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A PHYLOGENETIC CLASSIFICATION OF ORGANISMS OTHER THAN ANIMALS

This classification attempts to present a phylogenetic treatment of organisms which do not belong to the Kingdom **ANIMALIA** as narrowly defined, i.e. organisms possessing a blastula stage during their early development. There is no agreement about the exact number of kingdoms into which organisms can be accommodated and, bearing in mind that the kingdom (and any other taxonomic rank above that of species) is an abstraction, it is unlikely that there will ever be. While efforts are directed towards the creation of natural classifications, these are nonetheless artificial systems created for our convenience and to fit the state of our knowledge, the interpretation of which is always open to discussion. Certain organisms persistently refuse to be pigeonholed into easily definable taxonomic groupings. Fine details of phylogeny are often based on highly subjective considerations. There is no one classification system which is acceptable to all - indeed every biologist who has attempted to make some sense out of the evolutionary relationships between taxonomic groups has come up with a different scheme. The scheme presented here takes into consideration recent advances in systematics where considerable weighting is given to nucleic acid sequencing, flagellar types, mitochondrial structure and chloroplast structure and chemistry.

Until recently, the term **Phylum** was restricted to groups governed by the International Code for Zoological Nomenclature (ICZN) while the equivalent taxon in the botanical code (ICBN) was the **Division**. Since the 1994 (Tokyo) edition of the botanical code, the use of "phylum" is also allowed (but not imposed) for plants, a practice which is followed here for the sake of streamlining.

Most of the traditional groupings in which organisms used to be classified no longer have a taxonomic standing since they are **polyphyletic** (i.e. include organisms which do not share a common origin) or **paraphyletic** (when a taxon does not include all the descendents of the common ancestor). Nevertheless they are still useful to define the general character and level of organisation of the organisms concerned, and they are still valid to define areas of interest. Some of these, e.g. **Protozoa** and **Fungi**, are still used here, in a restricted sense, as names for kingdoms. Some of the main traditional groupings are:

PROTOZOA: unicellular/colonial; typically phagotrophic/parasitic and microscopic.

PROTOCTISTA (PROTISTA): includes protozoa, eukaryotic algae and fungi with undulipodiate stages or organisms clearly derived therefrom.

ALGAE: photosynthetic; predominantly aquatic; no well-defined vascular tissues, reproductive bodies not enclosed by multicellular walls.

FUNGI: as in "algae" but never photosynthetic and most often terrestrial; typically filamentous.

LICHENS: intimate associations between higher fungi, mainly **Ascomycota**, and green or blue-green algae.

EMBRYOPHYTES: photosynthetic; typically terrestrial; always with alternation of a haploid gametophyte with a diploid sporophyte; sporophyte embryo starts to develop within the parental gametophyte; reproductive bodies enclosed in multicellular walls. Includes "bryophytes", "pteridophytes" and "spermatophytes"

BRYOPHYTES: non-vascular embryophytes

TRACHEOPHYTES: the vascular embryophytes characterised by the possession of a vascular system with xylem and phloem

PTERIDOPHYTES: vascular non-seeding embryophytes

GYMNOSPERMS: seed-producing non-flowering embryophytes

ANGIOSPERMS: flowering embryophytes.

Note: Phyla with names ending in **-phyta** include photosynthetic organisms; those ending in **-mycota** are fungi or fungus-like, which are non-photosynthetic. Class names ending in **-phyceae** refer to algae, those ending in **-mycetes** refer to fungi while those ending in **-opsida** refer to higher plants. Other suffixes for phyla and classes denote either bacterial groups (if prokaryotic) or protozoan groups governed by the zoological code. All orders governed by the botanical code end in **-ales** while the families end in **-aceae**.

Domain: **PROKARYA** (= **PROKARYOTA**, **MONERA**)

Organisms with a prokaryotic organisation. Often capable of nitrogen-fixation. Prokaryotes are polyphyletic and many bacteriologists now recognise several kingdoms. Only a simplified classification is given here.

Kingdom: **ARCHAEA** (=ARCHAEOBACTERIA)

Unlike other prokaryote groups, the cell walls lack peptidoglycans. Their major lipids are ether-linked (as against ester-linked in all other organisms). They include all methanogenic, halophilic and thermoacidophilic bacteria. Generally anaerobic. It is probable that these are the most primitive existing organisms. None are phototrophic. A polyphyletic group which includes at least two main evolutionary lines. One is highly isolated while the other may be more closely related to the Eubacteria and Eukaryotes.

