki *et al.* 2004; Katinka *et al.* 2001; Keeling 2003; Keeling and Fast 2002; Keeling *et al.* 2005; Keeling *et al.* 2000; Keohane and Weiss 1999; Larsson 1986; Lee *et al.* 2010; Lee *et al.* 2009; Ormières *et al.* 1976; Slamovits *et al.* 2004; Vávra and Larsson 1999; Vinckier *et al.* 1993; Vivares and Metenier 2000; Wang *et al.* 2009; Williams *et al.* 2002; Williams and Keeling 2003; Williams *et al.* 2005; Williams and Keeling 2005).

Rozellids

Parasitic fungi with uniflagellate motile cells, wall-less amoeboid trophic cells, and walled cyst stages; no filamentous taxa are known. Encysted and flagellated cells contain conspicuous polyphosphate granules. Parasite attachment is dependent on host signalling factors, and on growth of the host cell wall; feeding occurs by phagocytosis of host cell organelles. One genus, *Rozella*, is known, and is principally parasitic of other fungal-like organisms (chytrids, blastocladiomycetes and oomycetes), although one species has been suggested to be a parasite of coleochaete algae, and recent metagenomic studies have uncovered multiple unisolated freshwater, marine and acidophilic taxa. Historically classified as chytrids, recent multigene phylogenies have supported a position basal to all osmotrophic fungi (chytrids, zygomycetes, blastocladales, ascomycetes, basidiomycetes); the position of rozellids relative to microsporidia is unknown. (Held 1972, 1974; Hibbett *et al.* 2007; James *et al.* 2006; Lara *et al.* 2010; Wool and Held 1976)

OPISTHOKONTS *INCERTAE SEDIS*

Corallochytrium

A species of aflagellated spherical marine protists, which are distinguished by undergoing up to 5 rounds of binary fission, producing up to 32 daughter cells which are released through a pore in the cell wall, as elongated amoebae. Nutrition is saprotrophic. This species was originally classed as a thraustochytrid (Stramenopiles) on the basis of morphology, but lacks the characteristic flagellated stags, sagenogenetosome and ectoplasmic nets of that group. Multigene studies strongly support a close relationship with ichthyosporids, whereas the use of α -amino adipate reductase in lysine biosynthesis suggests a closer relationship with holomycetes; the precise phylogenetic position of *Corallochytrium* is not agreed. (Carr *et al.* 2008a; Cavalier-Smith and Allsopp 1996; Cavalier-Smith and Chao 2003c; Chamberlain and Moss 1988; Kumar 1987; Medina *et al.* 2003; Steenkamp *et al.* 2005; Sumathi *et al.* 2006; Vørs 1992a).

AMOEBOZOA

A supergroup composed predominantly of amoebae and amoeboid flagellates: it includes nearly all the amoebae with lobose (broad, non-filose) pseudopodia, some of which have subpseudopodia. Some (pelobionts, myxogastrids, protostelids, *Phalansterium*, *Breviata*) have flagella, while others (canonical amoebae - Tubulinea, Flabellinida) do not. The group overlaps with the traditional concept of amoebae as one of the main groups of protozoa, but some of the taxa that would have been considered amoebae have now found homes elsewhere, mostly in the Excavata or Rhizaria. The group also overlaps significantly with the “Ramicristates” – a group defined by the presence of mitochondria that have branching, irregular mitochondrial cristae. The composition of each group requires further clarification as neither clear pictures of mitochondria, nor robust molecular phylogenetic information, are available for all members.

The supergroup was originally most clearly identified on the basis of molecular evidence from a concatenation of multiple genes, with details of membership emerging from more taxon-rich SSU rRNA and actin phylogenies. Membership of amoebozoa, or of some of its clearly-circumscribed subclades, can be determined using SSU rRNA phylogenies, but the relationships between subclades are best discovered using multiple gene phylogenies. Some traditional hypotheses of relationships within amoebozoa currently have no support as monophyletic clades, since the groups' defining features appear to be plesiomorphies throughout the amoebozoa: multi-gene phylogenies will illuminate this further when more taxa are sampled. These include Lobosea (canonical amoebae with broad, lobed or finger-shaped pseudopodia, and a simple life cycle of cysts and amoebae); Mycetozoa (slime moulds, which alternate between a motile amoeboid stage and a fruiting body stage); Conosa (flagellated amoebae with a cone and lateral band of microtubules, most with a single basal body); and Centramoebae (amoeboid taxa with an extranuclear “centrosome”, *i.e.* a striated microtubule organising centre giving rise to cytoplasmic microtubules).

The amoebozoa includes well-known parasites *Entamoeba histolytica* and *Acanthamoeba castellanii*, the classical amoeba *Amoeba proteus* and the model slime moulds *Dictyostelium discoideum* and *Physarum polycephalum*; genome or EST projects have been completed for each of these, revealing that amoebozoan genomes are intron-rich and have an unusually high proportion of signalling genes. There is considerable size variation in genomes, including the largest genome known (670 000 000 000 bases in *Amoeba dubia*). (Arisue *et al.* 2002; Baldauf and Doolittle 1997; Baptiste *et al.* 2002; Bolivar *et al.* 2001; Cavalier-Smith 1998, 2004; Dykstra 1977; Fahrni *et al.* 2003; Fiore-Donno *et al.* 2005; Fiore-Donno *et al.* 2008; Fiore-Donno *et al.* 2010; Frederick 1990; Glockner *et al.* 2008; Grebecki 1994; Grell and Schüller 1991; Guhl and Roos 1994; Kim *et al.* 2006; Kudryavtsev *et al.* 2005; Milyutina *et al.* 2001; Nassonova *et al.* 2010; Nikolaev *et al.* 2005; Olive 1975; Page 1987, 1988, 1991; Parfrey *et al.* 2006; Patterson 1994, 1999; Rogerson and Patterson 2002; Roos 1975; Shadwick *et al.* 2009; Silberman *et al.* 1999; Smirnov and Goodkov 1999; Smirnov *et al.* 2005b; Song *et al.* 2005; Spiegel 1981a, 1990; Spiegel 1991; Spiegel *et al.* 1995; Tekle *et al.* 2008; Ueda *et al.* 1997; Walker *et al.* 2003; Walker *et al.* 2001)

For ease of retrieval, taxa are organised below into amoebae, slime moulds and flagellated amoebae: it should be noted that this is an artificial distinction.

“AMOEBAE”

Tubulinea

A group of amoebae with diverse morphologies, recovered by molecular phylogeny, including "traditional amoebae" like *Amoeba* and *Chaos*; hartmannellids and echinamoebae; and leptomyxids; also the "shelled amoebae" or arcellinids. A possible synapomorphy is the ability to form tubular pseudopodia and mono-axial flow of cytoplasm in the entire cell or every pseudopodium. (Bolivar *et al.* 2001; Smirnov *et al.* 2005b)

Arcellinida

Testate lobose amoebae with a shell with a single aperture, with the shell made of proteinaceous material or agglutinated from organically- cemented sand, diatoms *etc.* Proteinaceous tests may be rigid or made of hollow building blocks that are made in the Golgi apparatus. Pseudopodia may be lobose and granular or hyaline, or finger-shaped, and may anastomose. SSU rRNA phylogenies indicate that the group is monophyletic and that organisms with proteinaceous and agglutinated shells do not form independent lineages. Actin phylogenies also place these organisms in the Tubulinea. (Bobrov 2004; Bonnet 1961, 1963, 1964, 1975; Lara *et al.* 2009; Mignot and Raikov 1990, 1992; Nikolaev *et al.* 2005; Ogden and Hedley 1980; Ogden and Meisterfeld 1989; Raikov and Mignot 1991)

Leptomyxida

Flattened, wide naked amoebae with diverse morphologies: uninucleate and elongate, multinucleate, plasmodial and reticulate or branched. Some species can change from wide, flat forms to cylindrical, monopodial, monoaxial-streaming forms. Anterior subpseudopodia are not produced. There is often a mass of trailing filamentous pseudopodia behind the amoeba. The group includes Leptomyxidae and Flabellulidae (from SSU rRNA analyses). (Amaral-Zettler and Caron 2000; Cann 1984; Fahrni *et al.* 2003; Michel and Smirnov 1999; Page 1971, 1972; Page and Willumsen 1983; Pussard and Pons 1976a, 1976b; Smirnov *et al.* 2009; Smirnov and Goodkov 1999; Vivesvara *et al.* 1993)

Tubulinida

A group identified on molecular grounds, including the lab amoeba *Amoeba proteus*, containing members of traditional groups Amoebidae, Echinamoebae, and Hartmannellidae (except those organisms in culture collections identified as *Hartmannella vermiformis*). These amoebae are monopodial or polypodial with a cylindrical cross-section of the pseudopodium. In Hartmannellidae there is a prominent nucleolus; *Saccamoeba* has hexagonal cup-shaped structures on the cell surface. In the Amoebidae the pseudopodia have hyaline tips, and there may be refringent crystals in the cytoplasm. One unnamed taxon has distinctive mitochondria with parallel spiral cristae. The Echinamoebae are small and flattened, with many fine, short, branching subpseudopodia extending from a hyaline anterior region. Under low-oxygen conditions they can convert to monopodial cylindrical forms. The echinopodia (spiny pseudopodia) include

central bundles of fibrillar material. The monophyly of the whole group (though not necessarily the traditional subgroups) is supported by actin and SSU rRNA phylogenies. Many currently under-characterised amoebae will probably fall into this group, for example *Hydramoeba*, parasitic on the cnidarian *Hydra*. (Anderson *et al.* 1997; Baumgatrner *et al.* 2003; Bolivar *et al.* 2001; Cavalier-Smith *et al.* 2004; Dyková *et al.* 2002; Fahrni *et al.* 2003; Kudryavtsev *et al.* 2005; Page 1967a, 1967b, 1986; Page and Robson 1983; Smirnov and Goodkov 1997; Smirnov *et al.* 2005b)

Flabellinida/ Discosea

A group of flattened amoebae that have cytoplasm with an anterior hyaline (glassy) zone and polyaxial cytoplasmic flow; including vannellids and dactylopodids; identified from SSU rRNA phylogenies. The group has been called the Discosea, defined on molecular grounds and the presence of flattened amoebae, though it should be noted that there is not evidence that *Multicilia* falls into the Discosea as has been suggested. (Cavalier-Smith 2004; Dyková *et al.* 2005b; Fahrni *et al.* 2003; Kudryavtsev *et al.* 2005; Peglar *et al.* 2003; Smirnov *et al.* 2005b)

Dactylopodida

Flattened amoebae with an anterior hyaline zone on which unbranching dactylopodia (finger-shaped pseudopodia) form, giving a spiny appearance to the cell; with polyaxial or non-axial cytoplasmic flow. Pseudopodia have an axial microfilamentous central region. The group includes members of the traditional families Paramoebidae, Vexilliferidae, and Mayorellidae. SSU rRNA phylogenies strongly support monophyly of the group.

The Paramoebidae includes *Neoparamoeba* species, the hosts of the “parasome” (eukaryotic euglenozoan parasites related to *Perkinsiella amoebae*). These include agents of amoebic gill disease, important in farmed salmon; though not all strains of all three *Neoparamoeba* spp have been demonstrated to be agents of AGD. Vexilliferids *Korotnevella* and *Vexillifera* have distinctive surface scales or glycostyles, and dactylopodid pseudopodia. Species are distinguished on the basis of scale morphology. Mayorellids are amoebae with short digitiform (mamilliform) subpseudopodia extending from the anterior hyaline margin during locomotion; *Mayorella* has a cuticle whereas *Dactylamoeba* has complex microscales on the cell surface. (Anderson 1977; Dyková *et al.* 2003; Dyková *et al.* 2000; Dyková *et al.* 2005b; Fiala and Dyková 2003; Goodkov 1988; Grell and Benwitz 1970; Page 1973, 1987, 1988, 1991; Peglar *et al.* 2003; Smirnov 1997, 1999a, 1999b; Smirnov *et al.* 2005b; Young *et al.* 2007)

Vannellids

Flattened, fan-shaped or linguiform amoebae with a hyaline anterior zone without subpseudopodia, polyaxial cytoplasmic flow and wheel-like rotation of the cell membrane. Where studied (in *Clydonella*, *Lingulamoeba*, *Vannella* and *Platyamoeba*), the cell surface is highly differentiated into pentagonal glycostyles, some with hair-like filaments, or hexagonal prisms, or short prismatic structures. The floating forms of these amoebae are round with radiating pseudopodia - similar to Dactylopodida. (Dyková *et al.* 2005a; Hülsmann and Haberey 1973; Kohsler *et al.* 2006; Page 1987; Page and Blakey 1979; Page and N.B.S. 1980; Peglar *et al.* 2003; Sims *et al.* 1999; Smirnov *et al.* 2005a; Smirnov 2001; Smirnov *et al.* 2007)

Acanthamoebae

The human parasite *Acanthamoeba castellanii* can cause amoebic keratitis, uveitis and encephalitis. Amoebae with clear, eruptive pseudopodia at front end of cell, and numerous, slender, tapering subpseudopodia (acanthopodia) giving the cell a spiny appearance. The glycocalyx is extremely thin. There is a centrosome (a striated fibrillar "root" that acts as a microtubule organising centre) in trophic amoebae. Cysts often have two layers: a thick, wrinkled, outer ectocyst and an inner polygonal endocyst, and a wall pore with an operculum. The cyst wall contains cellulose. Cyst morphology has traditionally been used to distinguish species but this is not congruent with molecular analyses using SSU rRNA or ITS. Molecular analyses indicate *Acanthamoeba* and *Balamuthia* form a clade, but *Comandonia* is not part of the group. Recent genomic analyses suggest extensive biosynthetic capacities might account for the diversity of habitats in which Acanthamoebae are found; *Acanthamoeba* is possibly the most commonly isolated genus of all naked amoebae from freshwater and soil habitats. (Amaral-Zettler 2001; Anderson *et al.* 2005; Bolivar *et al.* 2001; Carosi *et al.* 1977; Daggett *et al.* 1985; Fahrni *et al.* 2003; Kudryavtsev *et al.* 2009; Page 1967c, 1981; Stothard *et al.* 1998)

Cochliopodiidae

Amoebae with a flexible dorsal layer of trumpet-shaped carbohydrate scales. Moving amoebae are lens-shaped with a hyaline periphery (like the pseudopodia of Vannelliidae) and a granular central area. There is a distinctive electron-dense body near the Golgi apparatus. Molecular data suggests a placement for *Cochliopodium* inside the Amoebozoa but provides no specific support for relationships within the Amoebozoa. *Gocevia* and *Paragocevia* have been placed in the group in the grounds of cell shape and a fine filamentous dorsal tectum, but they lack the scales characteristic of *Cochliopodium* species. (Bark 1973; Dyková *et al.* 1998; Kudryavtsev 2004, 2005; Kudryavtsev *et al.* 2005; Kudryavtsev *et al.* 2004; Nagatani *et al.* 1981; Page 1987; Page and Willumsen 1980; Sadakane *et al.* 1996; Yamaoka *et al.* 1984)

Filamoeba* and *Flamella

Flattened, fan-shaped or spatulate amoebae; with a wider, hyaline anterior edge, from which finger-shaped pseudopodia (*Flamella*) or long thin branching filopodia (*Filamoeba*) extend. The cytoplasm contains many contractile vacuoles. Mitochondria in *Filamoeba sinensis* have tubular cristae that seem not to branch. SSU rRNA phylogenies suggest that *Flamella*, *Filamoeba*, *Comandonia* and *Arachnula* may form a clade. (Amaral-Zettler and Caron 2000; Dyková *et al.* 2005c; Kudryavtsev *et al.* 2009; Page 1967a; Peglar *et al.* 2003)

Gephyramoeba

Flattened amoebae, fan-shaped and often highly branched and irregular in outline, but not reticulate. New pseudopodia may be eruptive. There is often a long "tail", but no mass of trailing filaments as found in the Leptomyxids. (Amaral-Zettler and Caron 2000; Bolivar *et al.* 2001; Dyková *et al.* 2005c; Nikolaev *et al.* 2005; Pussard and Pons 1976c)

Grellamoeba

Large, flattened, irregularly branched amoeba, with a broad fan-shaped part extending into a long robust pseudopodium; pointed non-anastomosing subpseudopodia; floating forms with thick radiating pseudopodia; cysts spherical, ovoid or bean-shaped. Isolated from pikeperch kidney tissue. (Dyková *et al.* 2010)

Thecamoebidae

Amoebae with a thin pellicle that is often wrinkled or ridged; moving forms are oblong with a rounded anterior end. There is a thick cell coat which can be amorphous, filamentous or cuticular. Many forms are predators of other amoebae. The group as formulated by Schaffer 1926 (*Thecamoeba*, *Dermamoeba*, *Paradermoeba*, *Parvamoeba*, *Pseudothecamoebea*, *Sappinia*, *Thecochaos*) is not currently resolved by molecular data, but this is inconclusive as the placements of *Dermamoeba* and *Thecamoeba* are not robustly resolved in molecular phylogenies. *Sappinia* has been implicated in a case of encephalitis. (Dyková *et al.* 2008; Kudryavtsev *et al.* 2005; Page 1975, 1977, 1978; Schaeffer 1926; Smirnov 1999c; Walochnik *et al.* 2010)

Trichosphaerium

Multinucleate marine testae lobose amoebae, with alternation of generations. In the diploid phase there is a test (shell) with three- or four-sided pyramidal calcium carbonate spines embedded in a mucin sheath overlying a fibrillar layer; the haploid phase has a smooth test. Analyses of SSU rRNA, actin, and tubulins place this taxon within Amoebozoa, but not in a stable position. (Angell 1975; Angell 1976; Schuster 1976; Sheehan and Banner 1973; Tekle *et al.* 2008)

“SLIME MOULDS”

Dictyostelids

A clade well-supported by molecular analyses, including the model organism *Dictyostelium discoideum*: “cellular” slime moulds with stalked sorocarps, which develop from aggregated amoebae. The trophic stage is uninucleate, haploid aflagellated, filopodial amoebae, with a distinctive “centrosome” microtubule organising centre. When starved, these amoebae can aggregate in response to cAMP or other molecular (acrasin) signals generated by other individuals; they form a ‘slug’ with differentiated cells which subsequently become sori, stalk cells or stalk base cells. The stalk may be cellular, acellular (formed of cell walls of dead cells), and/or branched; it bears terminal sori of haploid spores. Haploid amoebae can fuse to form a zygote, which then ingests aggregating haploid amoebae and forms a dormant macrocyst; meiosis occurs to release haploid amoebae. The genome of *Dictyostelium discoideum* has been published. There are four clades in the dictyostelids that are not differentiable on the basis of morphology. (Alvarez-Curto *et al.* 2005; Baldauf and Doolittle 1997; Baptiste and Philippe 2002; Eichinger and Noegel 2005; Eichinger *et al.* 2005; Fiore-Donno *et al.* 2010; Guhl and Roos 1994; Romeralo *et al.* 2007; Romeralo *et al.* 2010; Roos 1975; Schaap 2007; Schaap *et al.* 1986; Schaap *et al.* 2006; Shadwick *et al.* 2009; Spiegel *et al.* 1995; Swanson *et al.* 2002; Ueda *et al.* 1997)

Myxogastrids

A well-supported clade of “acellular” slime moulds with alternation of generations and a filamentous nucleoid in the mitochondrion, including model organism *Physarum polycephalum*. The trophic stages are haploid flagellates and filose amoebae, which fuse to form a zygote, which divides to form a multinucleate diploid plasmodium composed of veins (rather than the reticulate amoeba of protostelids); cytokinesis and meiosis result in stalked or unstalked fruiting bodies containing haploid spores. The group also includes species that form only flagellates, amoebae and cysts - belonging to several subgroups of the myxogastrids which have hitherto been separated on spore characters. The mitochondria contain branching tubular cristae, and an electron-dense filamentous nucleoid (probably DNA, ultrastructurally and biochemically similar to a kinetoplast). The flagellar apparatus is within the variation described for protostelids below. A molecular study of EF1-alpha and SSU rRNA supported some groups within the myxogastrids distinguished on the basis of morphology and life cycle. Analyses using SSU rRNA with very dense taxon sampling show that the myxogastrids form a clade, but their placement in the Amoebozoa - and with respect to other "eumycetozoans" - is unstable. (Cavalier-Smith 2004; Fiore-Donno *et al.* 2005; Fiore-Donno *et al.* 2008; Fiore-Donno *et al.* 2010; Frederick 1990; Gely and Wright 1985; Guttes *et al.* 1966; Haskins and McGuinness 1988; Ishigami 1977; Karpov and Mylnikov 1997; Schuster 1965; Shadwick *et al.* 2009; Spiegel 1981a; Walker *et al.* 2003; Walker *et al.* 2001; Walochnik *et al.* 2004; Wright *et al.* 1988; Wright *et al.* 1980a; Wright *et al.* 1979, 1980b)

"Protostelids"

A collection of groups that is not currently supported by taxon-rich analyses of SSU rRNA, however the groups are placed together here pending more gene-rich analyses; including Protosteliids *sensu stricto*, Soliformoviids, Protosporangiids, Cavosteliids, Ceratiomyxids, Endostelium and Schizoplasmodiids. There is some support for *Phalansterium* (discussed separately below) falling as the sister taxon to *Ceratiomyxella tahitiensis* in the Schizoplasmodiids.

The protostelid groups collectively include “acellular” slime moulds with a sporocarp (a fruiting body containing one to four spores, with a cellulose-containing stalk and a basal disc), and a plasmodial stage, and with mitochondria that lack a filamentous nucleoid. The life cycle may be simple and uninucleate, or involve multiple divisions and multinucleate stages. The trophic stage is a uninucleate flagellate or filopodial amoeba, which may fuse with other individuals to form a large, reticulate, multinucleate plasmodium, or merely develop into a single prespore cell; this (plasmodium or prespore cell) then forms a sporocarp; spores germinate to form either uninucleate trophic amoebae, or a multinucleate protoplast which can change directly into the multinucleate plasmodium, or divide to form trophic flagellates which convert to amoebae and then to the plasmodium. The mitochondria have branching tubular mitochondrial cristae, without the filamentous nucleoid seen in myxogastrids.

The flagellar apparatus is characteristic of both protostelids and myxogastrids, consisting of a flagellated anterior basal body with a thick cylindrical element in the transition zone (of most taxa); a fibrillar root surrounding three quarters of the basal body, which nucleates a curtain of microtubules that runs posteriorly into the

cell, and a lateral microtubular root running from the right-hand edge of the curtain; and a posterior MTOC (the centrosome) which gives rise to diffusely arranged microtubules, and is connected to the proximal end of the basal body by striated fibres. Where present, the posterior basal body is perpendicular to the anterior one, and usually bears a layered “posterior parakinetosomal structure” on its anterior edge, which nucleates a lateral microtubular root. A fifth microtubular root arises from the posterior side of the posterior basal body. (Baldauf and Doolittle 1997; Fiore-Donno *et al.* 2008; Fiore-Donno *et al.* 2010; Furtado and Olive 1971; Hellsten and Roos 1998; Olive 1967, 1975; Shadwick *et al.* 2009; Spiegel 1981c, 1981a, 1981b, 1982, 1990; Spiegel 1991; Spiegel and Feldman 1985, 1988; Spiegel *et al.* 1986; Spiegel and J. 1988; Walker *et al.* 2003; Walker *et al.* 2001; Walochnik *et al.* 2004)

Phalansterium

Flagellates forming colonies of separate individuals, with cells producing and embedded in a matrix of mucilage granules. Each cell has a single apical flagellum surrounded by a continuous cytoplasmic collar. The single basal body is anchored by a concentric series of fibrillar collars, giving rise to a radially symmetrical cone of about 60 microtubules. The mitochondrial cristae are tubular. SSU rRNA phylogenies consistently place *Phalansterium* with *Ceratiomyxella tahitiensis*, an organism traditionally thought to be a “protostelid”: if this relationship is supported by further taxon-rich and gene-rich analyses, *Phalansterium* may have a more complex life cycle, and *Ceratiomyxella* may have a more complex flagellar apparatus than previously described. This taxon is superficially similar to *Spongomonas* and *Rhipidodendron* (Rhizaria). (Cavalier-Smith *et al.* 2004; Ekelund 2002; Hibberd 1983; Shadwick *et al.* 2009)

“FLAGELLATED AMOEBAE”

Archamoebae

Amoebae or amoeboid flagellates with unusually clear cytoplasm and chromatoid bodies (helical arrays of ribosomes, visible by both light- and electron-microscopy); they are microaerophilic or anaerobic, being secondarily amitochondriate with small 500 nm long mitochondrial-type organelles (mitosomes or hydrogenosomes) to which *cpn60* localises. Iron sulfur cluster assembly genes are laterally transferred from epsilon-proteobacteria. Molecular phylogenies of SSU rRNA and multiple genes place these taxa together. Archamoebae is used here *sensu* Cavalier-Smith 1983, 1997, Cavalier-Smith *et al.* 2004. (Aguilera *et al.* 2008; Arisue *et al.* 2002; Baptiste *et al.* 2002; Cavalier-Smith *et al.* 2004; Edgcomb *et al.* 2002; Fahrni *et al.* 2003; Gill *et al.* 2007; Silberman *et al.* 1999)

Entamoebae

Parasitic amoebae, including the agent of amoebic dysentery, *Entamoeba histolytica*; with clear eruptive anterior pseudopodia and frequent chromatoid bodies; mitosis is with an entirely intranuclear spindle. The number of nuclei in cysts is used as a taxonomic character. There are no flagellated stages. Mitosome-like organelles (degenerate mitochondria) are present. Most are intestinal parasites of vertebrates; one is a gingival parasite. The genome of

Entamoeba histolytica has been published: it is unusually AT-rich with many tRNAs. (Aguilera *et al.* 2008; Clark 1995; Espinosa-Canellano *et al.* 1998; Fahrni *et al.* 2003; Mai *et al.* 1999; Proctor and Gregory 1972; Siddiqui and Rudzinska 1965; Silberman *et al.* 1999; Song *et al.* 2005; Tovar *et al.* 1999)

Pelobionts

Free-living or endosymbiotic organisms forming amoeboid flagellates, amoebae and cysts; defined by the presence of a single basal body giving rise to a cone and ribbon of microtubules. The cone of microtubules may or may not connect to the nucleus. With hyaline cytoplasm which may form lobose or finger-shaped pseudopodia; the cell body is “clear” and pseudopodia form in an eruptive manner, in a way that differentiates pelobionts from the otherwise similar amoeboid-flagellates in the “Eumycetozoa” (“Slime moulds”) and Cercozoa. The flagellar beat is distinctively “languid” or slow - possibly due to the absence of the outer dynein arm from the flagellar axoneme. Amoebae may be small and with one or few nuclei; or large (150 µm long) with hundreds of nuclei. There are double membrane-bound organelles which are probably hydrogenosomes, which in some species of *Pelomyxa* and *Mastigella* are associated with endosymbiotic methanogenic archaea. Chromatoid bodies are rarely observed. One species is an endosymbiont in amphibians. *Pelomyxa palustris*, a large amoeba with multiple flagella, can form cells up to 500 µm long. *Rhizomastix* may also be a member of this group. (Arisue *et al.* 2002; Brugerolle 1991b, 1991a; Edgcomb *et al.* 2002; Fahrni *et al.* 2003; Gill *et al.* 2007; Griffin 1988; Milyutina *et al.* 2001; Silberman *et al.* 1999; Simpson *et al.* 1997a; Walker *et al.* 2001; Whatley and Chapman-Andresen 1990)

Multicilia

Carnivorous multflagellated protists, with multiple flagella arising randomly over the cell surface. There are short lobopodia on the cell surface. The cells appear to have no polarity and roll over the substratum on the flagella, which beat irregularly and without coordination; there are usually 20-30 flagella though small organisms have 2-4 and some giant organisms have up to 200. The anchorage for each separate flagellum consists of a single basal body surrounded by 4 perpendicular radiating microfibrillar discs, each giving rise to an incomplete multi-layered cone of very short microtubules, giving a staggered cone of microtubules which runs ‘upwards’ to the cell surface; there is also a microtubular ribbon that connects each flagellar apparatus to one of its neighbours. Mitochondrial cristae are flattened. There are multiple Golgi dictyosomes. The flagellar apparatus shows some superficial similarities to that of the euglenozoan *Stephanopogon*, but also to those of myxogastrids and protostelids - it requires further investigation. Analyses of SSU rRNA place *Multicilia* in the Amoebozoa but its location within the group is unstable. (Mikrjukov and Mylnikov 1998b; Nikolaev *et al.* 2006)

Other amoeboid taxa that seem likely to fall into the Amoebozoa; with light-microscopical identities, but not ultrastructural or molecular identities; include *Echinopyxis*, *Gibbodiscus*, *Janickia*, *Leptocystis*, *Malamoeba*, *Malpighamoeba*, *Ouramoeba*, *Ovalopodium*, *Pamphagus*, *Parvamoeba*, and *Playfairiana*.

EXCAVATES

An assemblage of predominantly heterotrophic flagellates, many of which live in oxygen-poor environments, and lack mitochondria but have organelles which may be homologous to mitochondria. Excavates typically contain a distinct type of longitudinal feeding groove, supported by the cytoskeleton, where suspended food particles are collected from a current generated by the beating of one or more posteriorly directed flagella, although some specific lineages lack this feature. Excavates contain a number of parasitic lineages, including several major human pathogens (e.g. *Trypanosoma brucei*, the causative agent of African Sleeping Sickness). Until recently, the evolutionary history of these taxa has been uncertain; however, recent, taxonomically broad multigene studies have robustly supported monophyly. Two major lineages are currently recognised- Metamonads and Discoba; one single genus, *Malawimonas*, is of unresolved position between these clades. The phylogenetic position of the excavates is subject to substantial debate: unrooted phylogenies typically place them as distinct from both unikonts and the grouping of the archaeplastids, SAR and CCTH clades; typically, this has been interpreted as excavates being an early-branching bikont clade, but recent reappraisals of the root of the eukaryotes have led to suggestions that they may be basal to the unikonts, or even a distinct offshoot from all other eukaryotic taxa. (Bodyl *et al.* 2010; Cavalier-Smith 2010; Hampl *et al.* 2009; Parfrey *et al.* 2010; Patterson 1990, 1999; Simpson and Roger 2002; Simpson 2003; Simpson *et al.* 2005; Simpson *et al.* 2002a; Simpson and Patterson 1999; Simpson *et al.* 2002d)

METAMONADS

A clade unifying Fornicates, Parabasalids, and Preaxostyla, all principally “amitochondriate” excavate lineages. Although the phylogenetic validity of this clade has historically been uncertain, it has been resolved with robust support by recent multigene analyses. (Brugerolle 1977; Hampl *et al.* 2009; Parfrey *et al.* 2010)

Fornicates

A clade with a cytoskeletal apomorphy: the ribbon-like bilaminar 30nm-striated “B fibre” originates on the second microtubular root and arches across the ventral face of the flagellar apparatus. The organisms with this feature include *Carpediemonas* and retortamonads; the monophyletic group also includes diplomonads, which lack a B fibre. This clade is also supported by multiple molecular analyses. (Bernard *et al.* 1997; Kolisko *et al.* 2005; Kolisko *et al.* 2010; Simpson and Patterson 2001; Simpson 2003; Simpson *et al.* 2005; Simpson *et al.* 2002b; Simpson *et al.* 2002d)

Carpediemonads

An array of four described fornicate genera- *Carpediemonas* (semicircular flagellates with three basal bodies and paraxial vanes on the posterior flagellum), *Kipferlia* (semicircular flagellates with a broad ventral vane on the posterior flagellum, and a feeding groove that extends at the right margin into a thin membrane), *Dysnectes* (semicircular or elongate flagellates with an active anterior flagellum and ventral and dorsal vanes on the posterior flagellum) and *Hicanonectes* (ovoid flagellates containing a longitudinal feeding groove with a sharply defined right wall, which forms a curved cytopharynx at the posterior

end)- identified from low-oxygen marine sediments. *Carpediemonas*, *Dysnectes* and *Hicanonectes* all contain conspicuous, acristate mitochondrion-like organelles, that superficially resemble the hydrogenosomes of parabasalids. Molecular data suggests that these genera are paraphyletic and diverge basally from other fornicates. (Kolisko *et al.* 2005; Kolisko *et al.* 2010; Simpson 2003; Simpson *et al.* 2005; Simpson and Patterson 1999; Simpson *et al.* 2002d; Yubuki *et al.* 2007)

Eopharyngia

A group uniting diplomonads and retortamonads, currently recognised by molecular phylogenies and by broad similarity of cytoskeletal organisation. A potential synapomorphy, pending further investigations, is the hooked appearance of microtubular root R1 at its origin. (Brugerolle 1991b, 1991a; Cavalier-Smith 1993; Kolisko *et al.* 2005; Simpson 2003; Simpson *et al.* 2005)

“Diplomonads + Enteromonads”

Small amitochondriate excavate flagellates, many of which have a “doubled” cell structure: each cell contains two nuclei, each attached to a flagellar apparatus (karyomastigont) supporting a feeding groove. Some species (enteromonads) have only one karyomastigont. Each karyomastigont is formed of four flagella arising from four basal bodies, three microtubular roots which support the feeding groove, and one striated rootlet; microtubular roots closely associated with the nucleus. Genetic information may be exchanged between sister nuclei of encysted cells. There is a “mitosome” organelle homologous to mitochondria and parabasalid hydrogenosomes.