Phylum: **CRENARCHAEOTA** (= SULFOBACTERIA; thermoacidophils): Organisms which live in habitats rich in sulphur and of high ambient temperature. Most require an optimum temperature of over 80°C, occasionally even over 100°C as in *Pyrodictyum* (optimum 105°C). *Thermoplasma*, which requires an optimum temperature of 55°C, may actually be an euryarcheote and may be related to the ancestors of the first eukaryotes.

Phylum: **EURYARCHAEOTA** (halophiles and methanogens): The methanogens (e.g. *Methanococcus*, *Methanosarcina*) are chemosynthetic organisms which use H₂ to reduce CO₂ and thence build up their organics while releasing methane; often endosymbiotic such as the organisms in the rumen of cattle. Halophils (e.g. *Halobacterium*, *Natronobacterium*) require habitats with a NaCl concentration higher than 9%, some surviving at concentrations of up to 30%. They employ a light-mediated reaction for ATP synthesis using rhodopsin pigments (related to those of animal retinas) as light receptors.

Kingdom: **BACTERIA** (= EUBACTERIA, NEOBACTERIA)

Prokaryotes with **peptidoglycan** (cf. murein) cell walls made up of alternating units of acetyl-muramic acid (AMA) and acetyl glucosamine (AGA) accompanied by short peptide chains attached to the AMA subunits which typically include the amino acid **diaminopimelic acid** (DAP). Major lipids are ester-linked, as in the Eukaryotes. A large assemblage of organisms covering a wide range of forms. May be heterotrophic, photoautotrophic, chemoautotrophic. Photoautotrophic forms may possess **chlorophyll a** or a variety of **bacteriochlorophylls**. Some bacteria possess flagella which are in no way homologous to eukaryote flagella (or undulipodia). Bacterial flagella are composed of the protein **flagellin** and do not contain microtubules. For convenience, bacteria are split into three categories (each not necessarily monophyletic) according to the nature of their cell-walls (or lack thereof).

GRACILICUTES (Gram -ve bacteria): Bacteria with thin peptidoglycan wall surrounded by a lipoprotein layer.

Phylum: **PROTEOBACTERIA**: A large assemblage of diverse bacteria; generally anaerobic, though many are oxygen-tolerant; photosynthetic or not; with or without flagella. Photosynthetic forms have **bacteriochlorophylls a & b**. Include the oxygen-tolerant **purple sulphur bacteria** (e.g. *Chromatium*, *Thiocapsa*) which use H₂S as hydrogen donor and deposit sulphur in their cells, as well as **purple non-sulphur bacteria** (e.g. *Rhodobacter*, *Rhodospirillum*). At any rate photosynthesis is only carried out under anaerobic conditions. Includes forms important in the nitrogen cycle such as the symbiotic nitrogen fixers *Rhizobium*, which produces root nodules in leguminous plants, and the free-living *Azotobacter*; and the nitrifying *Nitrobacter* and *Nitrosomonas*. Coliform bacteria (e.g. *Escherichia coli*) also belong here. Also important are the many species of the nitrogen-fixing *Pseudomonas* which includes plant pathogens, and human pathogens such as *Legionella* and *Salmonella*. and some **rickettsias**, these last being among the smallest and simplest bacteria. Also some more complex forms such as the relatively large filamentous *Beggiatoa*, very similar to colourless cyanobacteria, and the **myxobacteria** (e.g. *Chondromyces*, *Myxococcus*) which may form complex colonies. Eukaryote mitochondria are possibly derived from the purple sulphur bacteria.

Phylum: **SPIROCHAETA** (spirochaetes): A distinctive group of heterotrophic, generally anaerobic, bacteria with elongated spiral cells. Occur free-living in a variety of media, as well as endobiotically and parasitically. They are unusual in having flagella (2 - 200) lying in the space between the cell wall and the plasma membrane. Some (e.g. *Leptospira*) are obligate aerobes. A few, such as *Treponema*, which causes syphilis, are pathogens. It has been suggested that eukaryote flagella (undulipodia) and centrioles may be derived from endosymbiotic spirochaetes.

Phylum: **SAPROSPIRAE**: Gliding bacteria lacking flagella. Include the anaerobic *Bacteroides* and related forms, which are often found in mammalian intestines, as well as aerobic forms, such as the cellulose digesting *Cytophaga* and *Saprospira*, occurring in decaying vegetation.