Some species are free-living in low-oxygen environments, whereas others are parasitic in vertebrates, including the human gut parasite *Giardia lamblia* (a causative agent of waterborne enteric disease), and the fish parasite *Spironucleus salmonicidus*. Giardiins, a family of annexin-like proteins predominantly present on the plasma membrane and flagella, are essential for the viability of *G. lamblia* trophozoites, although their precise function in pathogenesis remains unknown. A draft genome sequence has been completed for *G. lamblia*, and reveals substantial reduction and compaction of content, including the complete absence of genes encoding structural regulatory factors in DNA replication. Early transcriptomic analyses of *G. lamblia* and *S. salmonicidus* have additionally revealed extreme divergence in gene expression between different species, and between different phases of infective life cycles, and several instances of presumed lateral gene acquisitions from bacterial donors. Molecular phylogenies have challenged the traditional taxonomy of this clade: diplomonads *sensu stricto* are believed to be paraphyletic and enteromonads polyphyletic, with giardiids basally divergent from enteromonads and other diplomonads; furthermore, one SSU study has suggested that giardiids may in fact be the direct sister-taxon to some retortamonads; under all circumstances, either multiple independent origins (in diplomonads) or secondary losses (in enteromonads) of the doubled karyomastigont are envisioned. (Andersson *et al.* 2007; Birkeland *et al.* 2010; Brugerolle 1975c, 1975b, 1975a, 1991b, 1991a; Brugerolle *et al.* 1974a; Brugerolle *et al.* 1973b, 1973a, 1974b; Dolezal *et al.* 2005; Eyden and Vickerman 1975; Kolisko *et al.* 2005; Kolisko *et al.* 2008;

Kolisko *et al.* 2010; Morrison *et al.* 2007; Poxleitner *et al.* 2008; Roxstrom-Lindquist *et al.* 2010; Simpson 2003; Simpson *et al.* 2002b; Tovar *et al.* 2003; Vickerman 1990; Wei *et al.* 2010)

Retortamonads

Amitochondriate excavate flagellates with four flagella arising at the anterior end of the feeding groove, from four basal bodies arranged either in pairs or in a cruciate pattern; there are two large microtubular roots that support the sides of the feeding groove and a discrete cytostome at the base of the groove, a dorsal fan of microtubules arising from fibrillar material, and two minor microtubular roots, as well as striated rootlets. Although one free-living species is known, the overwhelming majority of studied taxa are parasitic: *Chilomastix* is a gut commensal of humans. Recent SSU phylogenies have suggested that retortamonads may be paraphyletic, with *Chilomastix* basal to a clade of diplomonads, enteromonads and *Retortamonas*, and- in one study- a direct sister-taxon relationship between giardiids and *Retortamonas*. (Brugerolle 1973, 1977, 1991b, 1991a; Brugerolle and Metenier 1973; Cepicka *et al.* 2008; Kolisko *et al.* 2005; Kolisko *et al.* 2010; O'Kelly *et al.* 1999; Silberman *et al.* 2002; Simpson *et al.* 2005)

Parabasalia

A clade of amitochondriate flagellates with the synapomorphy of a parabasal apparatus: a striated root extending posteriorly from the flagellar apparatus, with attached Golgi dictyosomes. The feeding groove is secondarily absent. Some lineages are secondarily aflagellate or (in hypermastigids) multiflagellate; however, the basic flagellar apparatus consists of four flagella arising anteriorly, from three anteriorly-directed and one posteriorly-directed basal body, of which the posterior-directed flagellum may be attached to the cell by an undulating membrane (in trichomonads). The basal bodies are associated with a fan of microtubules attached to a striated fibre (the pelta-axostyle complex, which supports the cell membrane); there are no other microtubular flagellar roots, whose anchoring function may instead be fulfilled by the striated costa and parabasal striated root with its anchoring Golgi dictyosomes. Parabasalids contain hydrogenosomes, which are believed to be degenerate mitochondria lacking a genome; hydrogenosomes operate in respiration and may additionally retain functions in metalloprotein biosynthesis.

There are some free-living taxa but many are gut commensals of insects (hypermastigids, *e.g.* the termite gut endobiont *Mixotricha paradoxa*) or parasites of vertebrates (trichomonads, *e.g.* the human and bovine genito-urinary parasites *Trichomonas vaginalis* and *Tritrichomonas foetus*). Many endobiotic parabasalids harbour bacterial endosymbionts or ectosymbionts, which may be highly lineage-specific, and are highly sensitive to changes in host physiology. A draft genome sequence has been assembled for *T. vaginalis*; preliminary analyses indicate the presence of an almost complete array of meiotic genes, an RNAi interference pathway, and large numbers of introns and transposable elements, of which some appear to be transcriptionally and potentially transpositionally active. Molecular phylogenies robustly support a position in the fornicates, as a sister-group to all other identified taxa. Taxonomy of the group has recently been updated. (Brugerolle 1991a, 2004; Brugerolle and Joyon 1973; Brugerolle and Lee 2002;

Brugerolle and Metenier 1973; Brugerolle and Mignot 2003; Carlton *et al.* 2007; Carpenter *et al.* 2009; Carpenter *et al.* 2010; Cepicka *et al.* 2010; Cleveland and Grimstone 1964; Dolezal *et al.* 2005; Hampl *et al.* 2005; Honigberg 1963; Ikeda-Ohtsubo and Brune 2009; Lindmark 1973; Long *et al.* 2008; Lopes *et al.* 2009; Malik *et al.* 2008; Radek and Nitsch 2007; Simpson 2003; Simpson *et al.* 2005; Simpson *et al.* 2002d)

Preaxostyla

A clade with the cytoskeletal apomorphy: the “I fibre” has preaxostylar substructure (a double-cross matrix with a single fine outer sheet), homologous to the organisation in *Pyrsonympha vertens*. (Brugerolle 1970; Simpson 2003; Simpson *et al.* 2005)

Oxymonads

Amitochondriate flagellates that lack identifiable Golgi bodies, peroxisomes, hydrogenosomes or mitosomes. Oxymonads do not have a feeding groove but contain a flagellar apparatus characteristic of excavates, including a distinctive axostyle made of multiple parallel sheets of microtubules. There are two separated pairs of basal bodies; the anterior-most pair is associated with a pelta of microtubules which supports the cell membrane; the posterior-most pair is associated with striated (“B”, “C” and “I”) fibres, and microtubular roots characteristic of other excavates, and the axostyle. The I fibre has a preaxostylar substructure. The cell surface is covered by a glycocalyx, and- typically- bacterial ectosymbionts; some taxa may additionally have mushroom-shaped extracellular surface structures and a holdfast or rostellum for attachment to symbionts and to the host substratum.

Found exclusively as gut endosymbionts of termites, oxymonads vary greatly in size and habit from gut-wall attaching commensals hundreds of microns long (*Pyrsonympha*) to small flagellates (*Monocercomonoides*). Some oxymonads utilise an unusual genetic code, where canonical “amber” and “ochre” stop codons instead encode glutamine; the glycolytic pathways of *Monocercomonoides* and *Streblomastix* are believed to contain a number of non-canonical components, including a pyrophosphate-dependent phosphofructokinases and pyruvate kinases. The conserved presence of a preaxostyle and molecular data suggest a sister-taxon relationship to *Trimastix*; multigene phylogenies predominantly suggest a position basal to fornicates and parabasalids, although one recent study recovers a close relationship with the parabasalids. (Brugerolle and König 1997; Brugerolle and Müller 2000; Dacks *et al.* 2001; de Koning *et al.* 2008; Hampl *et al.* 2005; Hampl *et al.* 2009; Hongoh *et al.* 2007; Keeling 2001a; Keeling and Leander 2003; Liapounova *et al.* 2006; Moriya *et al.* 2003; Parfrey *et al.* 2010; Simpson *et al.* 2005; Simpson *et al.* 2002c; Slamovits and Keeling 2006)

Trimastix

Free-living excavate flagellates with four flagella inserting orthogonally at the anterior end of the feeding groove, with the posterior flagellum lying in the groove and with lateral vanes supported by microfibril-like material. The basal bodies are cruciate and give rise to three microtubular roots: a dorsal fan, and two roots which are attached to “C” and “I” striated fibres and which support

the ventral groove and a discrete cytostome at the base of the groove. The I fibre has a preaxostylar substructure. Mitochondria are absent, but *Trimastix* retains a number of clearly mitochondrial-derived genes; it is unknown whether these are functional. A largely canonical glycolytic pathway is employed, although there is evidence for the lateral acquisition of several genes (e.g. phosphoglycerate kinase) from bacterial donors. *Trimastix* lacks extracellular symbionts, a glycocalyx, surface structures and a holdfast. Molecular analyses predominantly support a sister-taxon relationship to the oxymonads, although one recent analysis suggests a position at the base of the metamonads. (Brugerolle and Patterson 1997; Dacks *et al.* 2001; Hampl *et al.* 2009; Hampl *et al.* 2008; Keeling and Leander 2003; Moriya *et al.* 2003; O'Kelly *et al.* 1999; Parfrey *et al.* 2010; Simpson 2003; Simpson *et al.* 2000; Simpson *et al.* 2005; Stechmann *et al.* 2006)

DISCOBA

A clade, well supported by molecular phylogenies, of the predominantly mitochondriate Heterolobosea, Euglenozoa and jakobids; a number of smaller lineages have been unified on the grounds of ultrastructure without molecular confirmation. There is no synapomorphy, although there are similarities of the flagellar apparatus. (Hampl *et al.* 2009; Parfrey *et al.* 2010; Simpson *et al.* 2005)

Heterolobosea

Excavate amoeboflagellates, flagellates, amoebae or slime moulds, with eruptive pseudopodia and an unusually fast amoeboid locomotion; the group has also been named Percolozoa. Species may lack flagella at all life stages (acrasid “slime moulds”), contain two or four flagella that insert at the anterior end of the feeding groove (e.g. *Percolomonas*), or contain multiple rows of flagella immediately below the dorsal lip (*Stephanopogon*); flagella typically arise from four basal bodies arranged either as a parallel tetrad, or as a mirror-image “L”, which give rise to three microtubular roots and a striated “I fibre”. Flagellar replication is unusual because it occurs in pairs of basal bodies rather than sequentially as in other taxa. Golgi stacks are absent. Ribosomal DNAs may be arranged on up to 5000 extrachromosomal plasmids, which are tightly aggregated within the nucleolus. Heteroloboseans are predominantly mitochondriate, containing discoid cristae; some genera (e.g. *Psalteriomonas*) contain hydrogenosomes, and a mitochondrial-targeted Fe hydrogenase is present in the mitochondriate soil amoeboflagellate *Naegleria gruberi*, implying that heteroloboseans may be facultatively anaerobic.

Species are free-living, heterotrophic, and have a cosmopolitan distribution: terrestrial, halophilic, psychrophilic and thermophilic taxa are known, and *N. gruberi* can facultatively parasitise the human central nervous system. A complete genome is available for *N. gruberi*: preliminary analyses reveal the absence (interpreted as secondary loss) of genes associated with a number of otherwise broadly conserved biosynthetic pathways such as gluconeogenesis, and purine and heme biosynthesis: supporting the widespread auxotrophy observed in these species. Multigene analyses recover either a sister-group relationship to the excavates or the jakobids. (Abad *et al.* 2008; Archibald *et al.* 2002; Broers *et al.* 1990; Brugerolle and Simpson 2004; Burki *et al.* 2008; de Graaf *et al.* 2009; De Jonckheere *et al.* 2009; Edgcomb *et al.* 2001; Fenchel and Patterson 1986; Fritz-

Laylin *et al.* 2010; Maruyama and Nozaki 2007; Page and Blanton 1985; Reeb *et al.* 2009; Robinson *et al.* 2007; Rodriguez-Ezpeleta *et al.* 2007a; Simpson *et al.* 2006a; Simpson 2003; Simpson *et al.* 2005; Simpson *et al.* 2002c; Yubuki and Leander 2008)

Jakobids

Mitochondriate, heterotrophic excavate flagellates with the synapomorphy of a sole flagellar vane with a diffuse origin on dorsal surface of the posterior flagellum. The two flagella insert at the anterior end of the feeding groove; they arise from two basal bodies, which give rise to a dorsal fan of microtubules originating directly against the anterior basal body, two main microtubular roots which support the edges of the feeding groove- the left root supporting the floor of the groove-, a singlet microtubular root, and non-microtubular striated “A” “B”, “I” and “C” fibres. Structured extrusomes (discobolocysts) are present. The mitochondria are irregularly flattened (*Jakoba*) or tubulocristate (*Histiona*, *Reclinomonas*, *Andalucia*). There is evidence that jakobids locate prey bacteria via chemosensory pathways.

A mitochondrial genome has been sequenced for *R. americana*, and a complete genome and transcriptome are currently being assembled. The mitochondrial genome of *R. americana* is the largest known, and retains several putatively “primitive” features including a bacterial-like RNA polymerase, a 5S rDNA, and potentially highly reduced versions of bacterial editing tmRNAs. Historically believed to be basal to heteroloboseans and euglenozoa, some recent multigene phylogenies have recovered an alternate position as an immediate sister-group to the heterolobosea. (Archibald *et al.* 2002; Burki *et al.* 2008; Edgcomb *et al.* 2001; Hampl *et al.* 2009; Jacob *et al.* 2004; Lang *et al.* 1997; Lang *et al.* 1996; Lara *et al.* 2006; Mohapatra and Fukami 2007; O’Kelly 1997; O’Kelly 1993; O’Kelly and Nerad 1999; Parfrey *et al.* 2010; Patterson 1990; Rodriguez-Ezpeleta *et al.* 2007a; Simpson and Patterson 2001; Simpson *et al.* 2008; Simpson 2003; Simpson *et al.* 2005)

Euglenozoa

A large and diverse group of flagellates, containing flagellar paraxonemal rods that differ in structure according to the flagellum, with an anterior tubular rod and a posterior (ventral or recurrent flagellum) lattice. The heterodynamic flagella, which often have fine hairs along the outside, arise from two basal bodies lying parallel or acutely to each other. The anterior basal body is associated with a single microtubular root similar to the dorsal fan in other excavates, which gives rise to peripheral microtubules that support the cell surface; the posterior basal body gives rise to two microtubular roots, one of which supports the cytostome (feeding apparatus), which may be highly complex. Four lineages are currently recognised: euglenids, kinetoplastids, diplomonads and symbiontidids. Multigene analyses recover two alternate positions within the Discoba- as a sister-taxon to Heterolobosea, and as basal to Heterolobosea and Jakobids. (Archibald *et al.* 2002; Baldauf *et al.* 2000; Brugerolle 1985; Brugerolle *et al.* 1979; Burki *et al.* 2008; Dawson and Walne 1994; Edgcomb *et al.* 2001; Farmer and Triemer 1988; Hampl *et al.* 2009; Kivic and Walne 1984; Leedale 1974; Leedale 1978; Leedale *et al.* 1970; Mignot 1964; Moreira *et al.* 2004; Parfrey *et al.* 2010; Rodriguez-Ezpeleta *et al.* 2007a; Roy *et al.* 2007a; Roy *et al.* 2007b; Schuster *et al.* 1968; Simpson *et al.*

2004; Simpson 1997; Simpson *et al.* 2005; Simpson and Roger 2004a; Taylor 1976; Triemer and Farmer 1991; Vickerman 1976; Vickerman and Preston 1976)

Euglenids

Euglenozoa with a coat or “pellicle” of sub-membrane strips of protein, arranged in spirally overlapping stripes, which in many species can glide longitudinally relative to each other and produce the distinctive euglenoid “metaboly” or squirming movement. There are two or four heterodynamic flagella arising from an apical groove (one flagellum may be too short to be visible by light microscopy); the presence of paraxial rods or lattices makes the flagella extremely thick. Carbon is stored as paramylon. There is a complex feeding apparatus in many species; both heterotrophic and phototrophic forms exist: phototrophic forms have a basal swelling on one flagellum, the paraflagellar body (an eyespot). Chromosomes are condensed in interphase. Mitochondrial DNA is in small circular chromosomes. Some petalomonad euglenids may have diverged prior to the evolution of the pellicle, and may possess kinetoplasts (see below): this needs further investigation.

Euglenids are primarily heterotrophic, but one lineage, including the laboratory model alga *Euglena gracilis*, has acquired a chloroplast by secondary endosymbiosis of a green alga; phylogenetic analysis suggests that the donor lineage may be basally divergent from all extant chloroplastid taxa, and transcriptomic analyses suggest that endosymbiont-derived genes may account for over one-fifth of the genomes of photosynthetic euglenids. The chloroplast genome of the photosynthetic *E. gracilis*, and the secondarily nonphotosynthetic *E. longa* have additionally been sequenced. Recent SSU phylogenies have suggested that euglenids are paraphyletic, with the bacterivorous genera *Petalomonas* and *Notosolenus* resolving as basal to all other euglenozoa; multigene phylogenies incorporating a more limited array of euglenids supports a basal divergence from diplomonads and kinetoplastids. (Ahmadinejad *et al.* 2007; Breglia *et al.* 2010; Dawson and Walne 1994; Farmer and Triemer 1988; Geimer *et al.* 2009; Gibbs 1978; Gockel and Hachtel 2000; Kivic and Walne 1984; Leander *et al.* 2001; Marin *et al.* 2003; Roy *et al.* 2007b; Simpson *et al.* 2004; Simpson 1997; Simpson and Roger 2004b; Takahashi *et al.* 2007b; Triemer and Farmer 1991; Yubuki *et al.* 2009)

Kinetoplastids

Euglenozoa of ecological and medical importance, including *Trypanosoma brucei brucei* and *T.b. rhodesiense*; *T. cruzi*; *Leishmania mexicana*, respective agents of sleeping sickness, Chagas’ disease, and kala azar in humans, and *T. brucei brucei* which causes nagana (wasting disease) in cattle. There are two flagella inserting into an apical pocket which also is the sole location of endo- and exo-cytosis. The mitochondrion contains a kinetoplast (DNA organised as an aggregation of multiple small minicircles), which may be a large single aggregation associated with the flagellar bases, or several aggregations throughout the mitochondrion. Uniquely, the majority of glycolysis is performed in modified peroxisomes (“glycosomes”), with glycolytic preproteins bearing internal transit peptides. Nuclear gene expression pathways involve spliced leader transcripts. Mitochondrial transcripts are rendered translationally competent via the insertion or deletion of internal polyuridine tracts; editing is mediated by two interconverting complexes, which are targeted by a unique

family of guide RNAs (gRNAs) to candidate sites on pre-mRNAs, and are themselves expressed via a novel and poorly understood pathway.

Five lineages are currently recognised from molecular analyses: Prokinetoplastids (aflagellate or flagellate kinetoplastids with a single, giant mitochondrion, including *Ichthyobodo*, a fish parasite, and “*Perkinsiella amoebae*”, an endosymbiont of the parasitic amoebozoan *Neoparamoeba*); Neobodonids (free-living biflagellate heterotrophic kinetoplastids, with an apical cytostome, and a conspicuous preflagellar rostrum); Parabodonids (biflagellate heterotrophic or osmotrophic kinetoplastids, both flagella lacking hairs, with an anterolateral cytostome, and a kinetoplast that does not form a continuous network; includes the polyphyletic fish parasite and commensal genus *Cryptobia*); Eubodonids (free-living biflagellate kinetoplastids, with non-tubular hairs on the anterior flagellum, an anterolateral cytostome, a kinetoplast that does not form a contiguous network); and Trypanosomes (parasitic, with diverse eukaryotic hosts, complex multi-host life cycles, a single emergent flagellum which may be attached to the body by an undulating membrane, a simple cytostome, and a small kinetoplast). Complete genomes are available for the trypanosomes *T. brucei*, *T. cruzi*, *Leishmania major*, *L. infantum* and *L. braziliensis*, a transcriptome has been annotated for the avirulent *Trypanosoma rangeli*, and genome sequencing is underway for the eubodonid *Bodo saltans*. Comparative genomic analyses have revealed large numbers of species-specific genes in *T. brucei* and *T. cruzi*, particularly at nonsyntenic chromosomal regions, and the recent expansion of several families of protein kinases, but remarkable conservation of gene content between *Leishmania* subspecies. Genomic studies have additionally largely refuted the hypothesis that kinetoplastids may have historically contained a chloroplast. Protein phylogenies have suggested a clade containing diplomonids and kinetoplastids to the exclusion of euglenids. (Berriman *et al.* 2005; Blom *et al.* 1998; Brugerolle 1985; Brugerolle and Joyon 1979; Brugerolle *et al.* 1979; Callahan *et al.* 2002; Caraguel *et al.* 2007; Dolezel *et al.* 2000; Dyková *et al.* 2003; El-Sayed *et al.* 2005; Galland *et al.* 2010; Golas *et al.* 2009; Grisard *et al.* ; Hannaert *et al.* 2003; Hashimi *et al.* 2009; Ivens *et al.* 2005; Jackson *et al.* 2008; Moreira *et al.* 2004; Parsons *et al.* 2005; Peacock *et al.* 2007; Simpson *et al.* 2004; Simpson *et al.* 2006b; Simpson *et al.* 2005; Simpson *et al.* 2002a; Simpson *et al.* 2002c; Vickerman 1976; von der Heyden *et al.* 2004; Waller *et al.* 2004; Weatherly *et al.* 2009)

Diplomonids

Euglenozoa with a complex apical ingestion apparatus, two flagella (without paraxial rods) inserting into a subapical pocket, and squirming motion. They lack the pellicle and kinetoplast characteristic of euglenids and kinetoplastids. Mitochondrial DNA is in small circular chromosomes. Two genera have been described- *Diplonema* and *Rhynchopus*- although many more lineages are known from environmental samples. Principally free-living heterotrophs from deep marine waters, some strains of *Rhynchopus* may be facultative parasites of crustaceans. Diplomonids contain an unusual, bacterial-derived isoform of GAPDH, which is also present in diatoms and haptophytes, suggesting multiple prokaryote-to-eukaryote and eukaryote-to-eukaryote gene transfer events. Similarly to kinetoplastids, diplomonids utilise spliced leader transcripts in nuclear gene expression; the ultrastructure of the feeding and flagellar apparatus

and protein phylogenies likewise suggest a close relationship to the kinetoplastids to the exclusion of euglenids. (Elbrächter *et al.* 1996; Kent *et al.* 1987; Lara *et al.* 2009; Marande *et al.* 2005; Montegut-Felkner and Triemer 1994; Qian and Keeling 2001; Rogers *et al.* 2007b; Roy *et al.* 2007a; Roy *et al.* 2007b; Simpson *et al.* 2004; Simpson *et al.* 2005; Simpson *et al.* 2002a; Simpson and Roger 2004b; Sturm *et al.* 2001; Triemer and Ott 1990)

Anehmia exotica

Aflagellated euglenozoan with an anterior cytostome with a rostrum on its anterior edge, and with a plastic body similar in appearance to diplomonads. There is no molecular information on this species. (Ekebom *et al.* 1996; Simpson *et al.* 1997a)

Bordnamonas tropicana

Euglenozoan with two thick flagella inserting subapically, and an apical ingestion apparatus. The anterior flagellum is held in an arc in front of the cell in a manner reminiscent of stramenopiles. There is no molecular information on this species. (Larsen and Patterson 1990; Simpson 1997)

Postgaardi mariagerensis

Euglenozoan with the cell surface supported by microtubules subtending an electron-dense layer, and a body covered with rod-shaped bacteria. There are two equal, thick flagella with paraxial rods, emerging from a deep anterior flagellar pocket; and a complex microtubular ingestion apparatus. With cruciform tubular extrusomes similar to those of euglenids. Cells contain a superficial layer of mitochondria-like organelles. This species has been grouped with the symbiontidid *Calkinsia* due to the shared presence of ectosymbionts, sublamellar mitochondria, and the lack of a kinetoplast; no molecular information is available. (Breglia *et al.* 2010; Cavalier-Smith 2004; Fenchel and Finlay 1995; Simpson 1997; Simpson *et al.* 1997b)

Symbiontids

A clade of elongated and ovoid heterotrophic euglenozoa, recovered from low-oxygen deep-sea and intertidal sediments; only two genera have been formally described, *Calkinsia* and *Bihospites*, although a number of other lineages are known from environmental samples. There are two heterodynamic flagella that insert within a subapical depression and contain paraxonemal rods; the longer anterior flagellum extends forward during translocation, which occurs with a gliding movement. Cell division occurs along the longitudinal axis, starting at the anterior end and progressing towards the posterior. Single or multiple batteries of tubular extrusomes are present, which may contain cruciform core elements. There is a layer of mitochondrial-like organelles below the cell surface, which lack cristae and kinetoplasts; the nucleus is located towards the anterior. The clade is named for the distinctive presence of large numbers of bacterial ectosymbionts; these may include arrays of rod-shaped bacteria and longitudinal strings of spherical bacteria. Molecular phylogenies resolve a position within the euglenozoa distinct from diplomonads, kinetoplastids and euglenids; the precise phylogenetic position is unknown. (Breglia *et al.* 2010; Yubuki *et al.* 2009)

EXCAVATES INCERTAE SEDIS

Malawimonads

A single genus- *Malawimonas*- of small, laterally flattened excavate flagellates. The two flagella insert in different places: the anterior flagellum inserts apically, is directed forwards in a curve during active beating, and has an acronematic tip; the posterior flagellum inserts at the head of the feeding groove, and bears a vane on its ventral surface arises from a distinct point on the flagellum. There are two basal bodies; a dorsal fan of microtubules arises around a two-stranded microtubular root arising from the anterior basal body. The ventral feeding groove is supported by two microtubular roots, with the right root supporting the floor of the groove; there are non-microtubular striated “A” “B”, “I” and “C” fibres. Mitochondrial cristae are discoid. There are extrusome-like organelles, which lack the ordered structure seen in jakobids. A mitochondrial genome has been completed for *Malawimonas jakobiformis*; complete genome and transcriptome projects are underway. The phylogenetic position of Malawimonads is uncertain; multigene analyses frequently recover positions external to the excavates, and a number of internal positions- as a sister-group to Discoba, Preaxostyla, Diplomonads and Parabasalids, and Metamonads- have received weak phylogenetic support. (Hampel *et al.* 2009; O’Kelly and Nerad 1999; Parfrey *et al.* 2010; Rodriguez-Ezpeleta *et al.* 2007a; Simpson 2003; Simpson *et al.* 2005)

ARCHAEPLASTIDS

Green plants and algae, red algae and glaucophytes: the eukaryotes with primary plastids, *i.e.* eukaryotes where plastids are bound by a double membrane and are inferred to have arisen from only one endosymbiotic event with a cyanobacterium. In some recent literature they have also been referred to as “Plantae”. Cell walls typically contain celluloses, xylans and mannans, and are rich in arabinogalactan proteins. Species are present in a diverse range of marine, freshwater, terrestrial and extreme habitats; in addition, all other photosynthetic eukaryotes (with two exceptions: see Rhizaria) and several currently nonphotosynthetic taxa contain or are believed to have historically contained archaeplastid-derived secondary and tertiary endosymbionts (see the Excavates, the CCTH and SAR clades). Parasitic red algae, green algae and plants are known, and a number of major eukaryotic parasites and pathogens may have historically contained archaeplastid-derived endosymbionts.

Archaeplastids are believed from nuclear multigene phylogenies to be monophyletic, and this is supported by a number of molecular synapomorphies- e.g the TFIIB-like type I transcription factor pBRp, and a conserved duplication of cytosolic FBA. Sister-group relationships between archaeplastids and the SAR and CCTH clades are largely well-supported, leading to suggestions that the three groups should be referred to as a photosynthetic “megakingdom” of “Plastidophila”; the exact branching relationships within this clade are not completely resolved. Chloroplast multigene phylogenies strongly support monophyly, implying that photosynthetic eukaryotes (with two exceptions: *see* Rhizaria, *Paulinella* and *Aurantiocordis*) arose via a single, ancestral primary endosymbiosis of a cyanobacterium, although alternative hypotheses for multiple chloroplast acquisitions have been proposed. It has recently been suggested, from genomic data, that the cyanobacterial primary endosymbiosis

may have been preceded by a cryptic chlamydiobacterial primary endosymbiosis, although this has only been studied in a small number of species. Archaeplastids are known to have been uptaken as secondary endosymbionts a minimum of five times by members of the excavates, CCTH and SAR clades. Profiling of nuclear-encoded, cyanobacterial and chlamydiobacterial-derived genes in archaeplastids suggests that both predominantly encode chloroplast-targeted proteins, implying that in both instances endosymbiosis solely contributed to the establishment of photosynthesis, in direct contrast to the retention of genes from studied secondary and tertiary endosymbioses encoding cytoplasmic and mitochondrial-targeted proteins. (Bhattacharya *et al.* 1995a; Bhattacharya and Medlin 1998; Burki *et al.* 2007; Burki *et al.* 2008; Cavalier-Smith 1981; Chu *et al.* 2004; Delwiche and Palmer 1997; Deschamps and Moreira 2009; Durnford *et al.* 1999; Gross *et al.* 2001; Hackett *et al.* 2007; Hampl *et al.* 2009; Howe *et al.* 2003; Huang and Gogarten 2007; Imamura *et al.* 2008; Lagrange *et al.* 2003; Larkum *et al.* 2007; Lockhart *et al.* 1992; Lockhart *et al.* 2005; Lockhart *et al.* 1998; Marin *et al.* 2005; McFadden 2001; McFadden and van Dooren 2004; Moustafa *et al.* 2008; Nozaki *et al.* 2009; Nozaki *et al.* 2003b; Nozaki *et al.* 2007b; Palmer 2003; Philippe *et al.* 2004; Popper and Tuohy 2010; Reyes-Prieto and Bhattacharya 2007; Reyes-Prieto *et al.* 2006; Rodriguez-Ezpeleta *et al.* 2005; Simpson and Roger 2004a; Stiller *et al.* 2003; Stiller *et al.* 2001; Suzuki and Miyagishima 2010; Westphal *et al.* 2003; Worden *et al.* 2009)

VIRIDIPLANTAE (GREEN ALGAE & PLANTS)

Green algae and plants, also referred to as Chloroplastids, with primary (double membrane-bound) chloroplasts which contain thylakoids arranged in stacks (girdle lamellae are absent), a pyrenoid, and chlorophylls a and b. There are no phycobilins (other than the phytochrome). Chloroplast DNA is arranged in numerous small nucleoids, not rings. The ey spot (when present) and the pyrenoid are located inside the chloroplast. The flagellar bases have a stellate structure linking the pairs of microtubules in the transition zone. Cell wall polysaccharides principally consist of celluloses and hemicelluloses (*e.g.* xylans and mannans), the backbones of which synthesised by an unique and highly diverse family of Golgi and plasma membrane-localised synthases. Uniquely, starch is deposited principally in the chloroplast stroma; this has been linked to the conserved duplication and potentially secondary cytoplasm-to-chloroplast retargeting of a number of genes involved in the starch biosynthesis pathway. Some multicellular species are used in East Asian cuisine (*e.g.* *Cladophora*, “umibudō”). Molecular phylogenies strongly support monophyly, and division into two principal lineages of chlorophytes and streptophytes; although similarities in chloroplast ultrastructure and a cytosolic FBA duplication suggest a specific sister-taxon relationship to red algae, molecular analyses have failed to recover a consistent position, with nuclear gene phylogenies predominantly suggesting a sister-taxon relationship to either red algae or glaucophytes, and chloroplast gene phylogenies supporting either a sister-taxon relationship to red algae or a basal divergence of chloroplastids from other archaeplastid lineages. (Burki *et al.* 2007; Burki *et al.* 2008; Cavalier-Smith 1981, 1987; Christensen 1994b; Delwiche 1999; Delwiche *et al.* 2004; Deschamps *et al.* 2008a; Deschamps *et al.* 2008b; Deschamps and Moreira 2009; Hackett *et al.* 2007; Johnson *et al.* 2004; Lechtreck and Melkonian 1991; Mattox and Stewart 1984; Melkonian 1984; Moestrup 1991; O’Kelly and Floyd 1984a, 1984b; Pickett-Heaps and Marchant 1972; Popper and Tuohy 2010; Reyes-Prieto *et al.* 2007; Rodriguez-Ezpeleta *et al.* 2005; Sluiman 1985; Watanabe and Floyd 1996)

Chlorophyta

Swimming cells with 2 or 4 flagella, inserting apically, laterally (Mamiellales) or posteriorly. Basal bodies are arranged cruciately, usually associated with 4 microtubular rootlets alternating between 2 and higher numbers of microtubules, or minor variations on this; 180-degree symmetry is present in many taxa such that if one basal body and its roots are rotated 180-degrees, they cover the second basal body, and its microtubular roots. Different groups have different relative offsets from the cruciate (directly opposed, DO) pattern of rootlets, either clockwise (CW) or counter-clockwise (CCW). Chlorophyte reproduction is predominantly isogamous, although some oogamous and anisogamous lineages are known. Chlorophytes have been suggested to have secondarily lost genes encoding the cytosolic mevalonate isoprenoid biosynthesis pathway. At least four secondary endosymbioses of green algae by other eukaryotes are known: in the euglenids (of a basally divergent lineage), the chlorarachniophytes (a lineage related to the CUT clade), the dinoflagellate genus *Lepidodinium* (a lineage of unresolved origin) and the katablepharid *Hatena arenicola* (a prasinophyte). In addition, the recent recovery of large numbers of chlorophyte-derived genes in CCTH and SAR clade lineages, including five genes in the carotenoid biosynthesis pathway, phosphoribulokinase and a microtubular striated fibre assembling, has led to the suggestion that members of one or both lineages may have historically possessed a chlorophyte-derived endosymbiont. (Floyd *et al.* 1980; Grauvogel and Petersen 2007; Harper *et al.* 2009; Minge *et al.* 2010; Miyamura 2010; Moustafa *et al.* 2009; O'Kelly and Floyd 1984b; O'Kelly and Floyd 1984a, 1984b; Okamoto and Inouye 2006; Petersen *et al.* 2006a; Petersen *et al.* 2006b; Takahashi *et al.* 2007a; Watanabe and Floyd 1996; Westphal *et al.* 2003)

“CUT clade”

Chlorophytes where the R4 broad microtubular rootlet extends from basal body 2 to the eyespot. With cellulose cell walls, and with apically inserting flagella on flagellated cells. The group is resolved by molecular analyses, although the internal branching relationships are currently subject to debate. (Floyd *et al.* 1980; Frommolt *et al.* 2008; Grauvogel *et al.* 2007a; Grauvogel and Petersen 2007; Grauvogel *et al.* 2007b; Harper *et al.* 2009; Minge *et al.* 2010; Miyamura 2010; Moustafa *et al.* 2009; O'Kelly and Floyd 1984b; O'Kelly and Floyd 1984a, 1985; Okamoto and Inouye 2006; Petersen *et al.* 2006a; Takahashi *et al.* 2007b; Teich *et al.* 2007; Watanabe and Floyd 1996; Westphal *et al.* 2003)

Chlorophyceae

Coccoid, flagellate, colonial and filamentous chlorophyceans, with a haplobiontic life cycle. In the flagellar apparatus, microtubular rootlets have 180-degree symmetry; the transition region consists of a short proximal stellate structure and a long distal one with a thick transverse plate on its proximal edge. Approximately twenty nonphotosynthetic species are known, and a number utilise alternate nonoxygenic photosynthetic pathways, *e.g.* the anaerobic photolysis of acetate. Five clades are currently recognised, on the basis of molecular analyses and flagellar root orientation: “CW” (former Chlamydomonadales); “DO” (Sphaeropleales, also with basal body core connections); Oedogoniales (filamentous; producing stephanokont flagellates); Chaetopeltidales (quadriflagellates with a perfect DO flagellar apparatus); and Chaetophorales (quadriflagellates with a CW+CW arrangement of pairs of basal

bodies). Complete genome sequences are available for the model alga *Chlamydomonas reinhardtii* and the colonial *Volvox carteri* (both Chlamydomonadales); chloroplast genomes are available for the sphaeropleale *Scenedesmus obliquus* and chaetophorale *Stigeoclonium helveticum*; and complete genomes and transcriptomes are under construction for the chlamydomonads *Botryococcus braunii* and *Dunaliella salina*. Comparative genomic analyses have identified arrays of genes involved in sex differentiation and multicellularity (in *Volvox*), and transcript editing, cell signalling, metabolism and metalloprotein biosynthesis (in *Chlamydomonas*). Some recent molecular analyses have suggested that this assembly may be paraphyletic, with oedogoniales and/ or chaetopeltidales forming an outgroup to ulvophytes and core chlorophytes; others support chlorophyte monophyly. (Alberghina *et al.* 2006; Belanger *et al.* 2006; Bold and Wynne 1985; Buchheim *et al.* 2001; Deason *et al.* 1991; Ferris *et al.* 2010; Godman and Balk 2008; Guillou *et al.* 2004; Hoops *et al.* 1994; Kirk 2003; Lewis and Lewis 2005; Lewis and McCourt 2004; May *et al.* 2008; Melkonian 1984; Merchant *et al.* 2007; Mishler *et al.* 1994; O'Kelly and Floyd 1984b; Pickett-Heaps 1975; Prochnik *et al.* 2010; Ringo 1967; Smith and Lee 2009; Timmins *et al.* 2009; Vernon *et al.* 2001; Wheeler *et al.* 2008; Wilcox and Floyd 1988; Zhang *et al.* 2008; Zimmer *et al.* 2008)

Ulvophytes

Predominantly diplobiontic filamentous chlorophytes, where flagellates have flagellar roots that are CCW offset and have 180-degree rotational symmetry, containing an upper and a lower pair of basal bodies perpendicular to the long axis of the cell, with proximal ends of the upper pair overlapping, and an extremely long transitional region composed of proximal and distal stellate structures. The cell body of flagellates may be covered with square scales. Thalli may be multinucleate and siphonous, and calcareous scales may be present. Cytokinesis is by furrowing; there is no phycoplast or phragmoplast. Principally marine, species are known from coastal (*e.g.* *Ulva*) and benthic (*Acetabularia*) as well as freshwater (some cladophorales), terrestrial and subaerial habitats (some trentepohliales). Species have been identified as epibionts on trees, red algae and sloth fur, and some trentepohliales are photosymbionts of orange lichen. In addition, marine ulvophyte zoospores have been observed to respond chemotactically to bacterial quorum sensing molecules, suggesting further layers of potential symbiotic and parasitic interactions. Mitochondrial and chloroplast genomes are available for *Pseudendoclonium akinetum*, and a mitochondrial genome for *Oltmannsiellopsis viridis*, both deep-branching unicellular ulvophytes. Several ulvophyte genera are used in North European and South-East Asian cuisine (*e.g.* *Cladophora*, “kaipen”). Ulvophytes are believed to be monophyletic, and are believed to be either close relatives of chlorophytes or a basal offshoot of the CUT clade. (Alberghina *et al.* 2006; Bold and Wynne 1985; Chapman 1984; Gauna *et al.* 2009; Graham and Wilcox 2000; Guillou *et al.* 2004; Lewis *et al.* 2005; Mattox and Stewart 1984; Melkonian 1984; O'Kelly and Floyd 1984a; O'Kelly and Floyd 1984b; O'Kelly *et al.* 2004; O'Kelly and Floyd 1983, 1984a; Pombert *et al.* 2006; Pombert *et al.* 2004, 2005; Rindi *et al.* 2006; Roberts 1984; Suutari *et al.* 2010; Tait *et al.* 2005; Zhang *et al.* 2008)

Trebouxiophytes

Coccoid and filamentous chlorophytes that reproduce asexually by autospores or biflagellated zoospores; no defining synapomorphies are known, although as per Ulvophytes, the flagellar apparatus is offset anticlockwise. Trebouxiophytes may be free-living, or epibionts and endobionts of plants, dinoflagellates, marine invertebrates, and lichens. Two nonphotosynthetic genera, *Helicosporidium* and *Coccomyxa*, are parasites of marine invertebrates, and *Prototheca* is a vertebrate parasite and the causative agent of protothecosis in humans. A complete genome has been assembled for the free-living photosynthetic trebouxiophyte *Chlorella*; in addition, mitochondrial and chloroplast genomes are available for *Helicosporidium* and *Prototheca*, revealing substantial genome reduction and several presumed convergences in genome organisation with fungi. Molecular phylogenies strongly support trebouxiophyte monophyly, and weakly suggest a basal divergence from the chlorophytes and ulvophytes. (Ahmadjian 1993; Alberghina *et al.* 2006; Crespo *et al.* 2009; de Koning and Keeling 2006; Friedl 1995; Guillou *et al.* 2004; Krienitz *et al.* 2003; Kroken and Taylor 2000; Marin and Melkonian 2010; O'Kelly and Floyd 1984b; Pombert and Keeling 2010; Saito *et al.* 2006; Tremouillaux-Guiller and Huss 2007; Turmel *et al.* 2009; Wolff *et al.* 1993; Wolff *et al.* 1994; Yaman and Radek 2005, 2007; Zhang *et al.* 2008)

“Prasinophytes”

A paraphyletic “grade” including several clades of unicellular chlorophytes; cells may be naked, covered with sub-microscopic organic body scales containing 2-keto-sugar acids, or a theca of fused scales. Many taxa have hair scales on the flagella, long basal bodies and a parabasal Golgi apparatus. The mitotic spindle persists during cytokinesis. Molecular analyses support a position for prasinophyte lineages within the chlorophytes, but suggest that the assembly may be paraphyletic or polyphyletic with regard to the CUT clade. Recent genomic studies have suggested extensive gene transfers between the prasinophytes and members of the SAR and CCTH clades, which may be consistent with a cryptic endosymbiosis of a prasinophyte into the “secondary” algae. (Becker *et al.* 1991; Becker *et al.* 1989; Becker *et al.* 1990; Christensen 1962; Fawley *et al.* 1999; Guillou *et al.* 2004; Marin and Melkonian 2010; Mattox and Stewart 1984; Melkonian 1984; Moestrup 1982, 1991; Moestrup and Throndsen 1988; Moustafa *et al.* 2009; O'Kelly and Floyd 1984b; Steinkötter *et al.* 1994; Sym and Pienaar 1993; Turmel *et al.* 2009; Vierkotten *et al.* 2004; Worden *et al.* 2009)

Chlorodendrales

Flagellated scaly chlorophytes with a double layer of scales, the outer layer of which is made of stellate scales fused into a theca; the inner layer being diamond-shaped; with specialised hair-shaped flagellar pit scales. Organisms have flagella in multiples of two, each flagellum bearing a double layer of scales (outer layer tiny and rod-shaped, inner layer square or pentagonal), as well as “T-type” lateral flagellar hair scales. Flagella beat with a breast-stroke pattern; they have x-2 x-2 flagellar rootlets with a CCW offset and 180-degree symmetry, and (in *Tetraselmis*) with an MLS-like structure (see Streptophyta) facing the cell membrane. The transition region is a short

proximal stellate structure and a long distal one, with a transverse septum between; a rhizoplast is present. There is an eyespot in the plastid. Studied lineages are sexual and anisogamous. The group includes *Tetraselmis convolutae*, endosymbiont of acoel *Convoluta roscoffensis*. Molecular analyses and similarities in the flagellar and cytokinetic apparatus weakly support a sister relationship between Chlorodendrales and the CUT clade. (Domozych *et al.* 1981; Guillou *et al.* 2004; Manton and Parke 1965; Manton *et al.* 1965; Marin and Melkonian 1994, 1999, 2010; Mattox and Stewart 1984; McFadden *et al.* 1986; Melkonian 1979, 1982, 1984; Miyamura 2010; Moestrup and Thronsen 1988; O'Kelly and Floyd 1984b; Salisbury *et al.* 1981; Steinkötter *et al.* 1994).

Mamiellales

Very small scaly flagellated or coccoid chlorophytes; cells may be naked or covered with a “spider web” of flattened rounded or elliptical scales. with “spider-web” scales covering the body and (where present) the 2 laterally inserted flagella. Flagella, where present, may be covered with scales; the flagellar roots are CCW offset, and the transition region has a proximal transverse plate and a short distal stellate structure. A single chloroplast is present in each cell, and contains chlorophylls a and b and prasinoxanthin; the eyespot is in the plane of cell division. Mamiellophytes are predominantly marine, but include the freshwater Monomastigales; studied taxa contain genes implicated in meiosis and mating, but sexual cycles have yet to be observed directly. The mamiellophyte *Ostreococcus tauri* is the smallest known eukaryote. Complete genome sequences are available for *O. tauri* and *Micromonas* RCC299; preliminary analyses have revealed reduction of coding and non-coding content, and extensive genome rearrangements and substantial divergence in gene content between and within species. Molecular analyses strongly support monophyly, and moderately support a sister-relationship to the CUT clade, chlorodendrales and pyconoccales. (Barlow and Cattolico 1980; Barlow and Cattolico 1981; Becker *et al.* 1991; Chrétiennot-Dinet *et al.* 1995; Derelle *et al.* 2006; Egeland *et al.* 1997; Egeland *et al.* 1995; Eikrem and Thronsen 1990; Fawley 1993; Fawley *et al.* 2000; Foss *et al.* 1984; Guillou *et al.* 2004; Marin and Melkonian 1994, 1999, 2010; Melkonian 1984; Miyashita *et al.* 1993; Moestrup 1984; Nakayama *et al.* 2000; O'Kelly and Floyd 1984a, 1984b; Piganeau *et al.* 2009; Robbens *et al.* 2007; Worden *et al.* 2009)

Prasinococoids

Naked coccoid chlorophytes containing prasinoxanthin, and mitochondrial membranes intruding into the pyrenoid. Two genera are known: *Prasinococcus* and *Prasinoderma*. Molecular analyses suggest a relationship basal to all other chlorophytes. (Fawley 1992, 1993; Fawley *et al.* 2000; Guillou *et al.* 2004; Marin and Melkonian 2010; Miyashita *et al.* 1993)

Pycnococcales

Flagellated and coccoid chlorophytes. Flagellates have two layers of body scales: rod-shaped or stellate on top, square or pentagonal underneath, with specialised hair-shaped flagellar pit scales. Two unequal flagella insert laterally or posteriorly, each bearing two layers of flagellar scales and lateral

flagellar hairs; the three flagellar roots are CCW offset, and there is a multilayered structure attached to the broad root. The transition region consists of a proximal short stellate structure, transverse plate, distal long stellate structure, and a distal transverse plate; a rhizoplast is present. Pycnococcales include the genus *Nephroselmis*, a close relative of the secondary green algal photosymbionts of the katablepharid *Hatena arenicola*; a complete chloroplast genome is available for *N. olivacea*. Molecular analyses suggest that this assembly may be paraphyletic or polyphyletic, with some members resolving as sister-taxa to chlorodendrales and the CUT clade, and others as deeper branches within the chlorophytes. (Fawley 1993; Fawley *et al.* 1999; Guillou *et al.* 2004; Melkonian 1980; Moestrup 1979, 1983; Moestrup and Ettl 1979; Moestrup and Throndsen 1988; O'Kelly and Floyd 1984b; Okamoto and Inouye 2006; Suda *et al.* 1989; Turmel *et al.* 1999a; Turmel *et al.* 1999b)

Pyramimonadales

Swimming scaly chlorophytes where the four, eight or sixteen flagella arise from an inversely pyramidal apical pit, and may be held posteriorly while swimming. There is a CCW offset of flagellar roots and an MLS-like structure on root 1; the transition region has a short stellate structure and a distal coiled fibre. There are three layers of complex scales: flagellar scales are square or pentagonal underneath, limuloid or spined in the middle, and have two opposing rows of hair-shaped scales on top; body scales are square, with smaller ones underneath and larger ones in two layers on top. Some species produce a double-walled cyst or phycoma (valuable in the fossil record, *e.g.* of *Tasmanites*), which is surrounded by a single wing in *Pterosperma*. Each individual has one or two chloroplasts, with two or four eyespots on the surface of pyrenoids. Some species produce a double-walled cyst or phycoma, which is surrounded by a single wing in *Pterosperma*. No parasitic or symbiotic taxa are known, although bacterial epibionts have been identified from the arctic species *Pyramimonas gelidicola*. A complete chloroplast genome is available for *Pyramimonas*. Molecular analyses suggest a basal divergence from other chlorophyte taxa. (Delwiche 1999; Guillou *et al.* 2004; Hori and Moestrup 1987; Ishida *et al.* 1997; Marin and Melkonian 1994, 1999, 2010; Melkonian 1984; Moestrup 1974; O'Kelly and Floyd 1984b; Ponomarenko *et al.* 2004; Turmel *et al.* 2009)

Scourfeldia

Single genus of chlorophytes with a naked cell body and two naked flagella; tips of flagella taper to contain a single microtubule. The transition region contains a proximal plate and a short distal stellate structure. No molecular information is available for this group. (Manton 1975; Melkonian 1984; Melkonian and Preisig 1982; Moestrup 1991)

Streptophyta

An array of principally freshwater and terrestrial, multicellular chloroplastids, although some marine and unicellular taxa are known. Flagella, where present, insert symmetrically into long basal bodies, and there are two dissimilar flagellar roots, of which the longer is associated with a multilayered structure and an anterior peroxisome or mitochondrion. The transition region is a continuous stellate structure

without conventional transverse plates or septa. Mitosis is open, and there is a persistent mitotic spindle at telophase. Cell walls contain cellulose, synthesised in muro by an unique family of proteins that are spatially regulated by cortical microtubules; xyloglucans may be present in cell walls, as may plasmodesmata formed by the expansion of dividing cell walls over the ER. Glycolate metabolism occurs in peroxisomes; eyespots and pyrenoids are largely absent. Streptophytes contain an unique duplicated cytosolic isoform of GAPDH, GapB, which contains an unique C-terminal extension derived from the Calvin Cycle redox regulator CP12, and BIP, a gene family involved in bud development. The assembly contains embryophytes (land plants) and a paraphyletic array of algae grouped as the charophytes. (Graham and Wilcox 2000; Lloyd and Chan 2008; Mattox and Stewart 1984; Melkonian 1984; Nedelcu *et al.* 2006; Petersen *et al.* 2006a; Pickett-Heaps 1975; Pickett-Heaps and Marchant 1972; Popper and Tuohy 2010; Westphal *et al.* 2003)

Mesostigma viride

Asymmetrical unicellular biflagellated and filamentous streptophytes. Flagellate cells contain two equal laterally-inserting flagella, a short stellate structure in the transition region, and are covered with distinctive “maple-leaf” shaped scales. uniquely amongst streptophytes, there are four, cruciate flagellar roots that are CCW offset. Mature filamentous cells lack plasmodesmata and are connected by the hollow tube of the cell wall. Eyespots are present in the plane of cell division. Historically of uncertain phylogenetic position due to ultrastructural and pigment similarities to both chlorophytes and streptophytes, recent phylogenomic analyses and the conserved retention of MVA pathway and BIP2 family genes have placed *Mesostigma* as a sister-group to *Chlorokybus* at the base of the streptophytes. (Grauvogel *et al.* 2007a; Guillou *et al.* 2004; Karol *et al.* 2001; Lemieux *et al.* 2007; Manton and Ettl 1965; Marin and Melkonian 1999; Martin *et al.* 2002; Melkonian 1982, 1984, 1989; Nedelcu *et al.* 2006; Rodriguez-Ezpeleta *et al.* 2007b; Rogers *et al.* 1981; Turmel *et al.* 2002b; Yoshii *et al.* 2003)

Chlorokybus atmophyticus

Two- to 4-celled sarcinoid packets surrounded by a thick layer of mucilage, lacking plasmodesmata, that divide by the formation of a thin septum. Biflagellate zoospores may form from individual cells in sarcinoid packets; flagella are unequal, insert subapically, there is a distinctive multilayered structure and unilateral root, and basal bodies are CCW offset. A large single microbody branches around the nucleus and is attached to the flagellar apparatus, and two mitochondria are also attached to the flagellar apparatus. The flagella are covered with hairs, and both the flagella and body are covered with square scales; cell walls form beneath the scales during germination. There are eyespots and simple superficial pyrenoids on chloroplasts and an elaborate pyrenoid with embedded thylakoids joining the chloroplasts. A complete chloroplast genome is available. Phylogenomic analyses strongly support a sister-group position to *Mesostigma*, basal to the streptophytes. (Becker and Marin 2009; Delwiche *et al.* 2002; Guillou *et al.* 2004; Karol *et al.* 2001; Lemieux *et al.* 2007; O’Kelly and Floyd 1984a, 1984b; Rodriguez-Ezpeleta *et al.* 2007b; Rogers *et al.* 1980)

Klebsormidiophytes

Streptophytes forming unbranched filaments without holdfasts, and lacking plasmodesmata. and with zoospores released through a pore in the cell wall. Zoospores are naked, and contain two unequal flagella, a multilayered structure, a unilateral root, and CCW offset basal bodies. Chloroplasts are parietal and lobed; centrioles may closely associate with peroxisomes. Species are found in freshwater, terrestrial and polar habitats, and several acidophilic species are known. The phylogenetic position of klebsormidophytes is unresolved, with molecular analyses variously suggesting a close relationship with coleochaetales, the zygnematales, and a position near the base of the streptophytes. (Baffico 2010; Cook 2004; Elster *et al.* 2008; Guillou *et al.* 2004; Marchant *et al.* 1973; McCourt *et al.* 2000; Mikhailiyuk *et al.* 2008; Nagao *et al.* 2008; Novis 2006; O’Kelly and Floyd 1984a, 1984b; Pickett-Heaps 1972; Sakayama 2008; Silva *et al.* 1972; Sluiman *et al.* 2008; Turmel *et al.* 2002a)

Zygnemophytes

Aflagellated, freshwater and acidophilic streptophytes, which may be unicellular, colonial, or filamentous. Filamentous taxa are unbranched and lack plasmodesmata, distinguishing them from other filamentous streptophytes. The cell wall is composed of crystalline cellulose microfibrils; some taxa (*e.g.* desmids) have highly ornamented cell walls and pores. Sexual reproduction occurs by the conjugation, with amoeboid gametes moving through a tube of the cell wall; chloroplast inheritance is uniparental. A complete transcriptome has been annotated for *Spirogyra pratensis*. The conserved presence of a nuclear-encoded *TufA*, and recent chloroplast phylogenomic analyses, place zygnemophytes as a sister-group to the embryophytes, although the validity of this association has been questioned. (Baldauf and Palmer 1990; Becker and Marin 2009; Bhattacharya *et al.* 1996; Bhattacharya *et al.* 1994; Guillou *et al.* 2004; Karol *et al.* 2001; Lemieux *et al.* 2007; Mattox and Stewart 1984; McCourt *et al.* 2000; Mix and Manshard 1977; Rodriguez-Ezpeleta *et al.* 2007b; Timme and Delwiche 2010)

Coleochaetales

Streptophytes that form branched filaments, which bear sheathed hairs (extensions of the cell wall, containing cytoplasm), and contain parenchymatous tissue, with terminal and marginal growth. Biflagellated zoospores have unique pyramidal, diamond-shaped scales on the flagellum and body, and hair scales on the flagellum; the flagella extend laterally from the point of insertion, and have a distinctive transition region containing stellate structures and striated transverse septa. There are several small anterior mitochondria near the flagellar apparatus. A phragmoplast is present during cell division. Some species may be epiphytes of charalean algae. Organelle genome sequences are available for *Chaetosphaeridium globosum*, and a transcriptome has been completed for *Coleochaete orbicularis*. Phylogenomic analyses support a position basal to the charales and embryophytes. (Baldauf and Palmer 1990; Delwiche *et al.* 2002; Graham 1982, 1984, 1996; Graham and McBride 1979; Graham and Wilcox 2000; Guillou *et al.* 2004; Kenrick and Crane 1997; Lemieux *et al.* 2007; Mahakham and Theerakulpisut 2010; Moestrup 1974, 1978; O’Kelly and Floyd 1984a, 1984b; Rodriguez-Ezpeleta *et al.* 2007a; Rodriguez-Ezpeleta *et al.* 2007b; Sluiman 1983, 1985; Timme and Delwiche 2010; Turmel *et al.* 2002a)

Charales

Streptophytes ranging in size from centimetres to tens of metres, with extremely complex body structures, typically consisting of a holdfast attached to the substratum, and multiple thalli containing a central axis of multinucleate, internodal cells and whorls of branches radiating from uninucleate, node cells, which accumulate crystals of calcium carbonate (hence the colloquial name “stoneworts”). Meristems are apical, with a single face of cell division (*c.f.* parenchymatous growth in embryophytes); exposed antheridia and oogonia are surrounded by sterile cells (*c.f.* embryophyte protected gametangia). There is rapid cytoplasmic streaming, which moves the many small chloroplasts around the cell. A phragmoplast develops from the persistent interzonal spindle during division. Male swimmers (flagellates) are highly elongated, helically coiled, covered in diamond-shaped scales, and are released through enlarged plasmodesmata of antheridial cells. Swimmer flagella are likewise covered in diamond-shaped scales, and insert at the anterior tip of the cell; flagella are partially embedded within the cell membrane, emerging separately about 1/3 of the way down the cell. The flagellar transition region includes a stellate structure with no apparent transverse septa; basal bodies seem to be “a structureless mass”; a root of interconnected microtubules separate the flagella from the mitochondrion. Similarly to plants, cell wall deposition is turgor-dependent. Commonly found in high pH freshwater habitats, charophytes are highly efficient at suppressing photosynthetic competitors; this is believed to be due to competitive nutrient occlusion but may additionally occur via allelopathic interactions. A complete chloroplast genome is available for *Chara vulgaris*. Phylogenetic analyses have linked charales either as the direct sister-group of embryophytes, or as basal to the zygnematophytes and embryophytes; the relationships between these lineages is debated. (Becker and Marin 2009; Delwiche *et al.* 2002; Graham 1990, 1993; Guillou *et al.* 2004; Hidding *et al.* 2010; Jeffrey 1967; Karol *et al.* 2001; Lemieux *et al.* 2007; Moestrup 1970, 1978; Pickett-Heaps 1968; Proseus and Boyer 2008; Rodriguez-Ezpeleta *et al.* 2007b; Sluiman 1983; Turmel *et al.* 2006; Turner 1968)

Embryophytes

Land plants: vascular plants, mosses, hornworts and liverworts. There are alternating diploid and haploid sporophyte and gametophyte generations, although this ranges from gametophyte dominance (in bryophytes) to the internalization of gametophytes within sporophyte reproductive tissue (in angiosperms and gymnosperms). Spores are produced in tetrads, and sperm architecture is unique, with ovoid, naked male swimmers. Where present on swimmers, flagella insert into a stellate transition region, with a three or four-layered multilayered structure wrapped around a morphologically distinct anterior mitochondrion, and incorporating a helical, “unilateral” curtain root of 15-60000 microtubules, set at 45 degrees to the long axis of lamellae in the multilayered structure. Chloroplasts have a consistent gene order in their DNA; pyrenoids are absent except in some hornworts. Uniquely amongst chloroplastid lineages, cell walls may contain significant quantities of xyloglucans and lignins; the complex hemicellulose rhamnogalacturonan II is believed to be specific to embryophytes. In addition to terrestrial and freshwater taxa, a small number of secondarily marine species is known. Over 200 angiosperm genera (*e.g.* *Viscum*- mistletoe; *Nuytsia*- West Australian Christmas Tree; *Cuscuta*- dodder; *Rafflesia*), grouped in eleven phylogenetically distinct lineages, are known to be parasites of other plants;

parasitic taxa may be either secondarily nonphotosynthetic or mixotrophic, and typically invade host species via the formation of specialised root systems (“haustoria”) or mycoheterotrophy. The signalling interactions between parasites and hosts involves the bidirectional translocation of secondary metabolites (e.g. strigolactones) and RNAs, and is of particular interest due to the similarities with the signalling pathways underpinning rhizosymbioses. A substantial number of genomes have been completely sequenced or are under assembly, ranging from model angiosperms (e.g. *Arabidopsis thaliana*) to important crop species (rice, soya), representative gymnosperms, lycophytes and bryophytes (*Pinus taeda*, *Selaginella moelendorffii*, *Physcomitrella patens*, *Marchantia polymorpha*), as well as the chloroplast genomes of nonphotosynthetic parasites (*Epifagus virginiana*). Analyses of plant genomes have recovered evidence for multiple whole genome duplication events in plant evolution, and a number of lateral gene transfer events, including a small number of gene acquisitions from fungal donors. (Badger *et al.* 1998; Bidartondo and Bruns 2005; Bidartondo and Duckett ; Blanc and Wolfe 2004; Bremer 1985; Brown and Lemmon 2008, 2009; Bungard 2004; Carothers and Duckett 1979, 1980; Delwiche *et al.* 2002; Duckett and Carothers 1979; Graham 1990, 1993; Jaillon *et al.* 2007; Jeffrey 1967; Karol *et al.* 2001; Kenrick and Crane 1997; McKay and Gibbs 1991; Mishler and Churchill 1985; Moestrup 1978; Norstog 1974; Oda *et al.* 1992; Ohyama *et al.* 1986; Popper and Tuohy 2010; Raubeson and Jansen 1993; Remington *et al.* 1999; Rensing *et al.* 2008; Renzaglia and Duckett 1988; Turmel *et al.* 2003; Westphal *et al.* 2003; Yu *et al.* 2002)

RHODOPLASTIDS (RED ALGAE)

“Red algae” *sensu lato*, also referred to as Rhodoplantae. Unicellular and multicellular archaeplastids that have lost flagella and centrioles at all life history stages, a significant change in cell biology from other eukaryotes. Multicellular taxa may contain pit plugs, “stoppered” connections between daughter cells resulting from incomplete cleavage. Primary plastids are enveloped by double membranes, lack chlorophylls b and c, have a genophore arranged in multiple small 1-2 μm diameter “blebs”, and contain non-aggregated thylakoids embedded with phycobilisomes containing the accessory pigments phycoerythrin (red pigment), phycocyanin (blue pigment) and allophycocyanins. Cell walls typically contain celluloses, xylans and mannans; lignin may be present. Uniquely amongst archaeplastids, rhodoplastids utilise a form ID rubisco obtained laterally from a proteobacterial donor, and deposit Floridean starch deposited free in the cytoplasm instead of within the chloroplast. Principally found in marine but also freshwater and extreme habitats, although species number is low; a small number of parasitic taxa are known, all of which are parasites of other red algae, and two lineages- the Erythropeltiales and the Rufusiales- are epibionts, respectively of marine macroalgae and sloths. Red algal-derived secondary chloroplasts are present in photosynthetic cryptomonads, haptophytes, stramenopiles and dinoflagellates, and thus red algal lineages are present in the majority of extant algal species; these chloroplasts are believed to have originated via a single secondary endosymbiosis, although there is debate over how and in which eukaryotic lineage this happened.