Phylum: **CHLOROFLEXA** (green non-sulphur bacteria): Oxygen tolerant, facultatively phototrophic bacteria; filamentous and with flexible cell-walls (e.g. *Chloroflexus*). Photosynthesising forms have **Bacteriochlorophyll a** and **b, c** or **e**.

Phylum: **CHLOROBIA** (green sulphur bacteria): Anaerobic, phototrophic bacteria lacking flagella containing **bacteriochlorophyll c, d** or **e** (occasionally **a**). Use H₂S, H₂ or NaS as electron donors (e.g. *Chlorobium*, *Chlorherpeton*).

Phylum: **CYANOBACTERIA** (= CYANOPHYTA, MYXOPHYCEAE; blue-green algae): The blue-green algae. Photoautotrophic organisms which always have **chlorophyll a** as well as the biloprotein (= phycobilin) pigments, mainly **phycocyanin** and **phycoerythrin** (a characteristic they share with the red algae, glaucophytes and cryptophytes). Never flagellate. No sexual reproduction known. Includes several nitrogen fixers. Representative genera: *Nostoc*, *Oscillatoria*, *Spirulina*, *Chroococcus*, *Lyngbya*, *Rivularia*, *Scytonema*.

Phylum: **PROCHLOROPHYTA** (= CHLOROXYBACTERIA):

Similar to the blue-green algae but having chlorophylls *a* and *b* while lacking biloproteins. Discovered little more than 25 years ago. *Prochloron* is endozoic in Didemnid tunicates. *Prochlorothrix* is a free-living freshwater type similar to the blue-green *Oscillatoria*. They are perhaps better included within the **Cyanophyta**.

FIRMICUTES (Gram +ve bacteria): Bacteria with thick peptidoglycan/protein wall but lacking a lipoprotein layer.

Phylum: **ENDOSPORA**: Endospore forming bacteria, motile or non-motile, which include the well-known genera *Bacillus* and *Clostridium*. Both aerobic and anaerobic. **Endospores** (with walls containing calcium dipicolinate) are resistant to desiccation and contain a copy of the parental genome; they serve as propagules and perennating structures. Occur in a variety of habitats as saprotrophs, endosymbionts or parasites. Some (e.g. *Clostridium botulinum*, the agent of food-poisoning; *Clostridium tetani*, of tetanus, *Bacillus anthracis*, of anthrax) are pathogens. The non-spore forming lactobacilli, streptococci and staphylococci may belong here. The soil-dwelling N-fixing facultatively phototrophic Gram -ve **heliobacteria** (e.g. *Heliobacterium*, *Heliospirillum*) which contain **bacteriochlorophyll g**, may also belong here. Unlike other photosynthetic bacteria, the bacteriochlorophyll is carried in the plasmalemma rather than in an intracellular membrane system. They can absorb light in the near infrared range. They may be involved in a mutualistic association with rice roots, supplying fixed nitrogen to the plants.

Phylum: **PIRELLULAE**: Lack peptidoglycans in their proteinaceous cell walls which are rich in cysteine and proline. Include free-living freshwater forms which often form colonies, either planktonic or attached by stalks to a variety of substrates. Examples are *Pirellula* and *Planktomyces*. In *Gemmata* the nucleoid is membrane bound, thus resembling a true nucleus. This is believed to be independently derived relative to the eukaryote nucleus. *Chlamydia* and related forms are obligate parasites of mammals and birds; these form desiccation resistant "elementary bodies" analogous to the endospores.

Phylum: **ACTINOBACTERIA** (= ACTINOMYCETES): Uni- or multicellular bacteria. Typically filamentous and forming mycelia as in fungi (as which they were originally classified), generally aerobic and living in a variety of habitats. May produce conidia-like propagules known as **actinospores**. Include the N-fixing *Frankia* and related forms which form woody root nodules in a variety of trees and shrubs such as alder and *Casuarinia*. *Streptomyces* is a source of the antibiotic streptomycin while *mycobacterium* is a pathogen causing tuberculosis. Include also the **corynebacteria** with club-shaped cells; some of these are a source of the flavour enhancer monosodium glutamate while *Corynebacterium diphtheriae* is a pathogen which causes diphtheria.