The traditional taxonomy, based on ultrastructure and life cycle, has undergone substantial recent revision from molecular data. The position of red algae within the Archaeplastida is unresolved: the presence of a conserved FBA duplication, chloroplast ultrastructure, and some molecular phylogenies support a sister-taxon

relationship to chloroplastids, others suggest a basal relationship to other archaeplastids, and recent chloroplast phylogenies have suggested a specific sister-group relationship to glaucophytes. (Baurain *et al.* 2010; Burki *et al.* 2007; Burki *et al.* 2008; Deschamps and Moreira 2009; Goff *et al.* 1997; Hackett *et al.* 2007; Keeling 2009c, 2009b, 2009a; Moon and Goff 1997; Müller *et al.* 2001b; Poeschel 1990; Poeschel and Magne 1987; Reyes-Prieto *et al.* 2007; Rodriguez-Ezpeleta *et al.* 2005; Saunders 2005; Silva *et al.* 2006; Silva 1996; Tabita *et al.* 2008a; Tabita *et al.* 2008b; Yoon *et al.* 2006a; Yoon *et al.* 2002a; Yoon *et al.* 2002b; Yoon *et al.* 2006b)

Cyanidiophytes

Unicellular red algae with thick, proteinaceous cell walls, tolerant of extreme environments; with an association between the ER and Golgi; with an endospore stage; and heterotrophic capability. Carbohydrates are principally stored as glycogen, although semi-amylopectins may also be present; amyloses are absent. A genome sequence has been completed for the extreme acidophile *Cyanidioschizon merolae*; an EST library has been constructed for the versatile acidophile *Galdieria sulphuraria*. The *C. merolae* genome is substantially reduced, is largely depleted of introns and transposons, lacks a number of otherwise broadly conserved eukaryotic genes including myosins, dyneins, and several SNARE complex proteins, and performs a number of unusual expression processes, including the production of tRNAs via a novel circular intermediate. Recent genomic analyses have suggested substantial divergence in gene content between *G. sulphuraria* and *C. merolae*, and a substantial number of lateral or endosymbiotic acquisitions of chloroplast-targeted genes from non-cyanobacterial donors. Molecular analyses strongly supports a position basal to all other red algae (Albertano *et al.* 2000; Barbier *et al.* 2005; Chapman 1974; Christensen 1962; Gross *et al.* 2001; Hirabaru *et al.* 2010; Koumandou and Howe 2007; Matsuzaki *et al.* 2004; Muravenko *et al.* 2001; Nozaki *et al.* 2007b; Ohta *et al.* 2003; Pinto *et al.* 2003; Saunders *et al.* 2004; Seckbach 1999; Shimonaga *et al.* 2008; Soma *et al.* 2007; Suzuki and Miyagishima 2010; Yoon *et al.* 2006a; Yoon *et al.* 2006b)

Rhodophytes

A diverse clade of unicellular and multicellular red algae. The clade is well supported by molecular analyses, and although no synapomorphies have been reported, the Golgi apparatus of most studied taxa is closely associated with the mitochondria; floridoside where present is enriched in amylopectin. (Saunders and Hommersand 2004; Scott *et al.* 2009; Shimonaga *et al.* 2008; Yokoyama *et al.* 2009; Yoon *et al.* 2006b)

Rhodellophytes

Unicellular rhodophytes with a single, highly lobed plastid, surrounded by plastoglobuli (lipid droplets). The Golgi apparatus may either be perinuclear or scattered, and its cisternae may appear fused; mannitol is present, and storage carbohydrates are predominantly semi-amylopectins with some amyloses. Reproduction occurs by cell division. Historically grouped with the porphyridiophytes as the porphyridiales, recent molecular analyses variously support a close relationship with the florideophytes and bangiales, and with the compsopogonophytes, porphyridiophytes and stylonematophytes. (Hirabaru *et al.* 2010; Müller *et al.* 2001b; Poeschel 1990; Saunders and Hommersand 2004;

Scott *et al.* 2009; Shimonaga *et al.* 2008; Silva 1996; Yokoyama *et al.* 2009; Yoon *et al.* 2002b; Yoon *et al.* 2006b)

Porphyridiophytes

Unicellular rhodophytes with a single branched or stellate chloroplast lacking an encircling thylakoid in the plastid; pyrenoids may be present. The Golgi apparatus is closely associated with the ER and mitochondria; reproduction occurs by cell division; floridoside is present, and is principally composed of semi-amylopectins, with small quantities of amylose. Historically grouped with the rhodellophytes as the porphyridiales, recent molecular analysis have failed to recover a consistent phylogenetic position for the porphyridiophytes. (Hirabaru *et al.* 2010; Müller *et al.* 2001b; Pueschel 1990; Saunders and Hommersand 2004; Shimonaga *et al.* 2008; Silva 1996; Yoon *et al.* 2006b)

Stylonematophytes

Unicellular, pseudofilamentous or filamentous rhodophytes; the Golgi apparatus is closely associated with the mitochondria and ER; reproduction may occur either by cell division or monospore production. Floridoside is absent, distinguishing the group from other Rhodophytes. Historically grouped with the porphyridiophytes and rhodellophytes as the porphyridiales, recent molecular analyses predominantly strongly support a close relationship with the porphyridiophytes and compsogonophytes. (Müller *et al.* 2001b; Pueschel 1990; Saunders and Hommersand 2004; Silva 1996; West *et al.* 2007; Yoon *et al.* 2006b; Zuccarello *et al.* 2008)

Rufusia

Branched filamentous rhodophytes, containing red to violet discoid or band-shaped chloroplasts; pyrenoids have not been observed; floridoside is present in the cytoplasm. A single species, *R. pilicola*, has been identified as an epibiont on the hair of two genera of sloths native to Latin America. Originally proposed from molecular analyses to be a basally divergent stylonematophyte, *Rufusia* has recently been suggested to form a separate, sister class to the Stylonematophytes due to the presence of floridoside and its unusual habitat. (Wujek and Timpano 1986; Yoon *et al.* 2006b; Zuccarello *et al.* 2008)

Compsopogonophytes

Rhodophytes with an ER-associated Golgi apparatus, and a central, thylakoid-free region in each chloroplast; pyrenoids are generally absent. Life history is biphasic; monosporangia and spermatangia are cut out from undifferentiated vegetative cells in some taxa by characteristic curved cell walls. Members of one order, the Erythropeltidales, are principally found as epibionts of marine macroalgae, but the nature of these associations have not been characterised. Molecular analyses weakly support a sister-group relationship with the porphyridiophytes, and a close relationship with the stylonematophytes. (Badger *et al.* 1998; Nelson *et al.* 2003; Saunders and Hommersand 2004; Silva 1996; West and Zuccarello 2009; West *et al.* 2007; Yokoyama *et al.* 2009; Yoon *et al.* 2006b; Zuccarello *et al.* 2010)

Bangiophytes

True rhodophytes that have a parenchymatous gametophyte, which –uniquely among red algae- produces carposporangia and spermatangia in distinct packets, by successive divisions. The sporophyte is filamentous and has pit plugs with a cap layer but no membranes, distinguishing this group from some other Florideophytes. The Golgi apparatus is associated with the ER and mitochondria. Conchospores may be formed. Members of the genus *Porphyra* are cultivated extensively in East Asian countries for use in food (e.g. as nori). A complete genome has been assembled for *Porphyra umbilicalis*, and a transcriptome for *P. purpurea*. Molecular phylogenies robustly support a sister-taxon relationship to the florideophytes. (Hirabaru *et al.* 2010; Hoef-Emden *et al.* 2005; Hommersand and Fredericq 1990; Müller *et al.* 2001a; Müller *et al.* 2003; Müller *et al.* 2001b; Oliveira *et al.* 1995; Saunders and Hommersand 2004; West *et al.* 2007; Yokoyama *et al.* 2009; Yoon *et al.* 2006b).

Florideophytes

True rhodophytes that grow as branched filaments, using apical and lateral cells, and pit plugs linking cells throughout the body. The life cycle consists of three phases (gametophytes, carposporophytes, tetrasporophytes), and a distinctive reproductive apparatus, consisting of terminal or lateral carpogonia bearing a long extension (trichogyne) for the attachment of spermatangia, and carpospores developing directly from the fertilised carpogonium. The ER, Golgi and mitochondria are closely associated. Chloroplasts are mostly parietal and discoid, although may in some species be centrally-placed and stellate; pyrenoids are present in most taxa. Five divisions are currently recognised: Hildenbrandiophytes (containing pit plugs with a single cap layer, covered by a membrane), Nemaliophycids (an extremely diverse group of marine and freshwater species, with pit plugs covered by two cap layers), Ahnfeltiophycids (with naked pit plugs, lacking both a cap and membranes), Corallinophycids (calcified florideophytes, with two-celled carpogonial branches, and pit plugs covered by two cap layers but no membrane) and Rhodymeniophycids (a diverse array of predominantly marine algae, with pit plugs covered by a membrane but no cap layers). Several rhodymeniophycid genera (e.g. *Asterocolax*, *Faucheocolax*, *Harveyella*, *Holmsella*) are parasites of other closely related Florideophytes; several species are extensively used as sources of gelling agents and stabilisers in food industries, such as *Gelidium* and *Gracilaria* (agar) and *Chondrus crispus* (carrageenan). Monophyly is supported by the presence of an unique actin duplication; molecular phylogenies robustly support a sister-group relationship to the Bangiophytes in a clade termed the “eurhodophytes”. (Delivopoulos and Kugrens 1985; Goff 1976; Goff *et al.* 1997; Hoef-Emden *et al.* 2005; Le Gall and Saunders 2007; Pueschel 1994; Saunders and Bailey 1997; Saunders *et al.* 2004; Saunders and Hommersand 2004; Saunders and Kraft 1997; West *et al.* 2007; Wetherbee and Quirk 1982; Yokoyama *et al.* 2009; Yoon *et al.* 2006b)

GLAUCOPHYTES

Small flagellated, coccoid or palmelloid eukaryotes with cruciate flagellar roots, a plasma membrane subtended by sacs or “shields”, and a Golgi apparatus proximal to the basal body. The blue-green chloroplasts, also referred to as “cyanelles” and

“muroplasts”, retain a large number of features either presumably derived from the bacterial ancestor or putatively more “primitive” than other primary plastid lineages, most notably a carboxysome (protein-encased, carbonic anhydrase-associated “bacterial pyrenoids”) and a peptidoglycan cell wall enclosed in a vacuole. The precise function of the peptidoglycan cell wall is not completely resolved; however, it has been suggested to have an essential role in the formation of the central furrow during cyanelle replication, and to act against the high stromal turgor produced by CCM activity. Chlorophyll *a*, phycocyanin and allophycocyanin are present; thylakoids are concentric, unstacked, and embedded with phycobilisomes; starch is deposited in the cytoplasm but not the cyanelle. No parasitic taxa are known, and glaucophytes are not known to have been uptaken as secondary endosymbionts by any extant eukaryotes.

Eleven genera are known, solely from freshwater habitats, and are divided into three groups: Cyanophorales (oval-shaped and ventrally flattened glaucophytes, with two unequal, hairy flagella that insert respectively into an apical and a ventral groove, and a parabasal Golgi body), Glaucocystales (coccoid glaucophytes containing star-like aggregates of rod-shaped cyanelles, a smooth, internalised flagellum, and a parabasal Golgi apparatus) and Gloeochaetales (palmelloid unicellular or colonial glaucophytes, with multiple small spherical cyanelles, and internalised flagella). Although similarities in the ultrastructure of the cell cortex and microtubular roots, and early molecular phylogenies suggested a sister-group relationship to the cryptophytes, more recent molecular analyses have robustly positioned glaucophytes within the archaeplastids, although there is conflicting information regarding its exact position relative to rhodoplastids and chloroplastids. A complete cyanelle genome sequence is available for the cyanophorale *Cyanophora paradoxa*. (Bhattacharya *et al.* 1995a; Bhattacharya and Weber 1997; Bourrelly 1960; Burki *et al.* 2007; Burki *et al.* 2008; Chu *et al.* 2004; Deschamps and Moreira 2009; Douglas and Raven 2003; Fathinejad *et al.* 2008; Heimann *et al.* 1989; Imai *et al.* 1999; Kiefel *et al.* 2004; Kies 1976; Mangeney and Gibbs 1987; Mignot *et al.* 1969; Nozaki *et al.* 2007a; Nozaki *et al.* 2009; Nozaki *et al.* 2003a; Raven 2003; Robinson and Preston 1971; Rodriguez-Ezpeleta *et al.* 2005; Sato *et al.* 2007; Schmidt *et al.* 1979; Schnepf 1965; Stirewalt and Bryant 1989; Takano and Takechi 2010; Thompson 1973; Westphal *et al.* 2003; Willison and Brown 1978)

“THE SAR CLADE”

An assembly of the large and diverse groups Stramenopiles, Alveolates, and Rhizaria, each of which contains flagellates, amoebae and parasites; and photosynthetic, mixotrophic and heterotrophic members. The SAR clade is also referred to as Harosa: the nomenclature of this group is currently under debate. Monophyly is robustly supported by nuclear multigene phylogenies, which suggest that the rhizaria are a basal outgroup to stramenopiles and alveolates. Ultrastructural synapomorphies are limited: stramenopile and alveolate taxa frequently contain two flagella, striated microtubular roots, and secondary red algal-derived chloroplasts that contain chlorophyll *c* and are encased by three to four membranes; mitochondrial cristae are predominantly tubular in all three taxa. Recently, a novel duplicated isoform of Rab1, a GTPase involved in ER-to-Golgi vesicle trafficking, has been identified in all three phyla, and may be a defining molecular synapomorphy, although there is weak evidence that this feature may be shared with some cryptomonads. The SAR clade contains a number of pathogenic and parasitic genera of major human interest,

including *Plasmodium* (causative agents of malaria) and *Phytophthora* (crop pathogens). Chloroplast gene phylogenies and the common presence of chlorophyll *c* strongly suggest a common origin for the chloroplasts of photosynthetic Stramenopiles, alveolates and CCTH/Hacrobia, and it is possible that the SAR clade and CCTH/Hacrobia are sister taxa that acquired a red algal chloroplast via a single, ancestral endosymbiosis. However, some nuclear multigene phylogenies have suggested that the SAR clade is in fact a basal offshoot of the CCTH/Hacrobia and archaeplastids and there is as yet no evidence that rhizaria historically contained a red algal endosymbiont lineage; as such, several alternative models- such as an origin of stramenopile and alveolate chloroplasts via the tertiary endosymbiosis of a haptophyte- have been suggested. (Baurain *et al.* 2010; Bodyl *et al.* 2009; Burki *et al.* 2009; Burki *et al.* 2007; Burki *et al.* 2008; Cavalier-Smith 2010; Elias *et al.* 2009; Hampl *et al.* 2009; Pawlowski and Burki 2009; Sanchez Puerta and Delwiche 2008)

STRAMENOPILES

A morphologically diverse clade, containing unicellular flagellate, amoeboid, mycelial and multicellular organisms. Flagella are of unequal length (the group is also called “heterokonts” because of this), and the long, mature flagellum carries tripartite tubular hairs that reverse the thrust of the flagellum. The flagellar apparatus contains up to four microtubular roots, and a striated rootlet is present in many taxa. Mitochondria have tubular cristae. Golgi bodies lie with forming faces adpressed to the nuclear envelope. Cell walls (where present) are made of cellulose. Chloroplasts are present in some but not all species; where present, they contain a distinctive girdle lamella consisting of three adpressed thylakoids that envelopes other lamellae. Chloroplasts themselves are enveloped by an outer membrane contiguous with the ER.

Stramenopiles may be autotrophic, mixotrophic and heterotrophic, and contain several parasites and pathogens of shellfish (*e.g. Aureococcus*), humans (*e.g. Blastocystis*) and higher plants (*Phytophthora*). Nuclear multigene phylogenies strongly support a sister-group relationship to the alveolates. Chloroplast gene phylogenies strongly support a red algal origin for all extant plastid lineages; however, the recent recovery of >1500 genes of green algal origin in sequenced diatoms, pelagophytes and oomycetes has led to the suggestion that stramenopiles may have historically contained a green algal endosymbiont, and/ or received repeated lateral gene transfers from green algal donors. (Andersen 2004; Atkins *et al.* 2000b; Burki *et al.* 2008; Dodge 1973; Guillou *et al.* 1999a; Massana *et al.* 2004; Moustafa *et al.* 2009; Nozaki *et al.* 2009; Patterson 1989, 1999; Reeb *et al.* 2009; Saunders *et al.* 1995; Van de Peer *et al.* 1996b; Van der Auwera *et al.* 1995)

Bicosoecids

Free-living heterotrophic flagellates with a posterior (smooth) flagellum which may attach to the substrate or lorica, and an anterior (usually hairy) flagellum directing currents of water over an ingestion area (a lip or a cytostome with cytopharynx) supported by a microtubular loop made of an L-shaped arrangement of microtubules, usually arranged as ‘8+3+x-fibre’. Basal bodies are at an oblique angle to each other, with BB1 oriented to the left; there are usually 4 microtubular roots with 2 additional singlet roots, in the same orientation in all taxa. A lorica may be present. The bicosoecids *Filos agilis* and *Nanos amicus* have been identified as epibionts of the chrysophyte *Apoikia lindahlia*, although whether this relationship is commensalist or parasitic is not fully understood.

Six major divisions of bicosoecid have been described from ultrastructural data: *Caecitellus* (naked flagellates with two unequal smooth flagella); *pseudodendromonads* (scaly or naked, colonial or free-living flagellates with two equal smooth flagella - *Adriamonas*, *Cyathobodo*, *Pseudodendromonas*); *Bicosoecidae* (loricate, solitary or colonial bicosoecids with two heterokont flagella, and a feeding collar, some with a paraxial rod in the posterior flagellum); *cafeteriates* (naked solitary bicosoecids with heterokont flagella and a feeding collar - *Cafeteria*, *Pseudobodo* and *Acronema*); *Siluania* (tiny solitary bicosoecid with a single hairy anterior flagellum and a reduced flagellar apparatus); and *Symbiomonas* (picoplanktonic flagellates with a single hairy anterior flagellum, endosymbiotic bacteria near the nucleus, tubulocristate mitochondria near the basal body, and a reduced flagellar apparatus). However, recent molecular data has implied that several of these divisions may be para- and or polyphyletic, with a basal division between freshwater and marine taxa. Molecular phylogenies weakly support a sister-group relationship with Placididea. (AlQassab *et al.* 2002; Atkins *et al.* 2000b; Cavalier-Smith and Chao 2006; Fenchel and Patterson 1988; Guillou *et al.* 1999a; Hibberd and Norris 1984; Hibberd 1976a, 1978, 1985; Karpov *et al.* 1998; Karpov *et al.* 2001; Kim *et al.* 2010; Kostka *et al.* 2004; Leipe *et al.* 1994; Massana *et al.* 2004; Mignot 1974b, 1974a; Moestrup and Thomsen 1976; Moriya *et al.* 2002; O’Kelly and Nerad 1998; O’Kelly and Patterson 1996; Park and Simpson 2010; Patron *et al.* 2007; Patterson *et al.* 1993a; Strüder-Kypke and Hausmann 1998; Teal *et al.* 1998; Verhagen *et al.* 1994)

Commaton

Heterotrophic gliding flagellates with a circular-oval (comma shaped) flattened cell body, and a proboscis. The single emergent flagellum bears tripartite hairs; two basal bodies have distinct microtubular roots and a rhizoplast. No molecular information is available for this group. (Thomsen and Larsen 1993)

Diplophrys

Small spherical aflagellate organisms with a scaly cell wall similar to thraustochytrids, an orange lipid droplet in the cell body, and tufts of pseudopodia arising from openings in the cell wall, which have been interpreted as similar to the ectoplasmic network of other labyrinthulids. Molecular data weakly supports a sister-group relationship with the labyrinthulomycetes, but the extreme divergence observed for *Diplophrys* render this classification uncertain. (Cavalier-Smith and Chao 2006; Dykstra and Porter 1984)

Labyrinthulids

Saprotrophic and heterotrophic stramenopiles with a cosmopolitan distribution across marine, freshwater and terrestrial habitats. Vegetative cells characteristically contain a sagenogenetosome (or bothrosome), an organelle which secretes a specialised ectoplasmic network that may be involved in adhesion and feeding; zoospores are biflagellate. Species have been identified on the surface mucilage of several marine invertebrate phyla, and have been suggested to form various symbioses based on fatty acid exchange. A parasitic relationship has been observed between the species *Thraustochytrium caudivorum* and its flatworm host, whereas the soil-borne *Labyrinthula terrestris* has been implicated as a causative agent of late blight in turf grass.

Molecular studies indicate that there are three major clades within the group: labyrinthulids (aflagellated spindle-shaped cells which are enclosed in single file by the ectoplasmic network, with a lipid body or eyespot present in the zoospore stages); thraustochytrids (solitary and immobile aflagellated cells, with multi-laminar scaly walls and globose sporangia, a small ectoplasmic rhizoidal network, and zoospores lacking an eyespot); and aplanochytrids (solitary aflagellated cells with multi-laminar scaly walls and globose sporangia, and ectoplasmic filaments which do not enclose the cells). The position of labyrinthulomycetes within the stramenopiles is unclear; molecular studies have weakly supported sister-taxon relationships to opalinids and to bicosoecids, and an early-branching position at the base of all other stramenopiles. (Alderman *et al.* 1979; Bahnweg and Sparrow 1972; Barr and Allan 1985; Bigelow *et al.* 2005; Cavalier-Smith and Chao 2006; Harel *et al.* 2008; Honda *et al.* 1999; Kazama 1972, 1980; Leander and Porter 2001; Leander *et al.* 2004; Leipe *et al.* 1996; Leipe *et al.* 1994; Moss 1985; Porter 1974; Riisberg *et al.* 2009; Scharer *et al.* 2007; Siboni *et al.* 2010; Tsui *et al.* 2009)

Pirsonia

Parasitoid flagellates that infect planktonic diatoms by injecting a pseudopodium through the host's frustule, then differentiating and budding. Motile flagellates have an anterior flagellum with tripartite hairs; the posterior flagellum and cell surface bear "knotted hairs". Mitochondria bear unique "straight" tubular cristae. Recent SSU data weakly supports a close relationship between *Pirsonia* and oomycetes. (Kim *et al.* 2010; Kühn *et al.* 2004; Kühn *et al.* 1996; Schnepf and Schweikert 1996; Schweikert and Schnepf 1997)

Placididea

Heterotrophic gliding flagellates with two unequal flagella containing a double helix in the transitional region; anterior flagellum bearing tubular hairs with two unequal terminal filaments; posterior flagellum attaching to the substrate. Mitochondria with tubular cristae. With a distinctive u-shaped microtubular root in an L-shaped "7+3" arrangement very similar to that seen in bicosoecids. The group includes *Wobblia*, *Placidia* and possibly *Pendulomonas*, though further investigation is needed. Molecular analyses place the group in a clade with bicosoecids and slopalinids. (Moriya *et al.* 2000, 2002)

Rictus

Small, benthic flagellates, with two flagella of uneven length, and a permanent cytostome that engages in feeding. Mitochondrial cristae are swollen, and chloroplasts are not present. A single species, *R. lutensis*, has been described. Similarities in the flagellar apparatus and organisation of microtubular roots, and SSU phylogenies weakly support a relationship with the bicosoecids, but a lorica was not observed, and the ultimate phylogenetic position remains unknown (Yubuki *et al.* 2010)

Sloomycetes

"Zoosporic fungi" (rhizoidal stramenopiles) with a flagellated zoospore stage which has a double helix in the flagellar transition zone. Cell walls are generally made of cellulose (though at least one taxon has chitin synthase genes, suggesting that chitin may be in the walls); lysine is made by the DAP pathway (as opposed to AAA pathway in true fungi). Storage products are glycogen and mycolaminarin;

lanosterol is synthesised directly from squalene oxide. A number of oomycete taxa (e.g. *Phytophthora*, *Aphanomyces*, *Sclerophthora*) are major biotrophic pathogens of higher plants.

Three major divisions are known: hypochoytrids (saprophytes with a lifecycle consisting of a stationary multinucleated rhizoidal thallus stage, and unflagellated zoospores with characteristic flagellar hairs); Developayella (marine heterotrophic flagellates, with a hairy anterior flagellum and smooth posterior flagellum both inserting into a deep right anterior ventral groove, which may either swim by flagellar motion, or attach to substratum via strands of cytoplasm); and Oomycetes/Peronosporomycetes (saprophytes with a lifecycle consisting of coenocytic hyphae, sexual mycelia and gametangia, and asexual biflagellate zoospores with distinctive, swollen basal body transitional plates, which are situated above the anterior flagellar insertion points). Complete genomic sequences and partial proteomic maps are available for three pathogenic oomycetes: *Phytophthora infestans* (the causative agent of potato blight), *P. ramorum* (sudden oak death) and *P. sojae* (soybean pathogen). Preliminary sequence analyses have revealed rapid rates of genome evolution, and the convergent evolution of a number of classes of proteins- e.g. cysteine protease inhibitors- with parasitic and hemibiotrophic fungi. Molecular data consistently suggests that, of all the major nonphotosynthetic stramenopile taxa, sloomycetes are the most closely related to the photosynthetic stramenochromes. The name is a contraction of “*sensu lato* oomycetes”. (Adl *et al.* 2005; Andersen 2004; Andersson and Roger 2002; Barr 1983; Barr and Allan 1985; Barr and Désaulniers 1989; Bartnicki-Garcia 1987; Ben Ali *et al.* 2002; Bhadauria *et al.* 2010; Dodds *et al.* 2009; Guillou *et al.* 1999a; Haas *et al.* 2009; Hausner *et al.* 2000; Kim *et al.* 2010; Leipe *et al.* 1996; Moriya *et al.* 2000, 2002; Mort-Bontemps *et al.* 1997; Mülisch 1993; Patterson 1999; Riisberg *et al.* 2009; Tong 1995; Tsui *et al.* 2009; Tyler *et al.* 2006; Van der Auwera *et al.* 1995)

Slopalinids

Flagellated stramenopiles with a ridged cell surface, which is supported by microtubular ribbons under the cell surface; with an amorphous fibre between the plasma membrane and terminal microtubule at the crest of each ridge; characteristic “struts” extending from the flagellar basal body to the cell surface; with a double-stranded helix in the flagellar transition zone. Several taxa are known to be endosymbionts of animals. Opalinids are intestinal commensals of cold-blooded vertebrates, with a complex life cycle intimately interconnected with hormonal secretions and thus the life cycle of the host. *Blastocystis* has been suggested to be an opportunistic parasite, which may infect humans by zoonosis, and is particularly associated with HIV infection; however, its significance as a potential pathogen remains poorly resolved.

Three major divisions are known, determined both from ultrastructure and (in the case of *Blastocystis*) SSU rRNA phylogenies: Opalinids (cigar-shaped or flattened slopalinids with many oblique rows of flagella, arising from an anterior morphogenetic centre, on ridges over the cell surface, and with two or more monomorphic nuclei); Proteromonads (flagellates with cell surface ridges supported by bands of microtubules, and with a multiplicative cyst with a central reproductive vacuole); and Blastocystis (aflagellated, anaerobic amoeboid organisms, with a characteristic crescent cap of heterochromatin around the nucleus, tubulocristate mitochondria, and lacking cytochromes, catalase and peroxidase). Molecular phylogenies suggest a sister-group relationship to

bicosoecids and placididea. The name is a contraction of “*sensu lato* opalinids.” (Brugerolle and Joyon 1975; Cavalier-Smith and Chao 2006; Iguchi *et al.* 2009; Kim *et al.* 2010; Kostka *et al.* 2004; Leipe *et al.* 1996; Nishi *et al.* 2005; Noel *et al.* 2005; Patron *et al.* 2006; Patterson 1985b, 1985a, 1988, 1989; Silberman *et al.* 1996; Stenzel *et al.* 1991; Zierdt 1986)

Stramenochromes

“Brown algae” *sensu lato*, unicellular or multicellular stramenopiles with chloroplasts containing chlorophylls a and c, and a distinctive girdle lamella consisting of three adpressed thylakoids; chloroplasts are surrounded by three or four membranes, the outermost of which is contiguous with the ER. Nonphotosynthetic lineages are believed to have originated via the secondary loss of chloroplasts from photosynthetic ancestors. Stramenochromes utilise a conserved, novel blue light “aureochrome” receptor, which may be involved in determining sexual versus vegetative reproductive strategies. A number of stramenochrome taxa have been identified as epibiotic or soil-borne symbionts of plants; it has been speculated that at least some of these relationships may be parasitic, pathogenic or opportunistic, but evidence for this is limited. Molecular phylogenies consistently recover moderate support for stramenochrome monophyly. (Bent *et al.* 2009; Ishikawa *et al.* 2009; Kim *et al.* 2010; Kostka *et al.* 2004; Patterson 1999, 2000; Riisberg *et al.* 2009; Takahashi *et al.* 2007b)

Actinophryids

“Heliozoan”, aflagellated, principally freshwater heterotrophic stramenochromes. Each arm is supported by a double polygonal spiral of microtubules which arises from differentiated areas on the nuclear membrane, and contains two distinct size classes of extrusome involved in prey capture. Contraction of the nuclear membrane, disruption of supporting microtubules, movement of arms and possibly expulsion of extrusomes are Ca²⁺-dependent. Siliceous plates or aggregates cover encysted cells. Chloroplasts are probably secondarily absent. Their heliozoan structure suggests a relationship with Dictyochophytes, whereas SSU data strongly supports a close relationship with the pelagophytes. (Arikawa *et al.* 2006; Arikawa *et al.* 2005; Cavalier-Smith and Chao 2006; Kakuta and Suzaki 2008; Nikolaev *et al.* 2004; Patterson 1979, 1986; Smith and Patterson 1986)

Aureanophytes

Unicellular, heterokont flagellates, with alternate sessile and swimming forms. Flagella are retained during the sessile stage underneath the cellulose cell wall. The longer flagellum bears tripartite tubular hairs; the shorter flagellum is smooth. Four flagellar roots are present, and a rhizoplast connects the basal body to the anterior end of the nucleus. Chloroplasts are central, lack a girdle lamella; the chloroplast DNA has a scattered genophore. Chloroplasts are arranged in pairs; each single chloroplast is surrounded by three membranes, and share a communal, fourth outer membrane between each pair. A single species, *Aurearena cruciata*, has been described, from intertidal habitats. Molecular data supports a sister-group relationship to the phaeothamniophytes. (Kai *et al.* 2008)

Bolidophytes

Small naked stramenochromes with a long hairy and a short smooth acronematic flagellum. Flagellar rootlets are absent, and there is no transitional helix, distinguishing this taxon from many other stramenochromes. There is one mitochondrion and one Golgi body. The single chloroplast has a girdle lamella, but lacks an eyespot; plastid DNA has a ring-type genophore. Molecular data suggests bolidophytes may be related to diatoms. (Cavalier-Smith and Chao 2006; Daugbjerg and Guillou 2001; Guillou *et al.* 1999a; Guillou *et al.* 1999b; Kim *et al.* 2010)

Chrysomerophytes

Stramenochromes with alternate multicellular filamentous and unicellular zoospore stages. The filamentous stage has cellulose cell walls which lack alginates, plasmodesmata and unilocular sporangia, thus separating the group from the phaeophytes. Zoospores lack a theca but are otherwise very similar to those of phaeophytes, having typical stramenopile flagella with four flagellar rootlets. There is a transitional helix above the plate in the flagellar transition zone. The chloroplast contains an eyespot of red lipid granules, situated at the base of the smooth flagellum; plastid DNA has a ring-type genophore. Molecular data moderately supports a basal position to the xanthophytes and phaeophytes. (Andersen 2004; Cavalier-Smith and Chao 2006; Kim *et al.* 2010; O’Kelly 1989; O’Kelly and Floyd 1985; Saunders *et al.* 1997)

Chrysophytes

Phototrophic or secondarily heterotrophic stramenochromes, occurring as free-swimming or sessile, solitary or colonial flagellates, amoeboid, coccoid, capsoid, filamentous, and parenchymatous forms; with terminal filaments on the hairs of the anterior hairy flagellum in zoospores (as in Synurales), and with a sophisticated arrangement of posteriorly-directed microtubular roots R3 and R4 in a feeding basket (which is superficially similar to that of bicosoecids). There are four microtubular roots. There is a transitional helix with 4-6 gyres above the plate in the flagellar transition zone, and a rhizoplast (striated flagellar root), attaching the nucleus to the immature basal body. Cells may be naked or covered by cellulose cell walls, gelatinous coverings, organic loricas, organic or silica scales. The chloroplast contains an eyespot of red lipid granules, situated at the base of the smooth flagellum, and has plastid DNA with a ring-type genophore; leucoplasts are present in taxa which lack chloroplasts. Species have predominantly been identified in freshwater habits, although taxa have been identified in ice samples, and as epibionts on polar and carnivorous plants.

The name Chrysophytes has referred in the past to much wider groups than its current sense, which only includes Chromulinales (swimming cells with only one flagellum visible- *Chromulina* and *Chrysomonas*), *Hibberdia* (swimming cells with only one flagellum visible, three microtubular roots), *Chlamydomyxa* (heterokont algae with aplanospore and plasmodial stages), paraphysomonads (unpigmented chrysophytes) and ochromonads (swimming cells with two flagella visible). Chrysophytes appear not to utilise an active carbon concentrating mechanism. Genomic sequences are not yet available; however, EST libraries have been constructed for *Ochromonas danica*. Molecular and morphological data suggest relationships with the Synurales and the

eustigmatophytes. (Andersen 1989, 2004; Andersen *et al.* 1999; Andersen and Wetherbee 1992; Ben Ali *et al.* 2002; Bouck 1972; Bourrelly 1966; Brugerolle and Mignot 2003; Heywood and Leedale 2002; Hibberd 1976a, 1978; Hibberd 1986; Kawai and Kreimer 2000; Kim *et al.* 2010; Leipe *et al.* 1996; Leipe *et al.* 1994; Maberly *et al.* 2009; Mignot 1977; Mignot and Brugerolle 1982; O’Kelly and Wujek 2001; Pearlmutter and Timpano 1984; Plancho and Wolowski 2008; Preisig and Hibberd 1982a, 1982b, 1983; Riisberg *et al.* 2009; Terauchi *et al.* 2010; Wenderoth *et al.* 1999)

Diatoms

“Glass-box” organisms, the source of diatomaceous earth; also called Bacillariophytes. Unicellular or colonial coccoid stramenochromes, where each vegetative cell lacks flagella, and is encased by a frustule (a box with a lid the same shape- *i.e.* two valves, along with girdle bands between the valves- all of which is a cell wall composed of bands or porous plates of silica). Spermatozoids are the only flagellated cells. Their single anterior hairy flagellum that lacks flagellar rootlets and the central pair of axonemal microtubules, and a transitional helix; it has a single basal body composed of microtubular doublets. Chloroplasts are golden-brown, have four membranes, lack an eyespot, have lamellae of three thylakoids, and have DNA in a ring-shaped nucleoid; some taxa (*Rhopalodia*, *Denticula*, *Epithemia*) additionally have colourless prokaryote-like endocytobionts that have been called cyanelles. The chloroplast ER characteristic of many other stramenopiles is absent from taxa with multiple chloroplasts; pyrenoids are absent from some lineages. The life cycle is diplontic and shows a slow size reduction over years because of repeated new cell wall formation inside the old rigid wall, then a fast size increase in the auxospore stage. The group is extremely speciose with over 10000 species, accounting for nearly half of recorded algal species diversity, is the dominant component of algal communities in temperate and subpolar oceans, and is as such believed to be a substantial contributor to planetary photosynthetic CO₂ assimilation. A number of diatom taxa are currently under investigation for potential use in a number of bioindustries, including biofuels and bionanotechnology. Several dinoflagellates contain tertiary, diatom-derived endosymbionts, and one endosymbiont lineage- of *Durinskia baltica* and *Kryptoperidinium foliaceum*- retains a nucleomorph and its own endogenous mitochondria.

Traditionally subgroups have been based on morphology, divided into centric (radially symmetrical) and pennate (bilaterally symmetrical). Centric diatoms are paraphyletic, and molecular groups only partly overlap with traditional groups, so subdivisions are likely to change. The two major subdivisions are currently the paraphyletic Coscinodiscophytina (circular or elliptical valves with patterns radiating from the central or subcentral annulus; girdle bands hoop-like or segmented; multiple small chloroplasts; oogamous reproduction with nonmotile eggs and flagellated sperm; auxospores with scales), and monophyletic Bacillariophytina (bilaterally or multilaterally symmetrical valves, with pattern radiating from a central elongate annulus or from a sternum; mucilage secretion occurring through special pores or slits in the cell wall; girdle bands hoop-like; few or a single chloroplast; oogamous (nonmotile eggs, flagellated sperm) or isogamous (amoeboid cells) reproduction; auxospores with band-like elements). Genome sequences are available for the

model centric and pennate species *Thalassiosira pseudonana* and *Phaeodactylum tricornutum*, and for the psychrophilic pennate diatom *Fragilariopsis cylindrus*. Early analyses of diatom genomes, transcriptomes and proteomes have revealed a number of diatom-specific and species-specific features, including genes encoding a complete urease cycle, ferritins, a structurally novel class of ice-binding proteins, and the use of a PEPC/ PEPCK-based C₄ photoassimilatory system. Diatoms are linked to Bolidophytes and Pelagophytes by SSU rRNA phylogenies (and possibly the reduced flagellar apparatus), but relationships with all other stramenochromes are unclear. (Andersen 2004; Andersen *et al.* 1998; Armbrust *et al.* 2004; Bayer-Giraldi *et al.* 2010; Bowman *et al.* 1992; Cavalier-Smith and Chao 2006; Chesnick *et al.* 1997; Daugbjerg and Guillou 2001; Guillou *et al.* 1999b; Heath and Darley 1972; Imanian and Keeling 2007; Janech *et al.* 2006; Kies 1992; Kim *et al.* 2010; Kooistra *et al.* 2003; Kroger and Poulsen 2008; Manton and von Stosch 1966; Marchetti *et al.* 2009; Medlin and Kaczmarska 2004; Moestrup 1982; Reinfelder *et al.* 2000; Round *et al.* 1990; Simon *et al.* 2009; Sorhannus 2001; Tamura *et al.* 2005; Van den Hoek *et al.* 1995; Van der Auwera and de Wachter 1997; Whitton 1973)

Dictyochophytes

“Heliozoan” stramenochromes with microtubular axonemes extending out from the surface of the nucleus to support radiating pseudopodial “arms” external to the cell body. The arms are supported by microtubules which arise either singly or in threes from differentiated areas on the nuclear membrane. Plastid DNA has a scattered granule-type genophore. Cells are naked or have a siliceous skeleton. When present in the flagellar apparatus, the transitional helix has up to 2 gyres below the transitional plate. The group includes dictyochids (known from the fossil record; photosynthetic, with a uniflagellated stage which has a siliceous exoskeleton and anastomosing cytoplasmic arms with peripheral chloroplast-containing lobes extending from the cell body; and a spherical biflagellated stage with a hairy anterior flagellum); pedinellids (photosynthetic and nonphotosynthetic, with microtubular triads supporting arms which radiate in a ring around the flagellum or over the entire body, a single long hairy flagellum which has a paraxial vane, and inserts in a pit, a basal bodies attached to the nuclear envelope); and Rhizochromulinales (photosynthetic, with an aflagellated trophic stage with very long, fine, beaded filopodia and a single chloroplast, and a zoospore stage with elongated cells bearing a single anterior hairy flagellum which inserts apically). Flagellar morphology, the absence of a chloroplast eyespot, presence of chlorophyll c₃, and molecular phylogenies, all support a close relationship with the pelagophytes. (Andersen 2004; Ben Ali *et al.* 2002; Daugbjerg 1996b, 1996a; Daugbjerg 2001; Guillou *et al.* 1999b; Hibberd 1979; Kim *et al.* 2010; Larsen 1985; Moestrup 1995; Moestrup and Thomsen 1990; O’Kelly and Wujek 1995; Patterson and Fenchel 1985; Riisberg *et al.* 2009; Saunders *et al.* 1995; Sekiguchi *et al.* 2003; Sekiguchi *et al.* 2002; Silva 1980; Smith and Patterson 1986; Van de Peer *et al.* 1996b; Van den Hoek *et al.* 1995; Van Valkenburg 1971a, 1971b; Zimmermann *et al.* 1984)

Eustigmatophytes

Cocoid unicellular marine and freshwater stramenochromes occurring as single cells or colonies, with polysaccharide cell walls. Zoospores have two flagella,

inserting apically. There is a transitional helix with six gyres above the plate in the flagellar transition zone. There are four microtubular roots, and a rhizoplast (striated flagellar root) attaching the nucleus to the immature basal body. Zoospores have a distinctive large orange-red eyespot made of carotenoid-containing globules free in the cytoplasm, located outside the chloroplast but adjacent to the mature flagellum. Chloroplasts are yellow-green, have a stalked pyrenoid on the inner side, in coccoid cells; girdle lamellae are absent; the outermost chloroplast membrane is contiguous with the ER and outer nuclear envelope. Mitosis is closed, and is dependent on barrel- and boomerang-shaped pole bodies speculated to be morphologically unique MTOCs; the inner nuclear membrane envelope divides prior to the outer nuclear envelope. Chlorophyll c is absent, and violaxanthin is used as a light-harvesting pigment. Eustigmatophytes are under particular investigation as candidate taxa for biofuel production, but no genome projects are underway. There is weak molecular support for a close relationship with the chrysophytes. (Andersen 2004; Andersen *et al.* 1998; Ben Ali *et al.* 2002; Cavalier-Smith and Chao 2006; Guillou *et al.* 1999b; Hibberd 1990b; Hibberd and Leedale 1970, 1971, 1972; Kawai and Kreimer 2000; Murakami and Hashimoto 2009; Riisberg *et al.* 2009; Rodolfi *et al.* 2009)

Pelagophytes

A diverse array of free-swimming flagellates, coccoid planktonic cells and attached filamentous and palmelloid colonial stramenochromes, some of which are known to cause “brown tide” algal blooms. The flagellar apparatus is highly reduced, consisting of a single hairy anterior flagellum with a dentate paraxial rod (in *Pelagomonas*), or two flagella of uneven length (in other taxa). The basal bodies are adpressed to the nucleus; there are no microtubular roots on uniflagellate cells and four roots on biflagellated cells. Flagellar hairs are bipartite but function the same way as in other stramenopiles. Cells may be naked, or covered with a thin organic theca, a cell wall, or a gelatinous layer. The group includes pelagomonads (uniflagellated or coccoid organisms) and sarcinochrysids (sarcinoid, capsoid, biflagellate or filamentous organisms with an organic cell wall). A genome sequence is available for *Aureococcus anophagefferens*, the dominant planktonic component of studied brown tides, and preliminary investigation has revealed a potential lateral gene transfer of a pelagophyte methionine adenosyltransferase into haptophytes. Pelagophytes are linked to dictyochids by the presence of chlorophyll c3, and by molecular phylogenies. (Andersen 2004; Andersen *et al.* 1993; Bailey and Andersen 1999; Gobler *et al.* 2005; Guidi *et al.* 2003; Guillou *et al.* 1999b; Heimann *et al.* 1995; Kamikawa *et al.* 2009; Riisberg *et al.* 2009; Saunders *et al.* 1995)

Phaeophytes

“Brown algae” *sensu stricto* or kelps – *e.g.* *Fucus*, *Hormosira*, *Sargassum*, *Laminaria* - large, structurally and developmentally complex multicellular stramenochromes. Thallus morphology varies from microscopic and filamentous to parenchymatous kelps many metres long. Most taxa have heteromorphic life cycles. With cell walls made of cellulose impregnated with alginates; cells are interconnected via plasmodesmata (a situation unique in the stramenopiles). Zoospores have two flagella inserting laterally (most other stramenopiles have flagella inserting subapically), and lacking transitional helices. Chloroplasts are

golden-brown, discoid, small and scattered throughout the cell; pyrenoids are absent from Dictyotales, Fucales, Laminariales and Sphacelariales, distinguishing them from the other eight major groups within the phaeophytes. Plastid DNA has a ring-type genophore; chloroplasts have a girdle lamella and an endoplasmic reticulum connection to the nucleus. In most taxa there is a typical stramenopile eyespot in the chloroplast with a flagellar swelling on the mature flagellum.

Twelve major divisions are currently recognised based on ultrastructure: Ascoseriales (parenchymatous sporophytes with intercalary growth, non-freeliving gametophytes and isogamous sexual reproduction), Cutleriales (small parenchymatous sporophytes growing apically and large male and female gametophytes growing trichothallically), Desmarestiales (pseudoparenchymatous large sporophytes, filamentous small gametophytes, trichothallic growth, and öogamous sexual reproduction), Dictyotales (parenchymatous gametophyte and sporophyte, growing apically or marginally, an isomorphic life cycle, and öogamous sexual reproduction), Ectocarpales (uniseriate filamentous gametophyte and sporophyte with ribbon-shaped plastids, an isomorphic life cycle, isogamous, öogamous or anisogamous reproduction), Fucales (parenchymatous diploid sporophytes which produce gametes by meiosis, no gametophyte stage, and öogamous reproduction), Ishige (isomorphic life cycle with alternation of generations, pseudoparenchymatous cortex with apical growth, terminal unilocular or seriate plurilocular sporangia and assimilatory filaments in cryptostigmata), Laminariales (small filamentous apically-growing gametophytes, large, parenchymatous sporophytes with intercalary growth, and öogamous sexual reproduction, sometimes with flagellated eggs), Scytothamnales (large parenchymatous gametophytes with intercalary growth, small filamentous sporophytes with apical growth, heteromorphic alternation of generations, stellate or axial plastids, and anisogamous reproduction), Sphacelariales (isomorphic alternation of generations with multiseriate filamentous gametophytes and sporophytes with apical growth, and with isogamous, anisogamous, or öogamous reproduction), Sporochnales (pseudoparenchymatous small gametophyte and large sporophyte with trichothallic growth, alternation of generations, and öogamous sexual reproduction), Syringodermatales (gametophyte stage with 2-4 cells, not free-living, parenchymatous sporophytes with apical and marginal growth, alternation of generations, and isogamous reproduction), and Tilopteridales (isomorphic alternation of generations with thallus growing from a trichothallic meristem, and öogamous sexual reproduction). Molecular analyses have suggested that a number of these divisions may be para- or polyphyletic. Mitochondrial and chloroplast sequences are available for several taxa, and a complete genome has been assembled for the filamentous phaeophyte *Ectocarpus siliculosus*. Preliminary analyses of phaeophyte genomes have revealed extensive lateral gene and intron transfers in some mitochondrial lineages, and potential instances of convergent evolution with multicellular archaeplastids and opisthokonts, such as rapidly diversified families of LRR- and TPR-domain proteins involved in pathogen sensing, and a flavonoid biosynthesis pathway that may be involved in UV protection. Molecular studies suggest a relationship between Phaeophytes and Xanthophytes. (Andersen 2004; Ben Ali *et al.* 2002; Bisalputra 1966; Cock *et al.* 2010; Draisma *et al.* 2001; Guillou *et al.* 1999b; Ikuta *et al.* 2008; Kawai *et al.* 2007; Le Corguillé *et*

al. 2009; Motomura and Sakai 1988; Oudot-Le Secq *et al.* 2001; Oudot-Le Secq *et al.* 2006; Pueschel and Stein 1983; Riisberg *et al.* 2009; Rousseau *et al.* 2001; Van den Hoek *et al.* 1995)

Phaeothamniophytes

Branching filamentous stramenochromes with similarities to Phaeophytes. Cell walls are single or lamellate in two pieces; siliceous cysts are absent. In zoospores, the flagella insert ventrally about 1/3 of the way down from the anterior end. The hairs on the immature (anterior) flagellum lack terminal filaments. There is a transitional helix above the plate in the flagellar transition zone; a striated flagellar root connects the basal bodies but does not extend to the nucleus. Cells contain one to three golden chloroplasts which lack pyrenoids but have a girdle lamella and plastid DNA with a ring-type genophore. There is an eyespot in the chloroplast associated with R4, a posteriorly directed microtubular rootlet arising from the mature basal body. The group includes the molecularly-recognised clades phaeothamniates and pleurochloridellates; molecular data strongly support a sister-group relationship to aureanophytes, and close relationships with phaeophytes and xanthophytes. (Andersen *et al.* 1998a; Andersen *et al.* 1999; Bailey *et al.* 1998; Kai *et al.* 2008; Riisberg *et al.* 2009)

Parmales

Tiny aflagellated coccoid marine phytoplanktonic cells, characterised by large round and triradiate siliceous plates forming walls which surround the protoplasm. A large chloroplast is present, and the outermost membrane is contiguous with the endoplasmic reticulum. Three genera have been described from field isolates from polar and subpolar oceans: no cultures exist, and flagellate stages have not been identified. A close relationship to chrysophytes has been postulated on morphological grounds, but no molecular information has been obtained for this taxon. (Booth and Marchant 1987, 1988; Bravo-Sierra and Hernández-Becerril 2003; Konno and Jordan 2007; Kosman *et al.* 1993; Marchant and McEldowney 1986)

Picophagea

Tiny, naked biflagellates; cells are phagotrophic and do not appear to contain chloroplasts. Flagella are of uneven length and insert anteriorly at 90° to each other; two terminal filaments are present on each flagellar hair. As compared to chrysophytes, picophagid cells lack a transitional helix, have only two flagellar roots, homologous to roots 1 and 3 of chrysophytes, and lack a rhizoplast. The nucleus is located above the basal body of the long flagellum. Historically classified as chrysophytes, recent molecular analyses have suggested that picophagea may be a basal offshoot of chrysophytes and synchronophytes. (Guillou *et al.* 1999a; Patil *et al.* 2009)

Pinguiphytes

Marine microalgal and colonial stramenochromes, which may be naked, with a gelatinous covering or a mineralized lorica. Species may be aflagellated, or with two heterokont flagella; or with only one smooth mature flagellum, a situation unique in the stramenopiles. Proximal to the flagellar transition zone there are

two rings either side of a helix, in some taxa; in others, there is a transitional helix above the single plate. There are three or four microtubular roots, and a rhizoplast (striated flagellar root) attaches the nucleus to the immature basal body. Chloroplasts have a girdle lamella and surrounding endoplasmic reticulum; there is no eyespot; plastid DNA has a scattered granule-type genophore. Pinguiphytes are of particular interest due to the large quantities of high-value polyunsaturated fatty acids- in particular eicosapentenoic acid- produced. Molecular phylogenies have suggested a close relationship to the pelagophytes, but with minimal support. (Andersen *et al.* 2002; Ben Ali *et al.* 2002; Honda and Inouye 2002; Hsiao and Blanch 2006; Kawachi *et al.* 2002a; Kawachi *et al.* 2002b; Kawachi *et al.* 2002c; Kostka *et al.* 2004; Magne 1975; O'Kelly 2002)

Raphidophytes

Large, unicellular, ovoid, rounded or club-shaped naked flagellates. The two flagella insert into a sub-apical pit on the ventral side, the immature hairy flagellum pointing forwards and the mature smooth one directed posteriorly in a ventral groove. There is no transitional helix in the flagellum. There is a compound microtubular root with a multilayered structure. A rhizoplast (striated flagellar root) is present, attaching the nucleus to the immature basal body. The Golgi is situated over the anterior surface of the nucleus. Cells contain seven or more green, yellow-green or yellow-brown ellipsoidal chloroplasts, which may either be radially distributed, with thylakoids vertical to the cell surface (*Chattonella*) or peripheral, with thylakoids parallel to the cell surface (all other taxa). Chloroplasts lack eyespots and the chloroplast ER characteristic of other stramenopiles; the DNA has a ring-shaped genophore. Chloroplasts are interspersed with mucus-discharging cysts beneath the cell membrane, which may be associated with cell hairs. Some species, such as the widely studied *Heterosigma*, form blooms or 'red tides' and may be toxic, and a range of bidirectional allelopathic interactions have been identified between raphidophytes and sympatric bacteria, diatoms and dinoflagellates. Molecular data suggests that raphidophytes are a basal relative to xanthophytes and phaeophytes. (Andersen 2004; Andersen *et al.* 1999; Ben Ali *et al.* 2002; Hara and Chihara 1985; Heywood and Leedale 2002; Kim *et al.* 2007; Potter *et al.* 1997; Riisberg *et al.* 2009; Sorhannus 2001; van Rijssel *et al.* 2008; Vesik and Moestrup 1987; Yamaguchi *et al.* 2010; Yamasaki *et al.* 2007)

Schizocladia

Marine filamentous stramenopiles with a zoospore stage. The vegetative thallus is made up of branched filaments; vegetative cells give rise to flagellated unicellular zoospores with heterokont flagella, with the anterior (long) flagellum bearing tripartite hairs and the smooth posterior flagellum having a basal swelling associated with the eyespot in the chloroplast. Flagella have a single transitional basal plate and a 5 or 6- gyred transitional helix distal to the plate. The chloroplast has a girdle lamella and plastid DNA has a ring-type genophore. Cell walls are impregnated with alginates but lack cellulose and plasmodesmata, thus distinguishing the group from filamentous phaeophytes. Molecular studies strongly support a sister-group relationship to the Phaeophytes. (Andersen 2004; Kawai *et al.* 2003; Kim *et al.* 2010; Phillips *et al.* 2008)

Synchromophytes

Mobile, floating and sessile mixotrophic or heterotrophic stramenochromes; all studied cells are amoeboid or encysted, and no flagella have been identified in any lineage. Pseudopodia project from a hyaline cortical cytoplasm. Chloroplasts, where present, are yellow-green, contain chlorophylls a and c2, are enveloped by two inner membranes, and are clustered in complexes of three to four, encased in two communal outer membranes, of which the outermost is contiguous with the endoplasmic reticulum. Golgi vesicles may be absent. Mitochondria in some cells are surrounded by vesicular bodies containing bacteria; these are hypothesised to be endobionts. Originally described as a single photosynthetic genus, *Synchroma*, identified from littoral habitats; recent molecular studies have incorporated two previously identified freshwater genera, the phototroph *Chlamydomyxa* and the heterotroph *Leukarachnion*; this composite class is currently without an agreed name. Molecular phylogenies suggest a probable sister-group relationship to chrysophytes and synurales. (Grant *et al.* 2009; Horn *et al.* 2007; Patil *et al.* 2009; Wenderoth *et al.* 1999)

Synurales

Flagellated stramenochromes, principally limited to high-pH, freshwater habitats, although a number of taxa have been identified as stomatocystic epibionts of Antarctic mosses. Cells have a distinctive, bilaterally symmetrical arrangement of silica scales, which have taxonomic value. Species have typical heterokont flagella, or a single immature hairy flagellum; flagellar hairs are tripartite, and the central shaft of each hair is covered with lateral fibres, as in the Chrysophytes. There is a transitional helix with 6-9 gyres above the plate in the flagellar transition zone; the flagellar apparatus contains 2-4 microtubular roots and a rhizoplast (striated root) which attaches the nucleus to both basal bodies. Chloroplasts lack chlorophyll c2, and the chloroplast ER characteristic of stramenopiles. There is no eyespot; plastid DNA has a ring-type genophore. Synurales appear not to utilise an active carbon concentrating mechanism. Morphology and molecular studies of SSU rRNA and *rbcL* indicate a relationship between Synurales and Chrysophytes. (Andersen 1987; Andersen 1989, 2004; Beech and Wetherbee 1990b; Beech and Wetherbee 1990a; Bhatti and Colman 2008; Coradeghini and Vigna 2008; Guillou *et al.* 1999a; Ludwig *et al.* 1996; Moestrup 1995; Neustupa and Nemcova 2007; Potter *et al.* 1997)

Xanthophytes

Yellow-green stramenochromes, with a variety of forms: predominantly coccoid cells with a cell wall or filamentous, multicellular forms with a cell wall made of H-shaped overlapping sections; or siphonous forms with branching multinucleate rhizoidal protoplast tubes. More rarely they exist as unicellular flagellates which form pseudopodia, amoebae, or tetrasporal colonies in a mucous sheath. In flagellates, flagella insert subapically and there is a double transitional helix with 6 gyres above the plate in the flagellar transition zone. There are four microtubular roots. A rhizoplast (striated flagellar root) is present, attaching the nucleus to the immature basal body. There is a typical stramenopile eyespot in the chloroplast with a flagellar swelling on the mature flagellum. Chloroplasts are discoid and green or yellow-green; plastid DNA has a ring-type genophore. Principally free-living in freshwater and marine habitats;

however, *Vaucheria karachiensis* has been identified as a dominant epibiont of mangrove pneumatophores. The sea slug *Elysia chlorotica* has been observed to harvest chloroplasts from *Vaucheria litorea*, and several lateral transfers of xanthophyte genes into the *Elysia* genome have been identified, implying that this kleptoplastid association may be longstanding.

Groups have traditionally been recognised on the grounds of gross morphology, however this is incongruent with molecular data. Robust groups currently include the Tribonematales (filamentous, coccoid or capsoid, some with H-shaped cell walls), and Vaucheriales (filamentous organisms with reproductive structures). Cell walls are made of cellulose and impregnated with silica; in chloroplasts, chlorophyll *a* is dominant, *c1* and *c2* are present in very small amounts, and fucoxanthin is absent. Nuclear gene phylogenies moderately supports a sister-group relationship to the phaeophytes. (Andersen 2004; Andersen and Bailey 2002; Ben Ali *et al.* 2002; Christensen 1994a; Ettl 1978; Hibberd 1990a; Maistro *et al.* 2009; Moestrup 1970; Ott and Brown 1972, 1974b, 1974a; Potter *et al.* 1997; Riisberg *et al.* 2009; Saifullah and Ahmed 2007; Schwartz *et al.* 2010)

ALVEOLATES

Predatory, phototrophic or parasitic organisms with cortical alveoli, *i.e.* contiguous sacs immediately below the cell membrane that are not part of other endomembrane systems, with only pores (micropores) interrupting the alveoli, and containing an unique family of structural proteins, alveolins. Mitochondria contain tubular or ampullar cristae. The flagellar apparatus usually includes a cross-striated root. Includes the ciliates, dinoflagellates and apicomplexans, and several smaller phyla; a large number of parasitic taxa are known, most notably within the apicomplexa (*e.g.* *Plasmodium falciparum*), but also within the ciliates, colpodellids, dinoflagellates, ellobiopsids and perkinsids. Multigene phylogenies, and the presence of the membrane trafficking protein Rab1a, strongly support a sister-group relationship to the stramenopiles, and a close relationship with the Rhizaria. (Burki *et al.* 2008; Cavalier-Smith 1993; Elias *et al.* 2009; Fast *et al.* 2002; Gajadhar *et al.* 1991; Gould *et al.* 2008; Leander *et al.* 2003b; Reeb *et al.* 2009; Siddall *et al.* 1997; Taylor 1976; Van de Peer *et al.* 1996b; Wilson *et al.* 1991; Wolters 1991)

Ciliates

A hugely speciose group of complex heterotrophic organisms with cilia (short flagella) arranged in kineties (anchored lines) over the surface. Cilia can arise from single or doubled basal bodies, and can form cirri (bundles, for walking on) or membranelles (flatly spread units, for creating water currents). The flagellar apparatus associated with each cilium is distinctive- with a microtubular ribbon, a striated rootlet, and a transverse microtubular ribbon, each arising from a defined and constant location on the flagellar (anterior) or posterior basal body. There is a complex cortex comprised of a pellicle with subsurface sacs (alveoli, which are arranged in species-specific mosaic patterns), subsurface plates (in some species), extrusomes, contractile fibres, and the anchorage structures of kineties. There is a complex mouth structure where endocytosis occurs. Several taxa have biomineralised elements (strontium or barium sulfate) in statoliths, or in calcium carbonate subsurface plates in *Coleps* species. Reproduction occurs by conjugation, and there is one spore-forming stalked taxon, *Sorogena*. A diverse

array of free-living ciliate species have been isolated, from marine, freshwater, soil and epiphytic environments. In addition, a number of ciliate species form close relationships with metazoa, such as entodiniomorphids, intestinal commensalists and debatably parasites of mammals, and *Ichthyophthirius multifiliis*, a commercially significant, obligate parasite of a number of fish species. Some taxa have algal endosymbionts, and these endosymbionts may in turn be harvested by other kleptoplastid organisms (e.g. *Dinophysis norvegica* harvesting cryptomonad endosymbionts of the ciliate *Myrionecta rubrum*); others have degenerate mitochondria (hydrogenosomes), and are dependent on methanogenic endosymbionts for respiration. While genes of red and green algal origin have been identified in ciliates, it is not yet clear that ciliates historically have possessed a chloroplast.

Ciliate nuclei are dimorphic: a large somatic macronucleus with highly amplified genes (where RNA synthesis occurs), and several small germline micronuclei (where genetic recombination occurs during conjugation). Macronuclear differentiation occurs via the excision of intergenic sequences and fragmentation of chromosomes, mediated by an unique class of small RNAs. Macronuclear genome sequences are available for *Tetrahymena thermophila* and *Paramecium tertauralia*, a corresponding micronuclear genome has been completed for *T. thermophila*, and EST libraries have been constructed for *Ichthyophthirius multifiliis*. Preliminary preliminary analyses of ciliate genomes has revealed evidence for several whole-genome duplication events, unusual intron structures, and suggested an unique codon usage pattern, wherein all three canonical stop codons may encode glutamine (UAA, UAG) or selenocysteine (UGA), although this has yet to be confirmed experimentally.