Phylum: **DEINOCOCCI**: Aerobic, non-motile bacteria, usually coccoid, sometimes forming small colonies. The diaminopimelic acid of the peptidoglycan cell-wall is here replaced by ornithine. Typically heat and radiation resistant. Includes genera such as *Deinococcus* and *Sarcina*. The rod-shaped Gram -ve *Thermus* may also belong here.

Phylum: **THERMOTOGAE** (= TOGOBACTERIA): A recently described group of anaerobic thermophilic bacteria. enclosed, singly (*Thermotoga*) or in groups (*Thermosipho*), by a sheath-like membrane (**toga**); *Fervidobacterium* lacks the toga.

TENERICUTES: Bacteria which lack cell-walls.

Phylum: **APHRAGMOBACTERIA** (mycoplasmas & phytoplasmas): Wall-less non-motile bacteria with cells bounded by a lipid trilayer. Include the simplest and smallest known prokaryotes (e.g. *Mycoplasma*, *Spiroplasma*). The plasmalemma of *Mycoplasma* is particularly rich in cholesterol which is typically absent in prokaryotes. Phytoplasmas are plant pathogens.

Domain: **EUKARYA (= EUKARYOTA)**

The remaining non-animal groups have a eukaryotic organisation with a well-defined double-membrane nucleus, real chromosomes (the bacterial chromosome is more properly termed a genophore), mitochondria (derived from prokaryote precursors) and a variety of other organelles. Most possess undulipodia (flagella/cilia) which consist of the 9 + 2 pattern of microtubules; these are composed of proteins called **tubulins**.

Kingdom: **PROTOZOA**

Phagotrophic, parasitic or, sometimes, saprotrophic; without true cell-walls (but may be provided with skeletons, tests, thecae, etc.); sometimes phototrophic through secondary endosymbiosis or by harbouring zooxanthellae or zoochlorellae. Mastigonemes, when present, never tubular. Mostly bear tubular or discoid mitochondrial cristae. Include several parasitic forms. Generally unicellular or colonial. Classification of the **Protozoa** is still very unsettled and only a generalised treatment is given here. It represents a basal paraphyletic complex from which other eukaryote kingdoms arose. These are here divided, for convenience, into two categories: flagellates and amoeboids. No phylogenetic relationship within these categories is implied.

FLAGELLATES:

Organisms whose main means of locomotion is by flagella. Some forms may also be amoeboid. Many flagellated organisms do not belong here, but rather with the chromists, fungi or true plants. With the exception of the euglenoids, often placed in a single paraphyletic phylum, the **Zoomastigina** (= zoomastigophora), a complex of groups which includes what are believed to be among the most primitive eukaryotes.

a. **Excavate phyla:** A possibly natural assemblage of unicells originally proposed for organisms with multiple flagella associated with a ventral feeding groove.

Phylum: **METAMONADA:** Endozoic anaerobic flagellates lacking true mitochondria, peroxisomes, Golgi bodies and ER. Contain 70S ribosomes (as in the *Microspora*, but in contrast to other eukaryotes which possess 80S). Contain **hydrogenosomes** (wherein pyruvate is oxidised and H₂ released), which are thought to be derived from mitochondria.

Class **Diplomonada** includes the binucleate organisms such as *Hexamita* and *Giardia*. This last is common in the colon.

Class **Retortamonada** are likewise endozoic but uninucleate and tetrakont (with 4 flagella) resembling half of a diplomonad. Examples are *Retortamonas*, *Chilomastix* and, possibly, *Carpediemonas*.

Class **Oxyomonada** are symbiotic in termite and wood-eating cockroach guts. Best known are the order **Pyrsonymphida** (e.g. *Pyrsonympha*, *Oxyomonas* and related types) with complex pulsating **axostyles**; cells contain endosymbiotic bacteria as well as symbiotic spirochaetes which may have locomotory function. Possibly close to the parabasalians with which they are sometimes united.

Phylum: **PARABASALIA** (= TRICHOZOA): Heterotrophic anaerobic undulipodiate forms lacking true mitochondria. Possess, near the anterior end, a **parabasal body** (a specialised Golgi apparatus involved in protein metabolism). Contain a **hydrogenosome** which may represent a modified mitochondrion. Includes many parasites. The order **Trichomonadida** includes multiflagellated organisms having a long axostyle. *Trichomonas* dwells in the mouth, intestine and urogenital tracts of humans. The order: **Hypermastigotida** includes the endosymbiotic termite flagellates, such as *Trichonympha*, with a capacity to digest lignin and cellulose; these have numerous flagella as well as endosymbiotic bacteria associated with the axostyle and numerous symbiotic spirochaetes projecting from the posterior end.