Ciliates are divided into two principal groups, Postciliatodesmatophora (ciliates with postciliatodesmata, microtubular ribbons arising from basal bodies, overlapping laterally and directed to the posterior of the organism) and Intramacronucleata (ciliates with a polygenomic macronucleus which divides via intranuclear microtubules), and then a number of smaller divisions based on very specific features of the ciliary cytoskeleton or silver line system, but the extent to which this is congruent with molecular phylogeny is currently unclear. Postciliatodesmophorid taxa include: karyorelictids (with non-dividing diploid macronuclei which are replaced at cell division by micronuclear division; postciliary ribbons are separated by two groups of microtubules; some taxa with barium or strontium sulfate statoliths), and heterotrichs (with polyploid macronuclei which divide via extranuclear microtubules; postciliary ribbons are separated by one microtubule; some taxa- folliculinids- live inside loricas). Intramacronucleate taxa include: spirotrichs (with kineties divided into left and right side oral cilia; left oral kineties leading clockwise into the mouth; some taxa with cilia bundled into cirri, used for walking; replication of DNA uses a migrating replication band in most taxa), Armophorea (with methanogenic endosymbionts and hydrogenosomes; group recognised on the basis of molecular studies of nuclear and hydrogenosomal genes), Litostomatea (each single ciliary basal body- monokinetid- with two transverse microtubular ribbons extending to adjacent kinety ridges on either side, a convergent posteriorly directed ribbon, and a lateral fibrillar root not overlapping with adjacent kineties), Phyllopharyngea (with radiating microtubular ribbons – phyllae- around the mouth; monokinetids with a reduced or absent transverse ribbon, convergent posteriorly directed ribbon converging with those of more anterior monokinetids, and subkinetal ribbons on

the inside of the rest of the flagellar apparatus; some taxa-suctorina- have nonciliated mature forms with tentacles); Nassophorea (with monokinetids and dikinetids with an anterior tangential transverse ribbon, a divergent postciliary ribbon, an anteriorly directed fibrillar root; large alveoli), Colpodea (ciliary dikinetids with one transverse ribbon and a postciliary microtubule associated with the ciliary basal body; and transverse and postciliary ribbons and a fibrillar root associated with the posterior basal body), Prostomatea (with oral dikinetids arranged radially, with microtubular ribbons extending laterally and overlapping to form the wall of a pre-cytostomal cavity; and associated dikinetids arranged in a brush), Plagiopylea (with endosymbiotic methanogens and hydrogenosomes arranged in “sandwich” formation; monokinetids with transverse ribbon, divergent postciliary ribbon and anteriorly-directed fibrillar root), and Oligohymenophorea (mouth with a distinct right dikinetid and three left polykinetids in a deep ventral cavity; monokinetids over the rest of the cell with radial transverse ribbons, divergent postciliary ribbons and overlapping anterior fibrillar roots). Phylogenomic analyses robustly support ciliate monophyly and a position within the alveolates, as a basal outgroup to dinoflagellates and apicomplexa. (Abernathy *et al.* 2007; Adl *et al.* 2005; Affa'a *et al.* 2004; Arnaiz *et al.* 2007; Bernhard *et al.* 2001; Budin and Philippe 1998; Chantangsi and Lynn 2008; Chantangsi *et al.* 2007; Eisen *et al.* 2006; Eisler 1992; Foissner *et al.* 2008; Gentekaki and Lynn 2009; Hackett *et al.* 2007; Harper *et al.* 2005; Hewitt *et al.* 2003; Israel *et al.* 2002; Jaillon *et al.* 2008; Johnson *et al.* 2004; Katz 2001; Lasek-Nesselquist and Katz 2001; Leander and Keeling 2003; Liu *et al.* 2004; Lynn 1985a; Lynn 1985b; Lynn 1988; Lynn and Small 1988; Lynn and Struder-Kypke 2002; Lynn and Struder-Kypke 2006; Matthews 2005; Miao *et al.* 2004; Park *et al.* 2008; Pomajbikova *et al.* 2010; Reeb *et al.* 2009; Reyes-Prieto *et al.* 2008; Schlegel and Eisler 1996; Small and Lynn 1981; Smith 1999; Struder-Kypke *et al.* 2007; Struder-Kypke *et al.* 2000; Wright and Lynn 1995)

Apicomplexa

Intracellular, intestinal or coelomic parasites of invertebrates and vertebrates, including *Plasmodium* species, causative agents of malaria; defined by the presence of an “apical complex” that functions in host cell attachment and invasion, in the asexual disseminative stage. The apical complex includes a “closed” conoid (helical sheet of microtubules forming a cone, with two anterior rings of microtubules, and an internal pair of longitudinal microtubules), a polar ring (ring-shaped MTOC just proximal to the conoid, giving rise to a subpellicular curtain of single microtubules), rhoptries (bottle-shaped secretion organelles that run longitudinally through the conoid and polar ring, and open at the anterior end of the cell), and enzyme-filled micronemes (filiform extensions of the endomembrane system). With a complex life cycle involving double or triple alternation of generations. Flagella are absent except from some microgametes: movement is by gliding or metaboly (squirming). Apicoplasts may also be present- plastids bound by four membranes, lacking thylakoids and photopigments, and with a circular genome with extremely reduced content, although they are absent from some taxa (*e.g.* *Cryptosporidium*); where present, they are of particular interest as candidate drug targets. Apicoplasts are closely associated with mitochondria, and have been suggested to be physically connected by some form of cytoskeletal apparatus. A number of unusual metabolic features, including a glycolytic pathway potentially shared between the cytoplasm and mitochondria, and haem biosynthesis potentially

shared between the cytoplasm, mitochondria and apicoplast, have been recorded in apicomplexan species.

The traditional morphological divisions of apicomplexa into haemosporidia, piroplasms, coccidia and gregarines have been overturned by recent molecular analyses. Four alternate divisions are currently recognised: archigregarines (with apical complex with a closed conoid, aflagellated trophozoites, syzygy and gamete formation; intestinal parasitism), cryptosporidians (closed conoid, two schizogonies; deeply embedded intestinal parasites of vertebrates), coccidians and piroplasmids (closed conoid, aflagellated trophozoites, syzygy and gamete formation; intracellular parasites of vertebrates, including *Plasmodium*), and eugregarines (including urosporidians) and neogregarines (with numerous longitudinal epicytic folds on which the cell glides and trophozoites lacking a conoid; some taxa with transverse septa between cell regions; a diverse array of taxa, some only recognised on molecular grounds, including coelomic parasites with metaboly instead of epicytic fold gliding; arthropod parasites, and annelid reproductive tract parasites). Full genome sequences are available for several apicomplexa, including species of *Plasmodium*, *Toxoplasma* (causative agents of toxoplasmosis), *Theileria* and *Babesia* (causative agents in cattle, respectively, of East Coast disease and tick fever) and *Cryptosporidium* (an intestinal parasite associated with secondary infection in HIV positive individuals). Phylogenomic analyses strongly support a position within the alveolates, as a sister-group to the dinoflagellates. Chloroplast gene phylogenies suggest that the apicoplast is the remnant of a red algal endosymbiont, although a number of genes of apparent green algal origin (e.g. *tufA*, *rpl16*, *rps3*) have been recovered. Recently, two functionally photosynthetic species- *Chromera velia* (see Chromerids) and CCMP3155- have been identified as either close relatives or basally divergent members of the apicomplexa and/or colpodellids, confirming a reductive origin for the apicoplast; the phylogenetic relationships and taxonomic status of apicomplexa, chromerids and colpodellids has not yet been accordingly reviewed. (Abrahamsen *et al.* 2004; Alvarez-Pellitero *et al.* 1997; Brayton *et al.* 2007; Carlton *et al.* 2002; Coppin *et al.* 2005; Dowse and Soldati 2004; Fleige *et al.* 2007; Fleige *et al.* 2008; Funes *et al.* 2002; Gardner *et al.* 2005; Gardner *et al.* 2002; Janouskovec *et al.* 2010; Kissinger *et al.* 2003; Kobayashi *et al.* 2007; Lau *et al.* 2009; Lim and McFadden 2010; McFadden 1999; McFadden *et al.* 1996; Moore *et al.* 2008; Nozaki *et al.* 2009; Pain *et al.* 2005; Patron *et al.* 2004; Reeb *et al.* 2009; Reichard *et al.* 2005; Saffo *et al.* 2010; Siddall *et al.* 1997; Templeton *et al.* 2010; Thompson *et al.* 2005; Vávra and Small 1969; Waller *et al.* 2004; Wilson *et al.* 1996; Xu *et al.* 2004; Zhu *et al.* 2001)

Colpodellids

Free-living predatory flagellates that feed by the myzocytotic uptake of prey cytoplasm. An apical complex is used to attach to and feed from host cells, consisting of a sheet of diagonal microtubules in a C-ring (conoid) on an apical rostrum close to a microtubular band, and thin micronemes and rhoptries that occupy the length of the cell. The anterior flagellum carries hairs or bulbs, and inserts in a pit. The flagellar apparatus is composed of two widely separated basal bodies giving rise to flagella which insert in opposite directions on a diagonal sagittal plane, proximal to the apical complex. The basal bodies are joined by a multilamellar connecting fibre. The anterior basal body gives rise to one apically-directed microtubular root of three microtubules; the posterior basal body gives

rise to an anteriorly-directed oblique root, which runs up to the rostrum, and a posteriorly-directed microtubular root. There may occasionally be three flagella, which is also seen in microgametes of apicomplexans. The pellicle includes cortical microtubules at the anterior end, and small polygonal alveoli, which may contain fibrous material. Dinoflagellate-like reproductive trichocysts and aflagellate resting cysts may form in some taxa. Ultrastructural studies do not resolve a consistent phylogenetic position for the colpodellids, with different species containing different numbers of dinoflagellate-, perkinsid- and apicomplexan- like features. Single-gene phylogenies predominantly support a closer relationship with the apicomplexa than with perkinsids and dinoflagellates, and reveal a potential sister-group relationship to the chromerids. (Gomez *et al.* 2009; Keeling and Leander 2003, 2004; Kuvardina *et al.* 2002; Leander *et al.* 2003a; Leander and Keeling 2003; Leander *et al.* 2003b; Leander *et al.* 2005; Moore *et al.* 2008; Mylnikov 2009; Mylnikov and Mylnikova 2008; Simpson and Patterson 1996)

Chromera

Free-living, photosynthetic alveolates, containing a micropore and cortical alveoli typical of alveolates, of considerable current interest due to their close phylogenetic affinities with apicomplexa. One or two golden-brown chloroplasts are present in each cell; each is a distinctive cone shape, bound by four membranes. A single, large mitochondrion is present; cristae are tubular, ampulliform and lamellar; the mitochondrion may be surrounded by vesicles of unknown function. Similarly to peridinin-containing dinoflagellates, chloroplast transcripts may be terminally polyuridylylated, and a form II rubisco is utilised; however, chloroplast genomes are either circular or long linear as opposed to being arranged in minicircles. Uniquely amongst photosynthetic alveolates, chlorophyll *c* is not present; and a novel accessory pigment, believed to be similar to isofucoxanthin, is used. Molecular phylogenies of nuclear genes variously place chromerids as closely related to apicomplexa and colpodellids, although a number of different positions have been suggested within this; phylogenies of chloroplast genes strongly support a sister-group relationship to dinoflagellates consistent with a common origin of the chloroplast lineage; as such, chromerids are the closest formally defined relatives of the apicomplexa to retain photosynthetically functional chloroplasts. One species, *Chromera velia*, has been identified from the stony coral *Plesiastrea versipora*. Recently, a flagellate CCMP3155 has been isolated from reef corals, which is functionally photosynthetic and groups in nuclear gene phylogenies with chromerids and apicomplexa; but the precise relationships between these lineages is uncertain. Complete plastid sequences are available for both lineages, and a full sequencing project is underway for *C. velia*. (Bråte *et al.* 2010; Guo *et al.* 2010; Janouskovec *et al.* 2010; Keeling 2009c; Moore *et al.* 2008; Obornik *et al.* 2009; Obornik *et al.* 2010; Okamoto and McFadden 2008; Sutak *et al.* 2010; Takishita *et al.* 2009; Weatherby *et al.* 2010 in press)

Perkinsids

Intracellular parasites of marine and freshwater molluscs and dinoflagellates, which in particular are a major cause of mortality in commercial oyster populations. Perkinsids contain an apical complex used for penetrating host cells, consisting of a sheet of diagonal microtubules in a C-ring (conoid), micronemes

and rhoptries that occupy the length of the cell, and both an anterior and a posterior ring. Cells may be uniflagellate or biflagellate; the conserved anterior flagellum bears a row of bipartite hooks or thick hairs on one side, and inserts in a pit, and a short, posterior flagellum is present in some species. The flagellar apparatus consists of two orthogonally inserting, very short basal bodies, connected by a striated fibre as in dinoflagellates and colpodellids. There are three microtubular roots, a striated rootlet, and distinctive fibrous structures around the basal bodies that are also seen in dinoflagellates. Micronemes are present beneath the cell surface; a refractive body of unknown function is adjacent to the nucleus. Mitosis is closed; aflagellated, parasitic trophozoites divide by successive binary fissions, and released trophozoites (spores) develop outside the host, to become flagellated zoospores. The potential presence of plastids in perkinsids is controversial; although *Perkinsus marinus* is known to contain and transcribe several putatively plastid-targeted genes, and is sensitive to inhibitors of plastid-localised biosynthetic pathways, and there is ultrastructural evidence for a four membrane-bound body in *P. atlanticus* that could be a relict chloroplast, there is at present no proteomic evidence that any putatively plastidic pathways retained in perkinsids are indeed plastid-localised. No genome sequences are yet complete, but EST libraries have been constructed for *P. marinus*. While the presence of a conoid suggests a close relationship with the apicomplexa; similarities in flagellar and nuclear structure, and multigene phylogenies, strongly support a sister-group position with the dinoflagellates to the exclusion of apicomplexa. (Bråte *et al.* 2010; Burki *et al.* 2008; Goggin and Barker 1993; Hoppenrath *et al.* 2009; Joseph *et al.* 2010; Kuvardina *et al.* 2002; Leander and Keeling 2003, 2004; Leander *et al.* 2005; Matsuzaki *et al.* 2008; Norén *et al.* 1999; Perkins 1996; Saldarriaga *et al.* 2003; Siddall *et al.* 1997; Slamovits *et al.* 2007; Stelter *et al.* 2007; Teles-Grilo *et al.* 2007; Villalba *et al.* 2004)

Dinoflagellates

Mostly free-living, heterotrophic, mixotrophic or autotrophic alveolates; most are biflagellate, but some amoeboid and syncytial taxa are known. The coiled transverse flagellum is held in a cingular groove, beating multiple waves in a spiral to the cell's left, and the longitudinal flagellum in a longitudinal sulcus; there are hooks on the anterior flagellum as in perkinsids, and paraxial rods on both flagella. Flagella insert on the ventral surface, and there are three flagellar roots accompanied by fibrous material; the striated connective between basal bodies seen elsewhere in alveolates is present. Cortical alveoli are well-developed, may contain cellulose plates, and usually contain square-based hollow-filament extrusomes, and some taxa have what appear to be relics of an apical complex-microtubular baskets underlying feeding tentacles (the peduncle), and the apical pore complex (extrusive organelles like rhoptries). The proposedly ancestral, red-algal derived chloroplast has a number of unusual features, such as the use of the soluble accessory pigment peridinin, and a form II rubisco laterally acquired from a proteobacterial donor. In addition, a diverse array of serial endosymbiotic, photosymbiotic and kleptoplastid chloroplast acquisitions from haptophytes (*e.g.* in *Karenia*), green algae (*Lepidodinium*) centric and pennate diatoms (*Galedinium*, *Kryptoperidinium*) and cryptomonads (*Dinophysis*) have been reported; notably, the pennate diatom-derived chloroplasts of *Kryptoperidinium* and *Durinskia* retain a nucleomorph and endogenous mitochondria. Nonphotosynthetic taxa (*e.g.* *Oxyrrhis*) are believed to have originated via secondary chloroplast loss.

Dinoflagellates are- from currently identified taxa- the most speciose group of algae, and free-living species are ecologically dominant components of marine communities. Dinoflagellates are important photosymbionts of an array of marine invertebrates (*e.g.* zooxanthellae with corals); in addition, approximately 5% of reported species are known parasites of marine invertebrates, and several free-living species are major components of fish-killing “red tide” harmful algal blooms. Five divisions have been defined by ultrastructure: Dinophyceae (with a dinokaryon throughout the life cycle, and amphiesmal vesicles often containing cellulose plates in highly specific arrangements; includes fossil taxa), Blastodinales (parasitic dinoflagellates with dinokaryon only in part of life cycle), Noctilucales (large free-living motile cells inflated by vacuoles, some taxa are phosphorescent; dinokaryon during part of life cycle only), Syndiniales (with histones in the nucleus, but dinoflagellate-type flagella), and Oxyrrhis (aplastidic, lacking cingulum and sulcus, with laterally inserting flagella, and closed mitosis). Genome structure is unusual, with a distinctive haploid nucleus (dinokaryon), with large permanently condensed chromosomes that lack standard histones, extremely reduced mitochondrial and chloroplast genomes, organisation of the chloroplast genome into small single- double- and pseudogenic minicircles, and evidence of multiple tandem gene duplication events in all three organelles. In addition, recent molecular studies have recovered a number of distinctive features of gene expression pathways, such as transcription of chloroplast minicircles via a rolling circle mechanism, and 3’ terminal polyuridylation of chloroplast transcripts. A complete genome sequence is not available for any dinoflagellate; however, the transcriptomes of two lineages of the genus *Symbiodinium* have been completed. Molecular phylogenies strongly support dinoflagellate monophyly within the alveolates, an immediate sister-group relationship to ellobiopsids and perkinsids, and close relationships with the apicomplexa, chromerids and colpodellids to the exclusion of ciliates. (Bhattacharya and Nosenko 2008; Calado *et al.* 1999; Chesnick *et al.* 1997; Dang and Green 2010; Garcia-Cuetos *et al.* 2010a; Howe *et al.* 2008; Iida *et al.* 2009; Imanian and Keeling 2007; Ki 2010; Leander and Keeling 2003; Nash *et al.* 2008; Rowan *et al.* 1996; Simon *et al.* 2009; Slamovits and Keeling 2008; Slamovits *et al.* 2007; Takishita *et al.* 2008; Taylor *et al.* 2008; Wang and Morse 2006; Yoon *et al.* 2002a; Yoon *et al.* 2005; Zhang and Lin 2003)

Ellobiopsids

Multinucleate alveolates that superficially resemble fungi, with each individual consisting of one or more tube-like structures containing transverse septa. Four genera- *Ellobiopsis*, *Ellobiocystis*, *Parallobiopsis* and *Thalassomyces*- are known, and the constituent species are chiefly ectoparasites of pelagic crustaceans, although one species is known to parasitise a benthic polychaetous worm. Parasitism may be species- and sex-specific in the host, and may substantially impact on the fecundity of host organisms. With a nutrient-absorbing root inside the host, and trophic/generative structures protruding through the host carapace, and with a biflagellated distributive stage that has not been described in detail. Molecular phylogenies support a position within the alveolates, as an immediate sister-group to dinoflagellates, to the exclusion of apicomplexa and perkinsids. (Albaina and Irigoien 2006; Galt and Whisler 1970; Gomez *et al.* 2009; Silberman *et al.* 2004; Walkusz and Rolbiecki 2007; Whisler 1990)

RHIZARIA

A major group of eukaryotes with fine “root-like, reticulate or filose” pseudopodia; currently identified only on the basis of molecular phylogenies of nuclear proteins and ribosomal genes, which strongly support the existence of the group as a clade. The group is resolved with strong statistical support in phylogenies of SSU rRNA and individual cytoskeletal proteins, and by phylogenomic approaches. The name Rhizaria was introduced by Cavalier-Smith in 2002 and has been used in several different ways in recent years, but in the absence of a synapomorphy it is used here in the sense of Nikolaev *et al.* 2004 (*i.e.* excluding Apusozoa) as the group identified by molecular phylogeny including Cercozoa, Foraminifera, and Radiozoa. The insertion of one or two amino acids between monomers of the polyubiquitin gene unites Cercozoa and Foraminifera to the exclusion of the “radiozoan” Acantharea and Polycystinea, although Foraminifera and Radiozoa have also been placed together in phylogenetic trees. Recent multigene studies have strongly supported a position for the Rhizaria at the base of the SAR clade; whether the Rhizaria historically contained a secondary, red-algal derived chloroplast lineage found in other SAR and CCTH clade taxa is currently unknown. Groups below are divided into Cercozoa (Filosa and Endomyxa), Foraminifera, Radiozoa and *incertae sedis* Rhizaria; however it is recognised that rhizarian systematics is currently developing quickly and likely to change. (Archibald and Keeling 2004; Archibald *et al.* 2003b; Bass *et al.* 2009a; Bass *et al.* 2009b; Bass *et al.* 2005; Berney and Pawlowski 2003; Bhattacharya *et al.* 1995b; Burki *et al.* 2006; Burki and Pawlowski 2006; Burki *et al.* 2007; Burki *et al.* 2008; Cavalier-Smith 2002, 2004; Chantangsi *et al.* 2010; Hampl *et al.* 2009; Howe *et al.* 2003; Keeling 2001a; Keeling 2009c, 2009b, 2009a; Longet *et al.* 2003; Moreira *et al.* 2007; Nikolaev *et al.* 2004; Parfrey *et al.* 2010; Pawlowski and Burki 2009; Polet *et al.* 2004; Rodriguez-Ezpeleta *et al.* 2007a; Simpson and Roger 2004a; Takishita *et al.* 2005)

Cercozoa

A morphologically and genetically diverse assemblage of protists including flagellates and amoebae that may form filose or reticulate pseudopodia, and may harbour endosymbiotic cyanelles or green algae; currently identified on the basis of molecular phylogenetic studies. An insertion of one or two amino acids at the monomer–monomer junctions of polyubiquitin is shared by all Cercozoa and Foraminifera (Archibald *et al.* 2003a). It has been suggested that an insertion of one amino acid found in the sequence from foraminiferans and some cercozoans represents an ancestral state, and an insertion of two amino acids represents a derived state (Bass *et al.* 2005); however the pattern seems to include multiple acquisitions and losses (Chantangsi *et al.* 2010). Flagellar apparatus characters have also been proposed by Cavalier-Smith (2008) as a synapomorphy found in flagellated cercozoans - the proximal hub-lattices and distal nonagonal fibers in the flagellar transition zone. Further work is needed to elucidate the distribution of these delicate, difficult to preserve ultrastructural characteristics. Several major studies including uncultured environmental sequences suggest that Cercozoa are as diverse on molecular grounds as the Foraminifera, and indicate that the lineages described below do not yet bear clear relationships to each other. The Cercozoa are currently divided into two major groups, the Filosa and the Endomyxa. (Archibald and Keeling 2004; Archibald *et al.* 2003a; Bass and Cavalier-Smith 2004; Bass *et al.* 2009a; Bass *et al.* 2009b; Bass *et al.* 2005; Cavalier-Smith 1998; Cavalier-Smith and Chao 2003b; Cavalier-Smith and

Chao 1997; Cavalier-Smith *et al.* 2008b, 2009; Chantangsi *et al.* 2010; Howe *et al.* 2009; Nikolaev *et al.* 2003; Nikolaev *et al.* 2004; Polet *et al.* 2004; Rodriguez-Ezpeleta *et al.* 2007a)

Filosa

A group recognised by molecular phylogeny, currently largely defined by exclusion (*i.e.* cercozoans that do not fit into the Endomyxa). The group contains numerous small colourless flagellates with filose pseudopodia, some flagellates with silica scales, and some filose amoebae with siliceous tests, as outlined below. Details of its membership will probably be considerably clarified in the near future. (Bass *et al.* 2009a; Bass *et al.* 2009b; Cavalier-Smith *et al.* 2008b, 2009; Howe *et al.* 2009)

Cercomonads

Filosan flagellates that produce filose, finger-shaped and branching pseudopodia; movement is by creeping, with the anterior flagellar beat stiffly describing a cone shape, and the posterior flagellum associating closely with the cell and trailing among pseudopodia behind the cell. The flagellar apparatus consists of two basal bodies at right angles, connected by fibrillar material, with three singlet microtubular roots; and in some taxa there is a broadly striated rootlet leading to an MTOC that nucleates a cone of microtubules, subtending the nucleus. Variation among taxa in the presence of carwheels in the basal bodies has been reported. There is an electron-dense “paranuclear body”. Numerous molecular phylogenetic studies suggest Cercomonads are highly diverse and important in ecological systems; alpha-taxonomy within the group has recently been revised by Bass and co-authors, based on a combination of SSU rRNA and light microscopical features. They possess the cercozoan molecular signature of a two-residue insertion in polyubiquitin. (Archibald and Keeling 2004; Archibald *et al.* 2003a; Bass and Cavalier-Smith 2004; Bass *et al.* 2009a; Bass *et al.* 2009b; Bass *et al.* 2005; Berney and Pawlowski 2003; Burki and Pawlowski 2006; Cavalier-Smith and Chao 2003a; Ekelund *et al.* 2004; Karpov 1997; Keeling 2001b; Keeling *et al.* 1998; Longet *et al.* 2003; Longet *et al.* 2004; Mignot and Brugerolle 1975a; Patterson and Zölffel 1991; Pawlowski and Burki 2009; Zölffel 1990)

Chlorarachniophytes

Filosan organisms that occur as reticulate amoebae with fine filose connections between cells, flagellates, and/or individual filose amoebae. There is a four-membraned chloroplast derived from a green algal endosymbiosis. The nucleomorph, nucleus of the endosymbiotic green alga, is still present between the two inner and two outer membranes, and holds the smallest known eukaryotic genome; it has been studied extensively because of its importance to ideas about lateral gene transfer and secondary endosymbionts in chloroplast evolution. In the flagellates, there is one apically inserting flagellum which wraps around the cell and trails posteriorly; it is covered with fine hairs emerging from a row of bumps on one side; the flagellar apparatus consists of two basal bodies, four microtubular roots, and lacks striated fibres. The original host organism may be related to *Leucodictyon* and *Reticulamoeba* (see below, Eukaryotes *incertae sedis*), to which it bears some morphological similarity. There are six genera, with species being distinguished on ultrastructural and

life-cycle characteristics; environmental surveys indicate undescribed diversity. There is a single insertion in the polyubiquitin gene. The chloroplast and nucleomorph genomes of the chlorarachniophyte *Bigeloviella natans* have been sequenced. (Archibald 2007; Bass *et al.* 2005; Bhattacharya *et al.* 1995b; Chantangsi *et al.* 2010; Geitler 1930; Gilson and McFadden 1996; Gilson and McFadden 1999; Gilson *et al.* 2006; Grell 1991a; Grell and Schüller 1991; Hibberd and Norris 1984; Ishida *et al.* 1997; Keeling *et al.* 1998; Ludwig and Gibbs 1989; McFadden *et al.* 1997; Moestrup and Sengco 2001; Ota *et al.* 2008; Palmer and Delwiche 1996; Rogers *et al.* 2007a; Slamovits and Keeling 2009; Van de Peer *et al.* 1996a; Williams *et al.* 2005)

Clautriavia & Auranticordis

The cell surface of these filosan organisms is covered in pores, and there are muciferous bodies immediately beneath the surface, giving a “warty” appearance. *Auranticordis* is a large, multi-lobed, orange tetraflagellate with recurrent hairy flagella. Most reports of *Clautriavia* are of small gliding flagellates, with a rigid, oval cell body with a subapical ventral cavity into which the single hairy recurrent flagellum inserts. A recent detailed description revealed an inconspicuous second recurrent flagellum. The flagellar apparatus of both genera includes a robust microtubular root attached to the anterior end of the nucleus; there is also a paranuclear body as seen in cercozoans. *A. quadrivirberis* has been reported to contain photosynthetic endosymbionts, which may be of cyanobacterial origin, and potentially represents a third primary chloroplast endosymbiosis, independent of archaoplastids and *Paulinella*. Reproduction is by fission of flagellates or by production of a large multinucleate plasmodium which subsequently divides and forms flagellates. Molecular data place *Pseudopirsonia* in the same clade. *Cholamonas* is similar to *Auranticordis* ultrastructurally. (AlQassab *et al.* 2002; Chantangsi *et al.* 2008; Chantangsi *et al.* 2010; Chantangsi and Leander 2010; Kühn *et al.* 1996; Lee and Patterson 2000; Massart 1900; Patterson and Zölffel 1991)

Desmothoracids (= “Clathrulinids”)

Filosan “heliozoan” protists where the cell body is surrounded by axopodia, which protrude through a perforated capsule made of silica mixed with organic matter; the capsule is often stalked. The microtubules supporting the axopodia are not organised in a regular pattern, and arise from a central nucleating site next to the nucleus. The life cycle involves mitosis within the capsule to produce flagellated swimmers, which metamorphose into amoebae. These produce a stalk-forming pseudopodium stiffened by hundreds of microtubules, which secretes the stalk and the new skeleton. Analyses of SSU rRNA place *Clathrulina* and *Hedriocystis* together in the Cercozoa. The group has also been called Clathrulinidae after the commonly-observed heliozoon *Clathrulina elegans*. It has been grouped with the gymnosphaerids in the “Nucleohelea”, on the basis of the central nucleating site for microtubules, though molecular work is needed to confirm this: gymnosphaerids also show morphological affinities to the radiozoan *Sticholonche*. (Adl *et al.* 2005; Bardele 1972; Bass *et al.* 2009a; Bass *et al.* 2009b; Nikolaev *et al.* 2004; Smith and Patterson 1986)

Euglyphids

Filose amoebae with a test formed of regularly-shaped siliceous plates held together by an organic cement. One member, *Paulinella chromatophora*, has endosymbiotic blue-green cyanelles which are independently derived from the cyanobacteria and unrelated to those seen in the Archaeplastida. Cyanelle genome sequences have been completed for two strains of *P. chromatophora*; preliminary analyses suggest that a small number of cyanelle-to-nucleus gene transfer events may have occurred, but proposed nuclear-encoded cyanelle-derived genes lack recognisable targeting sequences consistent with the evolution of a complex cyanelle protein import system.

On the basis of molecular phylogeny (of SSU rRNA) the group can be divided into five main groups: one clade containing Cyphoderiidae (circular or oval scales, angled test aperture) and Paulinellidae (long scales, positioned perpendicular to test aperture; with cyanelles); and another clade containing Assulinidae (strongly flattened test, only one scale type), Euglyphidae (thin test, with round or elliptical scales), and Trinematidae (test with bilateral symmetry). A two-residue insertion in polyubiquitin is present. The group has been placed with the thaumatomonads on the basis that both produce silica scales, however the molecular evidence for this hypothesis has recently begun to look questionable. Further investigations are needed both of morphology and molecules. Euglyphids may also be related to *Pseudodifflugia* and taxa that have not been studied by molecular techniques, such as amphitremids. (Archibald and Keeling 2004; Bass and Cavalier-Smith 2004; Bass *et al.* 2009a; Bass *et al.* 2009b; Bhattacharya *et al.* 1995b; Cavalier-Smith *et al.* 2009; Chantangsi *et al.* 2010; Heger *et al.* 2010; Kies 1974; Lara *et al.* 2007; Longet *et al.* 2004; Marin *et al.* 2005; McFadden 2001; Nakayama and Ishida 2009; Nikolaev *et al.* 2004; Nikolaev *et al.* 2005; Nowack *et al.* 2008; Reyes-Prieto *et al.* 2010; Wylezich *et al.* 2002)

Glissomonads

Small spherical, reniform or ellipsoid flagellates that glide on a trailing flagellum (and have a short, waving anterior flagellum); filose pseudopodia may rarely be present but are not as obvious as in cercozoans. The basal bodies insert at right angles and give rise to an undetermined number of single microtubules that extend into the cell. The taxonomy of the group has recently been revised (Howe *et al.* 2009) on the basis of SSU rRNA and light-microscopical characteristics; however there is a need for further electron-microscopical observations to identify the ultrastructural identity of members of the group. There is a double insertion in the polyubiquitin gene. Glissomonads are extremely abundant in soils around the world: considerable diversity is demonstrated by environmental sequencing rather than culture-based methods. (Adl *et al.* 2005; Bass *et al.* 2009a; Bass *et al.* 2009b; Bass *et al.* 2005; Cavalier-Smith and Chao 1997; Chantangsi and Leander 2010; Ekelund *et al.* 2004; Howe *et al.* 2009; MacDonald *et al.* 1977; Vickerman *et al.* 2002; Vørs 1992a)

Limnofila

A genus of marine protists with very fine, filose pseudopodia bearing granules (extrusomes); erected to include organisms with SSU rRNA sequences that group with one from a culture previously mis-assigned to *Gymnophrys cometa*,

with the culture renamed as *Limnofila borokensis* (Bass *et al.* 2009a). Ultrastructurally-studied species have flat mitochondrial cristae, bundles of 2—6 microtubules supporting the filopodia, two flagellar stubs that stop at the transitional region; they lack the distinguishing features of other groups. There is a flagellated stage in *L. borokensis* with long flagella. There is a double insertion between polyubiquitin subunits. (Bass *et al.* 2009a; Burki *et al.* 2007; Cavalier-Smith and Chao 2003b; Mikrjukov 1998; Nikolaev *et al.* 2003)

Massisteria

Small irregular or rounded star-shaped amoebae from which radiate thin pseudopodia with extrusomes; the pseudopodia may branch and anastomose. There are 2 inactive flagella with parallel basal bodies. Amoebae are normally sedentary but, under adverse conditions, the arms are resorbed, the flagella become active, and the organism becomes a motile non-feeding flagellate. There is a double insertion in the polyubiquitin gene of *Massisteria* characteristic of Cercozoa. (Atkins *et al.* 2000b; Bass and Cavalier-Smith 2004; Bass *et al.* 2009a; Bass *et al.* 2009b; Bass *et al.* 2005; Chantangsi *et al.* 2010; Mikrjukov and Mylnikov 1998; Nikolaev *et al.* 2003; Patterson and Fenchel 1990)

Metopion

Small disc-shaped flagellates with a very shallow ventral groove at the anterior end. The long posterior trailing flagellum and the (not always present) stumpy anterior trailing flagellum insert in the groove. The anterior margin of the cell contains refractile granules, and is swollen like a beak. Assuming the identification of this organism is correct in molecular papers (since the basis for the identification has not been published), phylogenies of SSU rRNA place this taxon within the Cercozoa. (AlQassab *et al.* 2002; Bass and Cavalier-Smith 2004; Bass *et al.* 2005; Bastien *et al.* 2004; Cavalier-Smith and Chao 2003b; Larsen and Patterson 1990; Mylnikov *et al.* 1999; Patterson and Simpson 1996; Tong *et al.* 1998)

Metromonas

Small lozenge-shaped gliding flagellates with a long posterior trailing flagellum detached from the body, and a short stumpy anterior trailing flagellum. The posterior flagellum can form a hook shape with the curve attached to the substrate: the cell then rocks back and forth like a metronome. There is a double insertion in the polyubiquitin gene. (AlQassab *et al.* 2002; Bass and Cavalier-Smith 2004; Bass *et al.* 2009a; Bass *et al.* 2009b; Bass *et al.* 2005; Chantangsi *et al.* 2010; Ekeboom *et al.* 1996; Larsen and Patterson 1990; Tong *et al.* 1998)

Pansomonads

A group including members of the genera *Aurigamonas*, *Cercobodo*, and *Agitata*. Heterotrophic flagellates with two hairy, heterodynamic flagella, both free from the body. A motile flagellate phase alternates with a sedentary, non-moving amoeboid phase. The flagellates of *Aurigamonas* have many stiff, radiating haptopodia (retractible arms stiffened with microfilaments with one extrusome on the end); one flagellum is long and propulsive, the other is short and crook-like. *Agitata* contains ovoid cells that glide agitatedly on their long

posterior flagellum; there are short pointed, filose, finger-like, lamellar and bulbous pseudopodia that can arise from anywhere on the cell surface. There is a one amino acid insertion between polyubiquitin monomers. (Bass *et al.* 2009a; Bass *et al.* 2009b; Chantangsi *et al.* 2010; Vickerman *et al.* 2005)

Sainouroids

Small, lozenge-shaped, gliding flagellates with a long posterior trailing flagellum detached from the body, and a short stumpy anterior trailing flagellum. The flagellar apparatus consists of two very short basal bodies interconnected by dense striated fibrous roots, that also attach the basal bodies to a centrosome and the nucleus; the fibrous roots give rise to one single microtubule (and a dorsal cape of microtubules in *Helkesimastix*); the centrosome also gives rise to radiating microtubules. The anterior flagellum is a stump without a 9+2 axoneme. Mitochondrial cristae appear discoid; and there is a paranuclear body (possibly a peroxisome). A double insertion in the polyubiquitin gene is present in *Sainoureon*, but a single one is in *Helkesimastix*. The group is recovered in SSU rRNA phylogenies and contains *Sainoureon*, *Cholamonas* and *Helkesimastix*. (AlQassab *et al.* 2002; Bass and Cavalier-Smith 2004; Bass *et al.* 2009a; Bass *et al.* 2009b; Bass *et al.* 2005; Cavalier-Smith *et al.* 2008b, 2009; Chantangsi *et al.* 2010; Ekeboom *et al.* 1996; Flavin *et al.* 2000; Larsen and Patterson 1990; Tong *et al.* 1998)

Spongomonads

Heterotrophic flagellates of the genera *Spongomonas* and *Rhipidodendron*, living in colonies embedded in a matrix of iron-rich mucous globules. The two equal flagella are directed apically but insert subapically into a shallow flagellar pocket, giving rise to radiating and longitudinal microtubular roots, joined by striated fibrillar roots. Members of each genus are superficially similar to members of the amoebozoan genus *Phalansterium*. (Adl *et al.* 2005; Bass *et al.* 2005; Cavalier-Smith and Chao 2003d; Hibberd 1976b, 1983; Strüder-Kypke and Hausmann 1998)

Thaumatomonads (=Thaumatomastigids)

Rounded heterotrophic flagellates with a distinctive combination of a short anterior scaly flagellum and a long naked posterior flagellum, and the ability to produce filose pseudopodia, usually from the ventral area of the cell. Many species are covered with siliceous scales and spines, which are produced in association with mitochondria. Some syncytial or colonial species exist; one has endosymbiotic bacteria. Thaumatomonads have been estimated to contribute on average about 5%-10% to flagellate abundance in different benthic habitats. SSU rRNA phylogenies place this group in the Cercozoa, sometimes with the (also siliceous) euglyphids; while this group (“Imbricatea”) has been supported in SSU rRNA trees in the past, the most recent trees with detailed taxon sampling suggest that silica biomineralisation may be more plesiomorphic in the Cercozoa. (Bass *et al.* 2009a; Bass *et al.* 2009b; Bass *et al.* 2005; Beech and Moestrup 1986; Cavalier-Smith and Chao 1997; Cavalier-Smith *et al.* 2009; Chantangsi *et al.* 2010; Chantangsi and Leander 2010; Ekelund *et al.* 2004; Karpov 1987; Karpov and Makarenkova 1989; Kim *et al.* 2006; Mylnikov and Karpov 1993; Patterson and Zölffel 1991; Preisig 1994; Preisig *et al.* 1994;

Swale and Belcher 1974; Thomsen *et al.* 1993; Thomsen and Ikävalko 1997; Wylezich *et al.* 2007)

Thecofilosea

A clade recognised on the basis of SSU rRNA trees, containing non-scaly filose amoebae: uninucleate cell surrounded by an organic flexible tectum or rigid test with one or two apertures for filopodia; with either two cilia or none; and tubular mitochondrial cristae. There is a single insertion between polyubiquitin monomers. (Bass *et al.* 2009a; Bass *et al.* 2005; Cavalier-Smith and Chao 2003a; Cavalier-Smith *et al.* 2008b, 2009; Chantangsi *et al.* 2010)

Cryothecomonas

Intracellular parasites of diatoms. Oval-shaped heterotrophic flagellates with two flagella, one directed anteriorly, one trailing; with a pronounced ventral groove from which pseudopodia emerge; with a delicate theca covering the cell except at the sites of flagellar insertion and ventral food ingestion. The flagella insert subapically; the two basal bodies are connected by a striated fibre and give rise to microtubular roots which connect the kinetosome to the nucleus. (Bass *et al.* 2009a; Chantangsi *et al.* 2010; Chantangsi and Leander 2010; Drebes *et al.* 1996; Kühn *et al.* 2000; Schnepf and Kühn 2000; Thomsen *et al.* 1991)

Ebriids

Large marine flagellates with a prominent basket-shaped internal siliceous skeleton. The flagella are often hard to see. The siliceous skeleton resembles those of dictyochids (Chromalveolata, Stramenopiles); the condensed chromosomes at interphase were thought to resemble those of dinoflagellates, but EM studies showed that this was not the case (they may resemble those of *Protaspis*). There is an extensive fossil record. (Chantangsi *et al.* 2010; Chantangsi and Leander 2010; Hargraves and Miller 1974; Hoppenrath and Leander 2006a; Korhola and Grönlund 1999; Lipps 1993; Preisig 1994; Tappan 1980; Taylor 1990; Tong *et al.* 1998)

Phaeodarea

“Radiolarian” or “heliozoan” deep-sea protists with an elaborately decorated skeleton and needles of amorphous silica mixed with organic components and traces of magnesium, calcium and copper. These protists were described by Haeckel in a famous series of engravings; however the Haeckelian concept of Radiolaria is made polyphyletic by the Phaeodarea falling apart from the rest of the group. Cytoplasm is divided into different areas by a thick central capsule, which has only three openings- the oral astropyle and two opposing parapyles through which the axopodia project. Outside the central capsule there is a yellow-brown globular pigmented aggregate, argued either to be waste material or involved in the metabolism of silica. The life cycle is complex and includes flagellated stages, however more comprehensive electron microscopical and life-cycle studies are needed. The group has traditionally been divided into: Phaeoconchia (central capsule enclosed within a bivalved shell, with separated dorsal and ventral boat-shaped lattice valves), Phaeocystina (central capsule suspended in the centre of the cytoplasmic network outside the capsule, skeleton absent or

incomplete with scattered, solitary spicules), *Phaeogromia* (central capsule located eccentrically, away from the mouth, in a simple lattice shell with a large opening at the oral end. The opening is surrounded by ‘teeth’ or ‘feet’ which may branch), and *Phaeosphaerida* (central capsule in the centre of a simple or double spherical lattice shell, with a simple opening), though whether this correlates with molecular phylogeny is unknown. (Anderson 1983; Bass *et al.* 2009a; Bass *et al.* 2005; Cachon and Cachon 1973; Cachon *et al.* 1990; Nikolaev *et al.* 2004; Polet *et al.* 2004; Reschetjnak 1966; Yuasa *et al.* 2005)

Protaspis

A genus of marine phagotrophic biflagellates, dorsoventrally flattened, shaped like elongated ovals with parallel lateral sides, with two heterodynamic flagella emerging through funnels that are positioned subapically, each within a depression and separated by a distinctive protrusion. A complex multilayered wall surrounds the cell. Like dinoflagellates and euglenids, the nucleus contains permanently condensed chromosomes and a large nucleolus throughout the cell cycle. Pseudopodia containing numerous mitochondria with tubular cristae emerge from a ventral furrow through a longitudinal slit positioned posterior to the protrusion and flagellar apparatus. Batteries of extrusomes are present within the cytoplasm and have ejection sites through pores in the cell wall. (Bass *et al.* 2009a; Chantangsi *et al.* 2010; Hoppenrath and Leander 2006b, 2006a)

Pseudodifflugia

Genus of filose amoebae with a rigid agglutinated test. There may be up to three nuclei present; cell division is by budding. Other organisms with similar morphology (amphitremids, chlamydropyrids, psammonobiotids, volutellids) not yet studied by molecular techniques may possibly form a group with *Pseudodifflugia*. (Bass and Cavalier-Smith 2004; Bass *et al.* 2009a; Chantangsi *et al.* 2010; Ogden and Hedley 1980; Wylezich *et al.* 2002)

Endomyxa

A group recognised by molecular phylogeny, typically plasmodial endoparasites of other eukaryotes. *Haplosporidia*, *Paradinium*, *Gromia*, and *Filoreta* all share the specific stem E23-13-1 in the SSU rRNA gene, and have a single insertion between polyubiquitin monomers. (Bass *et al.* 2009a; Bower and Meyer 2002; Cavalier-Smith and Chao 2003b; Cavalier-Smith and Chao 2003c; Cavalier-Smith *et al.* 2008b, 2009; Chantangsi *et al.* 2010; Tekle *et al.* 2007)

Ascetosporea

Parasites of arthropods that produce “simple” spores (in the context of former “sporozoan” taxonomy); the group is recognised now, and contains more members, on the basis of SSU rRNA phylogenies. There is a single polyubiquitin insertion. (Bass *et al.* 2009a; Berthe *et al.* 2000; Cavalier-Smith 2002; Skovgaard and Daugbjerg 2008; Sprague 1979)

Haplosporidia

Parasites or hyper-parasites of marine and freshwater invertebrates, which include significant pathogens of commercial importance such as *Haplosporidium nelsoni*, agent of MSX disease in the oyster *Crassostrea virginica*. Most taxa have a distinctive “open” spore case, which bears either a hinged operculum covering the opening, or a tongue covering the inner edge of the opening. A rudiment of the intranuclear mitotic spindle persists in the interphase nucleus (the “kernstab”). Life cycles remain understudied, but include spores, amoeboid cells which invade tissue, multinucleate plasmodia which divide in the coelom or extracellular space; haploid stages; and creation of the spore wall by division into nucleated and anucleated cells, the anucleated of which then engulfs the nucleated cell. Formerly thought to be alveolates, they are now affiliated with the Rhizaria on the basis of molecular studies. Despite the fact they include the genus *Urosporidium*, the haplosporidians should not be confused with the “urosporids” or “urosporidians” as used by (Leander *et al.* 2005) which contain the genus *Urospora* and belong to the apicomplexa: both haplosporidians and urosporidians are parasitic and have had a wildly unstable history of classification. Haplosporidia have a single insertion in the polyubiquitin gene. (Bass *et al.* 2005; Berthe *et al.* 2000; Burrenson and Ford 2004; Carnegie *et al.* 2000; Cochenec-Laureau *et al.* 2003; Flores *et al.* 1996; Longet *et al.* 2004; Perkins 1990, 1991; Reece *et al.* 2004; Siddall *et al.* 1995; Sprague 1979; Tekle *et al.* 2007)

Paramyxea

Economically important parasites of bivalve molluscs (*e.g.* *Marteilia*, parasite of Sydney rock oysters), crustaceans and annelids; which make multicellular spores by endogenous budding, and have centrioles of nine single microtubules. After nuclear division in the amoeboid “stem” cell, the daughter nucleus is surrounded by merging cisternae of endoplasmic reticulum, which make an intracellular, intravacuolar daughter cell. This can then happen in the intravacuolar cells as well. Different species perform endogenous budding to different degrees; endogenous cells may undergo cycles of meiosis. The spores are released into the environment from the host’s gut; thought the complete life cycle is unknown. Flagella are unknown despite the presence of 9-singlet basal bodies. Phylogenetic analyses have not yet resolved the placement of Paramyxea (Adlard and Ernst 1995; Berthe *et al.* 2000; Feist *et al.* 2009; Itoh 2004; Larsson and K ie 2005; Perkins and Wolf 1976)

Paradinida

Marine parasites of crustaceans, usually seen as large “gonospores” - large bag-like spores with a ridged surface, attached to copepods; but *Paradinium* species also reported in older literature as having a multinucleate plasmodial trophic phase, and a bi-flagellated dispersal phase. *Paradinium*, the “RP parasite” and the “spot prawn parasite” have been described recently in detail from a variety of habitats. (Bass *et al.* 2009b; Bower and Meyer 2002; Chatton 1920; Jepps 1937; Skovgaard and Daugbjerg 2008)

Filoreta

Amoebae that form extensive multinucleate reticulate plasmodial networks, with cells of various shapes and sizes connected by cytoplasmic strands. Strands vary in width from 0.1 μm to sheet-like expanses of cytoplasm, but very fine strands are always present, although the anastomosing reticulate network is short-lived. Cytoplasmic streaming can be bi-directional, but not always obviously; flow can be predominantly or completely in one direction, or switch direction. In contrast to *Leucodictyon* and *Reticulamoeba* (see below), cytoplasmic threads largely lack prominent granules. Round, smooth-walled cysts are produced. The group includes the organism recently described as *Corallomyxa tenera* (Tekle *et al.* 2007), though it has been moved (Bass *et al.* 2009a) to the new genus *Filoreta*. (Bass *et al.* 2009a; Pawlowski and Burki 2009; Tekle *et al.* 2007)

Gromia

Genus of large marine rhizopods with filose pseudopodia and a large ovoid proteinaceous test. Pseudopodia are non-granular and do not exhibit bidirectional streaming, distinguishing *Gromia* from foraminifera. The test has an oral capsule from which pseudopodia emerge; its light-brown wall is perforated by radially-directed canals, and it has a unique honeycomb membrane structure on its inner side, which distinguishes it from other testate filose amoebae. There is a motile stage with two flagella. Mitochondria are probably tubulocristate, though the published photographs have been interpreted as showing ramicristate mitochondria. Some species reach up to 38mm in diameter. (Archibald and Keeling 2004; Bass *et al.* 2009a; Bass *et al.* 2005; Burki *et al.* 2002; Chantangsi *et al.* 2010; Gooday *et al.* 2000; Hedley and Bertaud 1962; Hedley and Wakefield 1969; Longet *et al.* 2004; Longet and Pawlowski 2007; Nikolaev *et al.* 2003; Nikolaev *et al.* 2004; Patterson 1999)

Phytomyxea

Plasmodiophorids and phagomyxids, rhizarian “zoosporic fungi”- parasitoids or intracellular parasites of vascular plant roots or stramenopiles, which form multinucleate plasmodia and fruiting bodies in plant roots, chitin-walled cysts, zoospores and an invasive attacking stage which has unique modifications of the ER in the intracellular protrusion, the “stachel” and “rohr”. There is a characteristic cruciform nuclear division in unicells and plasmodia. Biflagellated zoospores have two exceptionally long basal bodies, each with an identical pair of two roots: one of two microtubules which extends to an indentation in the cell membrane; one which increases from 1 to 3 microtubules and extends to and along the cell membrane. The group includes plasmodiophorids and phagomyxids, demarcations between these groups currently being unclear. The group includes important agricultural pests *Spongospora subterranea*, potato “powdery scab” pathogen, and *Plasmodiophora brassicae*, cabbage club root disease agent. (Aist and Williams 1971; Archibald and Keeling 2004; Barr 1981; Barr and Allan 1982; Bass *et al.* 2009a; Bass *et al.* 2005; Braselton 1995; Bulman *et al.* 2001; Cavalier-Smith and Chao 2003b; Cavalier-Smith and Chao 1997; Cavalier-Smith and Chao 2003c; Chantangsi *et al.* 2010; Dylewski *et al.* 1978; Longet *et al.* 2004; Van de Peer *et al.* 2000)

Vampyrellids

Large round (globular), multinucleate, reticulate amoebae; with long, thick cytoplasmic arms ending in fan-like flat pseudopodia giving rise to filopodia; and with finely granular, streaming cytoplasm, which is often bright orange in colour. They feed by perforating the cell walls of algae and fungi, and ingesting the victim's cytoplasm. The feeding amoebae alternate with cysts; a bi-flagellated stage is known from *Platyreta*. Mitochondrial cristae are tubular; some organisms have helical arrays of ribosomes in the cytoplasm. Most are soil-dwelling; one is marine. They are similar to *Theratromyxa* and *Biomyxa* (Eukaryotes *incertae sedis*); they have been recently classified in the Aconchulinida with *Biomyxa*. (Bass *et al.* 2009a; Hülsmann 1993; Hülsmann and Grebecki 1995; Patterson *et al.* 1987; Röpstorf *et al.* 1993; Röpstorf *et al.* 1994)

Foraminifera

Highly diverse marine, freshwater and terrestrial rhizopods with large reticulate networks of granular pseudopodia which exhibit unique bidirectional rapid cytoplasmic streaming. The group is important in palaeontology. There is alternation of generations and very complex and variable morphology in the life cycle. There is a “fuzzy-coated” organelle of unknown function in the reticulopodia. Microtubules may be organised as single filaments or loose bundles, helical filaments, or helical filaments packed into paracrystalline arrays. Many taxa have membranous, agglutinated or calcareous chamber-bearing tests, which appear in the cambrian fossil record and are used as stratigraphic markers. Recent molecular studies have included the naked *Reticulomyxa* and deep-sea barium-sulfate producing xenophyophoreans in the group. Molecular environmental studies have also revealed considerable diversity that has not yet been correlated with morphology. Traditional taxonomy has been based on presence and complexity of tests (relating extant taxa to fossils), but this scheme is not supported by molecular studies. Broad groups include allogromiids + monothalamous textulariids (paraphyletic group with naked or single-chambered membranous or proteinaceous tests, or agglutinated tests in astrorhizids and multiple textulariid lineages), miliolids (with perforated porcellaneous calcite shells with chambers angled at 144 degrees to each other), fusulids (with fusiform microgranular calcite shells), and polythalamous textulariids and rotaliids (with multi-chambered spiral tests made of hyaline calcite, or multi-chambered agglutinated tests). Frequently, there are endosymbiotic eukaryotes in the pseudopodia: red algae, dinoflagellates, diatoms, and chlorophytes. Foraminifera used to be part of Granuloreticulosea, which no longer seems to be a natural group on the basis of molecular studies. The group probably includes some Xenophyophores and Komociacea (reticulate amoebae visible to the naked eye). They are often classified in the Retaria with Radiozoa, but support for this grouping varies considerably. EST libraries have been compiled for *Reticulomyxa filosa*. (Archibald and Keeling 2004; Aurahs *et al.* 2009; Bass *et al.* 2009a; Bass *et al.* 2005; Berney and Pawlowski 2003; Bowser *et al.* 1995; Burki *et al.* 2006; Dettmering *et al.* 1998; Grigelis 1978; Habura *et al.* 2008; Holzmann *et al.* 2003; Loeblich and Tappan 1989; Longet *et al.* 2004; Longet and Pawlowski 2007; Pawlowski 2000; Pawlowski *et al.* 1999; Pawlowski and Burki 2009; Pawlowski and Holzmann 2003; Pawlowski *et al.* 2001a; Pawlowski *et al.* 2001b; Tappan and Loeblich 1988)

Radiozoa

Two former member groups of the polyphyletic “Radiolaria”. Organisms with radiating arms, microtubule-supported axopodia, which extend outwards from a central cell body, though a porous organic capsule, to connect with a frothy external layer that contains digestive vacuoles and symbionts. There may be a skeleton or amorphous silica or strontium sulphate, varying from scattered spicules to geometrically ornate polygonal shells surrounding the central cell body. The siliceous skeleton of Polycystinea is secreted within a specialised envelope which determines shell shape. These protists were described by Haeckel in a famous series of engravings, however the Haeckelian concept of the Radiolaria is rendered polyphyletic by the Phaeodarea falling outside the group. Radiolaria is now often used in the more restricted sense given here as Radiozoa (*i.e.* excluding Phaeodarea): as explained in Adl *et al.* (Adl *et al.* 2005) Radiolaria is retained in the literature because it is a widely recognised name in biology and micropalaeontology. Radiozoa lack a polyubiquitin insertion, and their placement in phylogenetic trees varies: they have been classified with foraminifera in the Retaria, but support for this varies and the grouping may be a long branch attraction artefact. (Amaral-Zettler and Caron 2000; Amaral-Zettler *et al.* 1997; Bass *et al.* 2005; Chantangsi *et al.* 2010; Longet *et al.* 2004; Lopez-Garcia *et al.* 2002; Nikolaev *et al.* 2003; Nikolaev *et al.* 2004; Pawlowski and Burki 2009; Polet *et al.* 2004; Yuasa *et al.* 2005)

Acantharea

“Radiolarian” marine protists with radiating axopodia and spicules of strontium sulphate crystals arranged in 20-fold symmetry radiating from the centre of the cell. The cell is surrounded by a capsule of fibrillar material which interconnects myonemes that control the direction of the spicules. Axopodia contain hexagonal or dodecagonal bundles of microtubules. Endosymbiotic algae may be present. There is no fossil record as SrSO₄ is soluble in seawater. The group has traditionally been divided into Arthracanthida (with a thick capsule demarcating inner and outer areas, hexagonal bundles of microtubules in axopodia; symbionts, sexual reproduction without gamontocysts), Chaunocanthida (with pigmented cytoplasm and many small nuclei in the central cell body, clear outer cytoplasm, contractile matrix at the base of spicules, hexagonal arrays of microtubules in axopodia; reproduction in a scaled gamontocyst), Holocanthida (with pigmented cytoplasm and many small nuclei in the central cell body, clear outer cytoplasm, dodecaagonal arrays of microtubules in axopodia; reproduction in a gamontocyst), and Symphacanthida (with pigmented cytoplasm and one large nucleus in the central cell body, clear outer cytoplasm, anastomosing pseudopodia outside the central capsule; reproduction in a gamontocyst). Molecular phylogenetic studies of SSU rRNA have shown a sister relationship with Polycystinea (which also use SrSO₄) and *Sticholonche* (which also has hexagonal arrangements of microtubules in the axopodia), and a placement of this lineage in the Rhizaria, however these taxa lack the single or double insertion in the polyubiquitin gene characteristic of other Rhizarians. (Amaral-Zettler and Caron 2000; Amaral-Zettler *et al.* 1997; Bass *et al.* 2005; Febvre 1990; Longet *et al.* 2004; Lopez-Garcia *et al.* 2002; Nikolaev *et al.* 2003; Nikolaev *et al.* 2004; Pawlowski and Burki 2009; Polet *et al.* 2004; Yuasa *et al.* 2005)

Polycystinea

“Radiolarian” marine protists with axopodia and a skeleton of hydrated silica ranging from spicules to lattices with radiating spines. There is a rich fossil record of spumellariids and nassellariids. With cytoplasm divided into a central, nucleated optically dense area, and a peripheral ectoplasm which may bear symbionts; there is a membranous capsule surrounding the cell body, through which axopodia pass; axopodia have hexagonal arrays of microtubules. With a complex life cycle including biflagellated swimmers and vegetative colonies, some (Spumellariids) containing SrSO₄ crystals. The group has traditionally been divided into *Spumellaria* (spherical central capsule with evenly-distributed round pores in the capsule wall, skeleton of scattered spicules or latticed concentric shells) and *Nassellaria* (ovoid central capsule with pores at one end of the wall; skeleton is a tripod, a sagittal ring, or a helmet-shaped shell enclosing the capsule). Molecular phylogenies of SSU rRNA and actin place Polycystinea with acantharea and *Sticholonche*, in the Rhizaria, however these taxa lack the single or double insertion in the polyubiquitin gene characteristic of other Rhizarians. (Amaral-Zettler and Caron 2000; Amaral-Zettler *et al.* 1997; Bass *et al.* 2005; Cachon and Cachon 1973; Cachon *et al.* 1990; Longet *et al.* 2004; Lopez-Garcia *et al.* 2002; Nikolaev *et al.* 2003; Nikolaev *et al.* 2004; Pawlowski and Burki 2009; Polet *et al.* 2004; Yuasa *et al.* 2005)

Sticholonche

Spectacularly complex genus of reniform, bilaterally symmetrical marine protists with parallel rows of locomotory axopodia and rosettes of flattened siliceous spicules. Organisms swim by “rowing” with axopodia, because the hexagonally-packed microtubules supporting each axopod insert in ball and socket joints (of unknown proteins) on the nuclear membrane. Spatula-shaped flattened hollow spicules are present in 14 rosettes, positioned symmetrically in pairs on either side of the cell body or in the sagittal plane. The single SSU rRNA analysis that includes *Sticholonche* places it in a clade (100% bootstrap support) with Acantharea and Polycystinea. *Sticholonche* is the sole described member of the Taxopodida, though molecular surveys of the Sargasso Sea indicate considerable diversity closely related to *S. zanclea*. Gymnosphaerids have a similar organisation of microtubules in their axonemes, which also arise from a site next to the nucleus, but they are currently defined as Eukaryotes *incertae sedis* as no molecular data is available for them. (Cachon *et al.* 1977; Hollande *et al.* 1967; Hollande and Enjumet 1954; Jones 1975; Nikolaev *et al.* 2004; Pawlowski and Burki 2009; Yuasa *et al.* 2005)

Rhizaria *incertae sedis*

Heliomorphids (=“Dimorphids”)

“Heliozoan” type flagellates, formerly in the genera *Dimorpha*, *Acinetactis* and *Tetradimorpha*; with radiating arms (axopodia) that are stiffened by square-packed or irregular bundles of ca. 50 microtubules. The microtubular bundles all converge on a single centrosome, which is located in a pit on the anterior edge of the nucleus. The axopodia carry extrusomes which are easily visible. There are two (or four) flagella which insert orthogonally, with one emerging at the anterior end of the cell (surrounded by a mucus sheath in *Heliomorpha mucosa* = *Dimorpha mutans*); the other flagellum emerges at the side of the cell. The flagella have

extremely long basal bodies (similar to those in Phytomyxids) which converge on the centrosome, and are linked to it by one striated fibrillar rootlet and a microtubular rootlet each. Mitochondrial cristae are tubular, vermiform, and appear ramicristate. The taxonomy of the group has recently been revised (Bass *et al.* 2009) on the basis of SSU rRNA sequences, with the invalid genus *Dimorpha* being replaced by *Heliomorpha*. (Bass *et al.* 2009a; Brugerolle *et al.* 2002; Brugerolle and Mignot 1983; Brugerolle and Mignot 1984a, 1984b; Cavalier-Smith 1993; Cavalier-Smith and Chao 2003b; Mignot and Brugerolle 1991; Mikrjukov 2000b; Mikrjukov 2000a; Patterson and Zölffel 1991)

Other genera in the Rhizaria with light-microscopical and SSU rRNA identities include *Nanofila*, *Mesofila*, *Ventrifissura*, and *Verrucomonas*. (Bass *et al.* 2009a; Chantangsi *et al.* 2010)

“THE CCTH CLADE”

A group of free-living, heterotrophic, mixotrophic and autotrophic organisms, also known as Hacrobia, where it is named after the first two lineages identified to be related: haptophytes and cryptomonads. There are no known parasitic taxa in the group; but at least one (the kathablepharid *Hatena*) has a complex life cycle involving a facultative symbiont. Evidence for the group comes from both single-gene and multigene phylogenies, although currently no multigene phylogeny supporting the group's monophyly contains representatives of each of the proposed constituent taxa. A conserved isoform of the plastidic gene *rpl36*, acquired by lateral gene transfer from a bacterial donor, unites the cryptomonads and haptophytes. No ultrastructural synapomorphies have been reported, although similarities of the flagellar apparatus, sublamellar vesicles, and ejectisomes- are all observed in most CCTH groups. There is some debate concerning the phylogenetic position of this group: sister-group relationships to the archaeplastids or to the rhodophytes have been recovered in multigene phylogenies; however, phylogenomic analyses using solely slow-evolving gene datasets have recovered strong support for a sister-group relationship to the SAR clade. (Burki *et al.* 2007; Burki *et al.* 2008; Cavalier-Smith 2010; Hackett *et al.* 2007; Hampl *et al.* 2009; Nozaki *et al.* 2009; Okamoto *et al.* 2009; Rice and Palmer 2006)

Cryptomonads

Mostly “algal” cells with blue, brown or green chloroplasts; they are distinguished by characteristic flagella (with hairs), a geometric cell coat, and “ejectosome” type extrusomes. They have two flagella lined with stiff bipartite hairs: one row of short hairs on the short ventral flagellum, and two rows of long hairs on the long dorsal flagellum. Cells are coated in a periplast formed of geometrically positioned fibrous material on the cell membrane; this may be sheet-like, form hexagonal plates, or form rosette scales, in the same taxa at different times. Mitochondrial cristae are flattened. The flagella insert in a subapical, ventral groove, which is lined under the cell membrane with ribbon-like ejectisomes (explosive organelles that consist of two connected spiral ribbons held under tension); there are ejectisomes on the rest of the cell also. There are three microtubular roots, and a rhizostyle (microtubular root associated with multilayered material) that may or may not be keeled in shape; and a large fibrillar root. Brown, blue and red photosynthetic taxa, and colourless taxa that have lost plastids, contain or have contained a red algal-derived, secondary plastid, which bears phycocyanins,

phycoerythrins and chlorophylls a and c. Plastids are surrounded by four membranes, and contain a nucleomorph (reduced red algal nucleus), with an extremely diminished structure, including reduced or no introns, and limited intrachromosomal and interchromosomal recombination. In addition, plastids may retain a functional mitotic apparatus, although no ultrastructural evidence for a mitotic spindle or centrosome has yet been obtained.