The metamonads and parabasalians, together with the amitochondriate amoebae (**Pelobionta/Karyoblastera**) and the **Microspora** have been included in a polyphyletic assemblage called "**Archaeozoa**" (= *Archaeoprotista*, *Amitochondriata*, *Hypochondriata*) since they were thought to be primitively amitochondriate. However it appears that, at least some of these, have secondarily lost their mitochondria.

Phylum: **JAKOBA**: The jakobids are a small group of marine or freshwater free-living sessile flagellates bearing two acronematic flagella, with the posterior flagellum bearing a wing-like vane. Some are enclosed in a lorica. May be related to the retortamonads (phylum: *Metamonada*). *Reclinomonas* possesses the "most complete" mitochondrial genome known, with 97 genes. Some authorities suggest that the jakobids may be the most primitive eukaryotes since their mitochondrial genomes are closest to the bacterial condition, and the different genera possess mitochondrial cristae of different types: some discoid (*Malawimonas*), some tubular (*Reclinomonas*, *Histiona*), and some flattened (*Jakoba*). They may thus be a paraphyletic basal group which gave rise to the three main branches of eukaryotes: the "mainstream" protozoa + chromalveolates with tubular cristae, the discicristates with discoid cristae, and the choanoflagellates + animals + fungi + plants, all with flattened cristae.

b. **Discicristates**: organisms bearing discoid mitochondrial cristae.

Phylum: **DISCICRISTATA** (=DISCOMITICHONDRIA): Unicellular organisms with discoid mitochondrial cristae.

Class: **Euglenozoa** (= *Euglenophyceae*, *Euglenida*; euglenoids):

Unicellular forms with two pantonematic flagella arising from a "gullet". Chloroplasts with four membranes and containing chlorophylls *a* and *b*. Cell-wall absent but an extracellular theca is sometimes present. Many forms have a pellicle under the plasmalemma which may render the cell more or less rigid. Food reserve is the glucosan **paramylon** (otherwise only found in the **Prymnesiophyta**). Predominantly a freshwater group; typically free swimming (*Euglena*, *Phacus*, *Trachelomonas*), occasionally epibiotic (*Colacium*, which is usually attached to copepods and cladocerans). Many species are actually colourless and may be saprotrophic or parasitic (e.g. *Astasia*, with both free living species and parasites in copepods). Some are phagotrophic (e.g. *Peranema*). Often treated as a distinct phylum, the **Euglenophyta**.

Class: **Kinetoplastida**: Characterised by the presence of a large mitochondrion, the **kinetoplast**. Include notorious parasites such as *Trypanosoma* which causes sleeping sickness, and *Leishmania*, the agent of kala-azar; such parasitic forms often bear an undulating membrane attaching the flagellum along part of its length to the cell. Also free living types such as *Bodo*.

Class: **Pseudociliata**: Benthic marine ciliated unicells with several similar nuclei. Only known genus is *Stephanopogon*.

Class: **Hemimastigophora**: A single soil-dwelling species, *Hemimastix amphikineta*, recorded from Australia and Chile is so far known. Superficially resembles a ciliate.

Class: **Heterolobosea** (= *Amoebomastigota*, *Percolozoa*; amoeboflagellates and acrasids): Predominantly uninucleate amoeboid organisms, often with flagella. Include forms such as the pathogenic *Naegleria*, the quadriflagellate *Tetramitus*, the fast moving *Vahlkampfia* (all in the sub-class **Schizopyrenidea**), as well as the acrasid slime moulds (e.g. *Acrasis*, sub-class **Acrasiomycetidae**) which have many similarities with the *Dictyosteliomycetes* with which they were, until recently, united. The acrasids have no flagella except for *Guttulina* (= *Pocheina*).

c. **Neomonads** (= Phylum **Neomonada**): A rather mixed assemblage of flagellates, originally proposed as a kingdom, or treated as a phylum. Since the coherence of the group is questionable, the groups assigned to it are being retained as independent phyla.

Phylum: **APUSOZOA**: Originally associated with the opalinates which have now been transferred to the kingdom *Chromalveolata*. They are heterokont flagellates with tubular mitochondrial cristae such as *Apusomonas* and *Ancyromonas*.