The colourless, plastid-lacking *Gonionomonas* forms a sister group to all other taxa; these have been divided into six clades based on SSU rRNA analyses, which suggests that there have been multiple losses of photosynthesis (e.g. in *Chilomonas*, which has a leucoplast and evolved from *Cryptomonas*) and that brown, blue and red pigmentation do not correspond with basal subdivisions of the cryptomonads; instead cryptomonad phycocyanins evolved from red algal phycoerythrin. Cryptomonad-derived plastids are recovered in members of the dinoflagellate genus *Dinophysis*; these are believed to be uptaken by frequent and repeated kleptoplastoidy via a phagotrophic ciliate intermediate, although some lineages may represent genuine tertiary endosymbiotic acquisitions. A draft genome of the cryptomonad *Guillardia theta* is currently underway. Multigene phylogenies strongly suggest close affinities to telonemids and kathablepharids, and - more distantly - to haptophytes. (Archibald *et al.* 2001; Brett *et al.* 1994; Brett and Wetherbee 1986; Burki *et al.* 2007; Cavalier-Smith 1998; Douglas *et al.* 1991; Garcia-Cuetos *et al.* 2010b; Hackett *et al.* 2007; Harper *et al.* 2005; Hill and Rowan 1989; Hill and Wetherbee 1986; Hoef-Emden and Melkonian 2003; Hoef-Emden *et al.* 2005; Janson 2004; Keeling 2004; Keeling *et al.* 1999; Kugrens *et al.* 1999; Kugrens and Lee 1991; Lane *et al.* 2007; Marin *et al.* 1998; McFadden *et al.* 1994; Mignot 1965; Mignot *et al.* 1968; Okamoto *et al.* 2009; Okamoto and Inouye 2005a; Park *et al.* 2008; Patron *et al.* 2007; Patron *et al.* 2004; Patterson 1989; Perasso *et al.* 1992; Roberts *et al.* 1981; Takishita *et al.* 2002)

Kathablepharids

Free-living heterotrophic flagellates, oblong or cylindrically ovate, with two subapically-inserting flagella and the whole body covered in a bi-layered organic sheath with lamellae between the layers forming spiral rows around the cell body. The cell membrane is supported by a layer of sub-pellicular microtubules. With a complex conical, apical feeding apparatus (composed of a cytostome, cytopharyngeal rings, and longitudinal arrays of microtubules) and peripheral ER; with tubular mitochondrial cristae; and with several types of single-coil ejectisomes. The flagella appear thick, and may be covered with an outer layer of scales; they insert in an apical groove; the transition zone consists of a proximal electron-dense septum, a transverse plate and (in one taxon) a distal spiral outside the 9 pairs of microtubules. There are 4 microtubular flagellar roots, a striated root and a fibrous root. Heterotrophy may occur via attachment to the apex and engulfment, engulfment via the flexible expansion of cytoplasm, or myzocytotic consumption of cytoplasm, and individuals may swarm to engulf prey.

Five genera are currently known. One species, *Hatena*, exists with a green algal symbiont, with an eyespot that has been suggested to be formed from both symbiont and host membrane components; there is no evidence of plastids or plastid genes in kathablepharids. Morphological similarities in the feeding apparatus and peripheral ER have historically been used to suggest a sister-group relationship with the alveolates; however, flagellar rootlet configurations and recent molecular analyses have favoured a position within the CCTH/Hacrobia, as

the sister taxon to cryptomonads. (Clay and Kugrens 1999a; Kim and Graham 2008; Kim *et al.* 2006; Lee and Kugrens 1991a, 1991b; Lee and Kugrens 1992; Okamoto *et al.* 2009; Okamoto and Inouye 2005a, 2005b, 2006; Vørs 1992a, 1992b)

Picobiliphytes

Small (6 µm long) planktonic organisms of unknown general appearance, which have been described as a distinct clade in analyses of environmental 18S rRNA sequences from marine picoplanktonic samples. The cells have been identified in multi-eukaryotic samples by fluorescent *in situ* hybridisation but have not been described using standard light- or electron microscopy. Distributed throughout subarctic, temperate and subtropical marine waters; prevalence does not substantially relate to latitude, but may be principally limited to euphotic zones. Picobiliphytes have an organelle containing phycobilins, similar in fluorescence profile to the plastids of red algae and cryptomonads. A small body proximal to this organelle that stains for nucleic acids, hypothesised to be a nucleomorph, has been identified, but may not be present in all lineages. Phylogenetic analyses suggest that picobiliphytes are the sister group of cryptomonads and katablepharids, to the exclusion of haptophytes. (Cuvelier *et al.* 2008; Li *et al.* 2008; Not *et al.* 2007a; Not *et al.* 2007b)

Haptophytes

Free-living mixotrophic or autotrophic flagellates with two flagella and a haptonema (a locomotory, attachment and feeding organelle supported by microtubules). Amoeboid, coccoid, colonial and filamentous stages may occur, life cycles can involve complex alternation of generations and sizes range from the nanoplankton to macroscopic (*Phaeocystis*). There are up to four microtubular roots and striated and fibrillar roots. Mitochondrial cristae are tubular. There is endoplasmic reticulum surrounding the chloroplast, continuous with the outer membrane of the nucleus, and under the cell membrane over nearly all the cell. The one or two chloroplasts contain chlorophylls a and c, with distinctive lamellae made of three thylakoids, and lacking a girdle lamella.

Haptophytes can themselves be endosymbionts of dinoflagellates (resulting in HNOF-type plastids in dinoflagellates). Nuclear multigene phylogenies strongly support a close relationship to cryptomonads, and some single-gene phylogenies suggest a specific sister-group relationship to centrohelids. However, some phylogenies of chloroplast-encoded and -targeted genes support a relationship with stramenopiles and alveolates to the exclusion of cryptomonads, which has been interpreted as evidence for a tertiary endosymbiotic acquisition of plastids from a haptophyte donor. (Andersen 2004; Bachvaroff *et al.* 2005; Billard 1994; Bodyl *et al.* 2009; Burki *et al.* 2008; Cavalier-Smith 1998; Christensen 1962; Edvardsen *et al.* 2000; Green and Leadbeater 1994; Hackett *et al.* 2007; Harper *et al.* 2005; Ishida *et al.* 2007; Keeling 2004; Kim *et al.* 2006; Li *et al.* 2006; Moestrup 2000; Okamoto *et al.* 2009; Patron *et al.* 2007; Patron *et al.* 2004; Ryall *et al.* 2003; Sanchez-Puerta and Delwiche 2008; Thomsen 1986; Yoon *et al.* 2002a; Yoon *et al.* 2002b; Yoon *et al.* 2005)

Prymnesiophytes

Haptophytes with calcareous scales (coccoliths); isokont flagella (identical length, “pushing” beat making the cell swim backwards or “breast stroke” beat making the cell swim forwards) of which the mature flagellum is autofluorescent; There are two microtubular roots on each basal body. The anterior (immature) basal body gives rise to two small roots, while the posterior (mature) basal body gives rise to one broad root directed towards the chloroplast, and one smaller root which may nucleate microtubules in mitosis. There is a long coiled haptonema. A variety of organic or calcium carbonate scales occur on many species; siliceous scales have been observed in the species *Hyalolithus neolepis*. Calcified scales are well-preserved in the palaeontological record, forming chalk deposits (e.g. the white cliffs of Dover), and playing a major role in the long-term global carbon cycle. The observed sensitivity of scale formation to a number of environmental factors including CO₂ abundance, pH and temperature has led to the suggestion that prymnesiophytes may be a particularly clear sensor of recent climate change. There is a complex life cycle, which may in part be regulated by internal viruses; scale morphology and calcification varies between diploid or haploid life stage. The prymnesiophytes also include *Reticulosphaera*, a reticulate amoeboid organism superficially similar to chlorarachniophytes or *Leucodictyon*. *Phaeocystis*, *Prymnesium* and *Chrysochromulina* are agents of fish-killing planktonic blooms. A complete genome sequence is available for *Emiliana huxleyi*, and draft sequence assemblies of two species of *Phaeocystis* are currently underway. (Beech *et al.* 1988; Billard 1994; Cavalier-Smith 1986, 1996; Edvardsen *et al.* 2000; Eikrem and Moestrup 1998; Frada *et al.* 2008; Green and Hori 1994; Green and Leadbeater 1994; Halloran *et al.* 2008; Hibberd 1976a; Iglesias-Rodriguez *et al.* 2008a; Iglesias-Rodriguez *et al.* 2008b; Inouye and Kawachi 1994; Moestrup and Thomsen 2003; Zondervan 2007)

Pavlovophytes

Naked haptophytes, with heterokont flagella (short mature flagellum and long immature flagellum with knobs - modified scales - reversing thrust in some taxa, giving a “pulling” beat which makes cells swim forwards); with a short uncoiled haptonema. The anterior (immature) basal body has no associated roots. The posterior (mature) basal body gives rise to a fibrillar structure, and a small and a broad microtubular root in opposite orientations to those of prymnesiophytes. Stigmata may be found in the plastid, though they are not associated with the flagellum as in stramenopiles. Three subclasses are recovered by 18S rRNA phylogenies, each bearing a distinctive array of photosystem pigments. (Beech *et al.* 1991; Cavalier-Smith 1986; Edvardsen *et al.* 2000; Eikrem and Moestrup 1998; Green 1980; Green and Hori 1994; Green and Leadbeater 1994; Inouye and Kawachi 1994; Jordan *et al.* 1995; Tengs *et al.* 2000; Van Lenning *et al.* 2003)

Centrohelids

“Heliozoan” aflagellated protists with radiating arms (axopodia) stiffened by bundles of *ca.* 150 microtubules in a distinctive triangular pattern of arcs around a central hexagon. The microtubules converge on a central multilayered MTOC, with each bundle ending conically with the central microtubules ending closest to the MTOC. The arms have ball-and-cone extrusomes which are easily visible. The cell body is rounded and may be covered with siliceous or organic spines or scales,

which have taxonomic value. There is a radiating system of endocytic vesicles near the cell surface; there are many Golgi bodies dispersed through the cell. Mitochondrial cristae are flat, similar to those of nucleariids (Opisthokonta). Heterotrophy occurs via entrapment on the axopodia, expulsion of extrusomes, and immobilisation of prey prior to engulfment; some species are observed to form swarms, which fuse to form a single multinuclear cell with a communal spherical food vacuole before engulfment. Originally considered on morphological grounds as aflagellate members of the heliozoa, molecular data has suggested closer relationships to various photosynthetic taxa including rhodophytes and haptophytes; most recently, phylogenomic analyses have recovered strong support for a sister-group relationship to telonemids, within the CCTH/Hacrobia. (Bardele 1977a; Bardele 1977b; Burki *et al.* 2009; Cavalier-Smith and Chao 2003a; Febvre-Chevalier and Febvre 1984; Mikrjukov 1996; Nikolaev *et al.* 2004; Okamoto *et al.* 2009; Sakaguchi *et al.* 2007; Sakaguchi *et al.* 2005; Sakaguchi *et al.* 2002; Smith and Patterson 1986; von der Heyden *et al.* 2004; Zlatogursky 2010)

Telonemia

Predatory flagellates with a complex cell coating: a multilayered subcortical lamina of microtubules and fibres oriented at *ca.* 90 degrees to each other. There are vesicles beneath the outer cell membrane that contain “paracrystalline objects”. The two equal flagella arise from near-parallel basal bodies, which give rise to the microtubules of the sheath. The flagella insert on either side of a short antapical rostrum, they have tripartite tubular hairs. Food uptake occurs in an antero-ventral depression which is not covered by the sheath. The submembrane vesicles may be homologous to subcortical alveoli of alveolates. Cell sizes vary substantially, with a five-fold range in diameters measured in cultured species. One genus, *Telonema*, is known, containing two species; however, environmental 18S rRNA sequencing suggests that the genus contains many more than two species and has a cosmopolitan distribution, including freshwater, pelagic and deep-sea habitats. Molecular analyses have variously placed telonemids with cryptomonads and with stramenopiles; recently, phylogenomic analyses have suggested a close relationship to the centrohelids, within the CCTH/Hacrobia. (Bråte *et al.* 2010; Burki *et al.* 2009; Burki *et al.* 2008; Klaveness *et al.* 2005; Lefevre *et al.* 2008; Patterson *et al.* 1993b; Shalchian-Tabrizi *et al.* 2006; Shalchian-Tabrizi *et al.* 2007; Tong *et al.* 1998; Vørs 1992a)

“EUKARYOTES INCERTAE SEDIS”

Some eukaryotic taxa remain unplaced: through being inadequately described, genuinely difficult to place, or genuinely not closely related to any other group.

Apusozoa

A group of small, bi-flagellated, gliding protists, traditionally including the genera *Apusomonas*, *Amastigomonas* and *Ancyromonas* (= *Planomonas*). Protein and ribosomal RNA trees with eukaryote-wide sampling suggest that some combination of the apusomonads and *Ancyromonas/Planomonas* may be closely related to the Opisthokonts. However, apusomonads exhibit the dihydrofolate reductase–thymidylate synthetase gene fusion supposedly characteristic of bikonts: suggesting that Apusozoa may be of particular interest to the study of eukaryotic evolution because they show affinities with both ‘unikonts’ and ‘bikonts’. Support for the

group uniting apusomonads with *Ancyromonas* is frequently weak: solid hypotheses of homology, linking apusozoa to each other and/or to other eukaryotic groups, await a broader understanding of both apusomonads and *Ancyromonas*. Possible homologies between the flagellar apparatuses of ancyromonads and apusomonads (and excavates) include a splitting root on the right side of the posterior basal body and a singlet root, both supporting a longitudinal groove associated with the posterior flagellum. The anterior flagellar apparatus in each includes a root supporting structures to the left of the anterior flagellum. (Atkins *et al.* 2000a; Atkins *et al.* 2000b; Brown *et al.* 2009; Cavalier-Smith 2003b, 2009; Cavalier-Smith and Chao 1995; Cavalier-Smith and Chao 2010; Cavalier-Smith *et al.* 2008a; Cavalier-Smith *et al.* 2004; Heiss *et al.* 2010; Heiss *et al.* in press; Kim *et al.* 2006; Marande *et al.* 2009; Stechmann and Cavalier-Smith 2003)

Ancyromonas

Small gliding reniform flagellates with a single-layered dorsal organic sheath, and a short anterior flagellum and a long trailing posterior flagellum. There are two basal bodies, each with its own flagellar pocket. The anterior basal body associates with a microtubular doublet root that runs from between the basal bodies to support the cell's rostrum, and a short singlet root. The posterior basal body is associated with a conventional microtubular root; a curved ribbon of ~8 microtubules near the basal body, that splits proximally; and a posterior singlet root; all supporting the flagellar pocket and posterior flagellar channel. Mitochondria have flattened cristae. The genus *Ancyromonas* was recently replaced with a new genus, *Planomonas*, however the basis for this is contentious. A mitochondrial genome sequencing project is underway. (Atkins *et al.* 2000a; Cavalier-Smith and Chao 2010; Cavalier-Smith *et al.* 2008a; Cavalier-Smith and Chao 2003c; Heiss *et al.* 2010; Lee and Patterson 2000; Mylnikov 1990; Tong *et al.* 1998)

Apusomonads

Gliding flagellates with a double-layered dorsal organic sheath that lies over the dorsal face of the cell and ensheathes the basal part of the anterior flagellum. Apusomonads have two flagella, the first extends anterior or antero-laterally, the second trails behind the cell. The two basal bodies insert almost at right angles and give rise to four microtubular roots, two of which determine the margins of the ventral face of the cell, supporting the groove that holds the trailing flagellum. The posterior flagellum inserts orthogonally to the anterior one, at the base of a proboscis-like sleeve that extends anteriorly from the marginal folds of the dorsal sheath, and partly encloses the anterior flagellum. There are ventral pseudopodia. Mitochondrial cristae are tubular. Flagellar transformation has been suggested to follow the anterior-posterior pattern. On the basis of SSU rRNA, light microscopy and TEM, the taxonomy of the group has recently been revised to include the genera *Amastigomonas*, *Apusomonas*, *Thecamonas*, *Podomonas*, *Manchomonas* and *Multimonas*. A mitochondrial genome sequencing project is underway for *Apusomonas*. (Cavalier-Smith and Chao 2010; Cavalier-Smith *et al.* 2008a; Cavalier-Smith and Chao 2003c; Heiss *et al.* in press; Karpov 2007; Karpov and Mylnikov 1989; Karpov and Zhukov 1980; Karpov and Zhukov 1984, 1986; Mikrjukov and Mylnikov 2001; Molina and Nerad 1991; Mylnikov 1989; Mylnikov 1990; Vickerman *et al.* 1974)

Abollifer

Small oval, dorsoventrally flattened flagellates with an anterior ‘lip’ surrounding a deep depression into which the flagellum inserts. The cell surface is rigid and granulated and a pellicle may be present. A shorter trailing flagellum is sometimes present. (Vørs 1992a)

Biomyxa

Large amoebae with long, stiffened branching pseudopodia extending from a central irregular area. The pseudopodia are granular and motile, which suggests a relationship with the amoeboid members of the Rhizaria. They have recently been classified with Vampyrellids in the Aconchulinida; however no molecular information is available for this taxon. Sequences in recent literature that were named *Biomyxa* have been reclassified as *Limnophila*. (Bass *et al.* 2009a; Ekelund *et al.* 2004; Leidy 1879)

Breviataes

A group currently based on molecular phylogeny, which groups two otherwise uncharacterised SSU rRNA sequences, with the SSU rRNA sequence from *Breviata anathema* (studied in recent years as *Mastigamoeba invertens*). Analyses of many concatenated genes place *Breviata anathema* as the sister group to the rest of the Amoebozoa; in this phylogenetic position it is important in considerations of broad eukaryotic phylogeny. Organisms assigned to *B. anathema* are amoeboid flagellates with a constant rounded body shape and filose branching pseudopodia at anterior and posterior ends; a single flagellum with two basal bodies; with a distinctive ‘fan’ of microtubules arising from the anterior (flagellar) basal body; and a pseudopodial feeding area subtended by four microtubular roots arising from the very short posterior basal body. There is a large, branching mitochondrion-like structure without cristae, which may have some mitochondrial functions. (Cavalier-Smith 2004; Dawson and Pace 2002; Edgcomb *et al.* 2002; Minge *et al.* 2009; Roger and Simpson 2009; Stiller *et al.* 1998; Walker *et al.* 2006)

Collodictyonids (= Diphylleids)

Flagellates with a deep ventral feeding groove, and with two (*Diphylleia*, *Sulcomonas*) or four (*Collodictyon*) flagella inserting apically and orthogonally, with a distinctive flagellar apparatus. The transition zone of the flagella distinguishes collodictyonids from all other eukaryotes, with an electron-dense sleeve around the central microtubules, and an internal granule between the end of the central microtubules and the transitional plate. One basal body gives rise to a curved dorsal microtubular/fibrillar loop, from dorsal the side of which radiate bundles of microfibrils; the second basal body gives rise to left and right ventral roots of microtubules and fibrillar material, which support the sides of the feeding groove. The other two basal bodies in *Collodictyon* also give rise to microtubular roots. The horseshoe arrangement of dictyosomes is also unusual in the eukaryotes. SSU rRNA phylogenies have not yet resolved the placement of *Diphylleia* in the eukaryotes. (Brugerolle 2006; Brugerolle *et al.* 2002; Brugerolle and Patterson 1990; Cavalier-Smith 2003a; Cavalier-Smith and Chao 2010; Cavalier-Smith *et al.* 2008a; Klaveness 1995; Patterson 1999)

Colponema

Small reniform flagellates with subsurface alveoli and a ventral feeding groove. The two flagella insert orthogonally, the anterior one arising through a pore and bearing non-tubular mastigonemes, and the posterior one inserting in a ventral sulcus and bearing a wide vane. The flagella are anchored by two fibrillar roots each; the anterior flagellum has a striated root and a fibrillar root that gives rise to a dorsal ‘curtain’ of microtubules; while the posterior flagellum has fibrillar roots that give rise to microtubular roots that support the sides of the ventral groove. The ventral groove can emit fine filopodia and is the region of phagocytosis. Mignot and Brugerolle argued that the cell structure (flagellar apparatus, mastigonemes, cell cortex) suggests an affinity with *Cyanophora* (Archaeplastidia, Glaucophyta) or with certain excavate taxa, however the usual current interpretation by most authors is of alveolate affinities. No molecular information is available for this taxon. (Adl *et al.* 2005; Brugerolle 2002; Leander and Hoppenrath 2008; Lee and Kugrens 1992; Mignot and Brugerolle 1975b; Mylnikov 2008; Mylnikov and Tikhonenkov 2009; Mylnikova and Mylnikov 2010)

Copromyxids

“Cellular” slime moulds with tall conical branching sorocarps, which develop from aggregated amoebae. The trophic stage is a uninucleate lobose amoeba with broad anterior pseudopodia and filose posterior pseudopodia. These amoebae aggregate to form a non-streaming pyramid up to several millimetres high. Mitochondrial cristae are tubular, which suggest that copromyxids belong to the Amoebozoa rather than with the Acrasids, where they have been classified, or the Fonticulids, which have discoidal cristae. No molecular information is available for this group. (Nesom and Olive 1972; Raper *et al.* 1978; Spiegel and Olive 1978)

Discocelis

Small disc-shaped flagellates that adhere tightly to sand grains; with an anterior velum and two anteriorly inserted unequal flagella. The cell periphery and velum are supported by ribbons of microtubules. Three flagellar roots of a few microtubules each arise from the flagellar basal bodies; two roots run along the ventral cell membrane while the third supports the posterior edge of the velum. There is a microbody-like paranuclear organelle and a row of extrusomes bordering the cell periphery. Mitochondria have short tubular cristae. This organism is well-described and easily recognisable, but its morphology does not suggest any particular relationship with other eukaryotes, and there is no molecular information available. (Ekebom *et al.* 1996; Hausmann *et al.* 2002; Tikhonenkov *et al.* 2006; Tong *et al.* 1998; Vørs 1988)

Glissandra

Small gliding flagellates with an almost spherical body. The two flagella insert side by side into an anterior ventral groove; they are held against the substrate when the cell glides, one held anteriorly, one held posteriorly. The tip of the anterior flagellum moves back and forward during gliding, similar to that of *Petalomonas* (Euglenozoa, Excavata); there are similarities (none of them strong) with Euglenids (Excavata), cercomonads and thaumatomonads (Rhizaria). (AlQassab *et al.* 2002; Lee 2006; Patterson and Simpson 1996)

Gymnosphaerids

“Heliozoan” protists with one or more axopodia supported by hexagonally packed bundles of microtubules arising from a central nucleating site next to the nucleus, similar to that seen in desmothoracids (Rhizaria). Cells are naked (*Actinocoryne*) or have siliceous spicules (*Hedriaophrys*) or are covered in mucus (*Gymnosphaera*); they may be attached to the substrate by a contractile or non-contractile stalk with an amoeboid base. Mitochondrial cristae are tubular. Cells may be uninucleate or multinucleate, and may reproduce by budding from the “head”. *Gymnosphaera* and *Actinocoryne* produce biflagellated motile cells. The life cycle is complex (but unresolved) and may have an annual timescale. The axopodial microtubules are packed in the same pattern as those of *Sticholonche* (Rhizaria), but in *Sticholonche* the axopodia arise from ball and socket joints on the nuclear membrane, instead of just one area next to the nuclear membrane. No molecular information is available for this taxon, though morphology suggests that it is probably part of the Rhizaria. (Bass *et al.* 2009a; Febvre 1975; Jones 1975, 1976; Mikrjukov 2000b; Mikrjukov 2000c, 2000a)

Hemimastigophora

Multiflagellated protists with dorsal and ventral subsurface plates with diagonal symmetry. The flagella are arranged in one or more longitudinal kineties: the single basal body associated with each flagellum is anchored by two microtubular roots, one of which is closely associated with the cell surface. *Hemimastix* has a longitudinal kinety down each side of the cell (between the diagonally symmetrical dorsal and ventral plates); *Paramastix* has a wreath of flagella around the top of the cell; *Spironema* has a single spiral kinety in a groove down the cell; *Stereonema* has longitudinal rows of flagella down the cell. *Spironema* moves with euglenoid-like metaboly. Mitochondrial cristae are sacculate (arguably tubular or discicristate, pending further TEM investigation). Distinctive concentric extrusomes are present. No molecular information exists for this taxon, but morphology suggests a possible relationship with the euglenids. A potential relationship with the Apusozoa has been discussed in the literature. (Cavalier-Smith *et al.* 2008a; Foissner and Foissner 1993; Foissner *et al.* 1988)

Kiitoksia

Tiny spherical cells with one or two short trailing flagella, which insert ventrally. The cell body is 1-3 μm in diameter. Cells move by gliding on surfaces. There is no ultrastructural or molecular information available. (Tong *et al.* 1998; Tong *et al.* 1997; Vørs 1992a)

Lagenidiopsis

Sand-dwelling shelled amoebae, with a globular organic shell where the aperture extends into the middle of the shell as a tube. The amoeba’s pseudopodia are thin and filose. No TEM or molecular studies have been carried out, so it is not yet possible to assign this taxon to either the Amoebozoa or Rhizaria, though it is probably a rhizarian. (Bass *et al.* 2009a; Golemansky 1974; Sudzuki 1979)

“Leucodictyon + Reticulamoeba”

Reticulate amoeboid meroplasmodial organisms where the small cell bodies are contained in loaf-shaped fine organic loricae, and fine reticulopodia interconnect the cell bodies. The reticulopodia rarely contain extrusomes; they also contain vesicles

which transport food to the cell bodies. Cell bodies are uninucleate and the nucleus contains a rodlike fibrous element. Mitochondrial cristae are tubular. Binary fission or budding of the cell bodies occurs when food is sparse; it produces one cell that stays in the lorica, and a swimming or gliding biflagellated stage. The flagella are unequal: the anterior flagellum of the zoospore is short and propels the cell by gyration, whereas the posterior flagellum is long and trails behind the cell. The flagellar apparatus consists only of a short fibre connecting both basal bodies, and some microtubules running into the cell; there are granules in the lumen of the centriole that may possibly indicate an affinity with *Massisteria*. An unpublished partial SSU rRNA sequence (Pawlowski *et al.* 2003 Genbank submission, AY268044) suggests that *Reticulamoeba* is a member of the Rhizaria, and that the structural similarity of these taxa to chlorarachniophyte hosts may be due to a relationship between the taxa. *Leucodictyon* and *Reticulamoeba* are also superficially similar to *Reticulosphaera* (Haptophyta), and Stereomyxids. (Bass *et al.* 2009a; Grell 1991b, 1994, 1995; Grell and Schüller 1991)

Meteora

Small oval-shaped, colourless cells with two long axial appendages and two short characteristic lateral ‘arms’ which ‘row’ continuously. The lateral arms possess one granule each, which may be extrusomes like those seen in *Dimorpha* (Rhizaria; Heliomorphidae). Movement is by gliding in the axis of the long axial appendages, free swimming is unknown. There is no molecular or ultrastructural information for this taxon. (Hausmann *et al.* 2002)

Palpitomonas

Colourless, phagotrophic cells with two flagella. The flagella are long (20µm) and almost equal in length; one bears mastigonemes. There are two basal bodies, and two microtubular roots, each associated with the basal body of the non-mastigonemal flagellum. one root has a multi-layered structure similar to those seen in charophyte green algae. In swimming the anterior flagellum beats vigorously, and the posterior trails and may attach to the substratum; in both swimming and attached cells, a distinctive “wobbling” motion is observed. Cells are highly vacuolated, and lack recognisable cell walls or loricae. There is a single mitochondrion, containing flat cristae and several lobate structures, which surrounds the Golgi apparatus. One species, *P. bilix*, identified from subtropical coastal waters. A close relationship either with green algae, telonemids or cryptomonads has been suggested based on ultrastructure, as has a potential relationship with the biflagellate *Kamera lens* on the basis of cell shape and motion during swimming. Phylogenies of six nuclear genes reveals moderate support for a close relationship to either the archaeplastids or the CCTH clade, but the taxonomic position remains ultimately uncertain. (Patterson and Zölffel 1991; Woodcock 1916; Yabuki *et al.* 2010)

Palustrimonas

Small heterotrophic flagellates. The anterior flagellum inserts into a pocket, and has a “flailing” beat. The posterior groove extends most of the length of the cell; the posterior flagellum beats stiffly and is about 2 times the length of the cell. This taxon shows some similarity to *Colpodella* and *Colponema*; also to *Phyllomitus*. (Patterson and Simpson 1996)

Petasaria

Uniflagellated cells with a rounded body and distinctive large siliceous hat-shaped scales, and unmineralized, small cobweb-like scales. *Petasaria heterolepis* is thought to be widespread in oceanic waters but is currently only known from a whole mount SEM preparation. The shape of its scales suggests that it may be a haptophyte related to the silica-scale bearing *Hyalolithus neolepis*. (Moestrup 1979; Preisig 1994; Yoshida *et al.* 2006)

“*Phyllomitus* + *Pseudophyllomitus*”

Small colourless flagellates with 2 flagella that insert at the head of a groove. In *Phyllomitus* the flagella adhere to one another. These genera are distinguished from *Palustrimonas* by their single groove. (Lee 2006).

Quadricilia

Spherical flagellates with four long, acronematic flagella that insert at the same apical point. The cells can be amoeboid with broad, smooth pseudopodia. The single species known has been found in association with diatom blooms. (Auer and Arndt 2001; Vørs 1992a)

Schizocladus

Large deep-sea reticulate plasmodia (up to 1cm high) embedded in a mucilaginous matrix. The multinucleate plasmodium is bush-like with dichotomous branches, and funnel-shaped. There are no solid wall structures, though there are exogenous particles of other organisms' exoskeletons, and endogenous calcite and barite crystals embedded in the mucus. The body surface is smooth with apparent longitudinal striations. Each branch of the cell contains an elastic internal supportive rod of unknown composition. This taxon is similar to Xenophyophores, Komokiacea and Foraminifera, but lacks solid wall structures. Despite the similarity of names it is unrelated to the brown alga *Schizocladia*. (Cedhagen and Mattson 1992)

Spiromonas

Multiflagellated crawling protists that resemble ciliates, but lack nuclear dimorphism seen in ciliates. The cell is sac-like with a complex mouth at the anterior end; the lips are hyaline and non-ciliated; the cell membrane invaginates to form a gullet supported by microtubules, which is about a quarter of the cell's length. The microtubules of the gullet arise from a twisted fibrous structure in the anterior “lip”, and form complex sheets and rods; the cortical microtubules arise from the same area. Flagella are arranged in longitudinal rows, interconnected in each row by longitudinal fibrous bands. The flagellar anchorage consists of microtubules embedded in fibrillar material, arising as a ring at the base of the basal body and extending up to the cell surface to form a band on either side of the flagellum. Mitochondrial cristae are discoid- similar to those in Euglenozoa, suggesting a possible relationship with *Stephanopogon*. No molecular information is available for this group. (Alexeieff 1929; Brugerolle 2002; Brugerolle *et al.* 1979; Wolters 1991)

Stereomyxids

Amoebae with long, fine branching pseudopodia; which fuse to form reticulate plasmodia in multinucleate members of *Corallomyxa*, but not *Stereomyxa*. With a distinct trilaminar centrosome. No molecular information is available on

stereomyxids. Possibly includes *Leukarachnion*. The group has also been classified as the Acarpomyxea Page, 1976. A recent paper describing *Corallomyxa tenera* was about an organism that has been reattributed elsewhere in the Rhizaria. (Bass *et al.* 2009a; Gothe *et al.* 1999; Grell 1966, 1988, 1991a; Grell and Benwitz 1970; Page 1987; Tekle *et al.* 2007)

Stygamoeba

Flattened amoebae, thin and very elongate, stick-like, with a deep anterior hyaline zone. Cytoplasmic streaming is present. One species has flattened mitochondrial cristae instead of the usual Amoebozoan tubular or branching mitochondrial cristae. There is no molecular information on this taxon. (Sawyer 1975; Smirnov 1996)

Thalassomyxa

Large marine plasmodia with thin stiff pseudopodia, with a large network of pseudopodia with filose extensions (“captor strands”). The amoebae undergo periodic changes between trophic stages (plasmodia) and distributive stages (budded-off small round free-floating amoebae, which can undergo binary divisions, fusion, or multipartite fissions). These amoebae are similar to other large plasmodial amoebae; however no molecular data exists for this taxon. (Bass *et al.* 2009a; Grell 1985, 1991a, 1992, 1994)

Theratromyxa

Multinucleated, reticulate plasmodial amoebae, which consume nematodes. Reticulate pseudopodia are broad and the organism creeps with a “flowing” motion of the cytoplasm. *Theratromyxa* is similar to Vampyrellids (Rhizaria) and has been classified with them, but its life cycle and shape of mitochondrial cristae (which are defining features of Vampyrellids) are unknown. There is no molecular information for this taxon. (Bass *et al.* 2009a; Sayre 1973; Sayre and Wergin 1989; Zwillenberg 1953)

Toshiba

Gliding or swimming elongated apple-shaped heterotrophic cells with two equal flagella inserting apically. Pseudopodia may be produced when swimming or gliding. (Patterson and Zölffel 1991)

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