Phylum: **ISOMITA**: Like the *Apusozoa* they were originally assigned to the opalinates. They include isokont flagellates with tubular mitochondrial cristae.

Phylum: **CHOANOZOA** (= CHOANOFLAGELLATA; collar flagellates, choanoflagellates): Includes mainly freshwater colourless phagotrophs, with flat mitochondrial cristae (as in animals, plants, and fungi) but there are a few species with plastids (e.g. *Desmarella*); they are characterised by the presence of a collar-like structure surrounding the flagellum. Some texts incorporate them in the chromist phylum **Chrysophyta** as the class **Craspedophyceae**, but it has now been established that they are not so related, except that their plastids may be chrysophyte derived. Some systematists also include the collar flagellates in the Kingdom **Animalia** since they are believed to be related (possibly ancestral) to the sponges.

Apart from typical choanoflagellates, the parasitic ***Ichtyosporea***, with vesicular mitochondrial cristae, have been assigned here. Originally classified with the fungi, they include a variety of fish parasites such as *Dermacystidium* as well as the mammalian (including human) pathogen *Rhinosporidium* which affects the nasal mucosa.

The ***Bicosoecida*** is now included in the *Kingdom Chromalveolata* (q.v.) as also the ***Opalinata*** and ***Proteromonada*** which have recently been united into the phylum ***Slopalinida***

AMOEBOID GROUPS

Organisms whose main locomotory structures are pseudopodia though several have flagellated stages or phases. Not all amoeboid organisms belong in the phyla included here, some being more akin to groups here included among the flagellates and the chromists.

a. **Xenophyophoreans**: Amoeboid organisms of unknown affinity.

Phylum: **XENOPHYOPHORA**:

An unusual group of deep sea amoeboid organisms ranging from some 2 mm to several centimetres in size. Their protoplasm includes numerous barite crystals and they are covered by a rigid test in which is incorporated a collection of foreign matter (**xenophyae**) such as diatom, radiolarian, foraminiferan skeletons, sponge spicules, inorganic detriti etc.

b. **Retarians**: Amoeboid organisms in which the pseudopods are usually long and narrow such as filopodia, reticulipodia, axopodia.

Phylum: **CERCOZOA**:

Protozoa with both flagellate and amoeboid stages, often simultaneously, e.g. *Cercomonas*. May also be related to the *Myxomycota*, *Chlorarachniophyta*, *Plasmodiophoromycota*. The phylum is sometimes expanded to include all the retarian groups and in this form is sometimes treated as a distinct kingdom.

Phylum: **PLASMODIOPHOROMYCOTA**:

A small group of endoparasitic or, at any rate, endophytic species occurring in various plants. Traditionally regarded as "slime moulds". A microscopic multinucleate plasmodium inhabits host cells. Motile biflagellate zoospores/gametes are produced. Some species, e.g. *Plasmodiophora brassicae*, which causes club-root disease of cabbages, are of economic importance. Includes one class, the ***Plasmodiophoromycetes***. Probably close to the *Cercozoa*

Phylum: **RADIOZOA** (=Actinopoda; radiolarians):

Usually planktonic phagotrophs with axopodia (long narrow pseudopodia supported by an axial rod). The ***Radiolaria*** are important marine planktonic forms with an internal skeleton and an encapsulated nucleus.

Class: **Phaeodaria**: Radiolarians with a skeleton made of silica and poorly characterised organic substances. Skeleton consists of an intricate meshwork of markedly hollow tubes. Representative genera: *Astracantha*, *Phaeodina*, *Coelodendrum*.

Class: **Polycystina**: Radiolarians with a skeleton consisting of opal (hydrated amorphous silica). Skeleton consisting of several elements which look solid in light microscopy though actually containing minute tubes and pores. Polycystines contain zooxanthellae (dinoflagellates) or zoochlorellae (chlorophytes), rendering them secondarily photosynthetic. Representative genera: *Collozoum*, *Thalassicolla*.

Class: **Acantharia**: Radiolarians with a skeleton made of strontium sulphate and consisting of 20 radial spicules radiating from the centre of the cell. Acantharians are associated with green endobiotic haptophytes on which they depend for most of their nourishment. representative genera: *Acanthocola*, *Acanthometra*, *Amphiacon*.

Phylum: **HELIOZOA** (sun animalcules): Traditionally placed close to the radiolarians. Predominantly freshwater forms without a distinct skeleton though may have siliceous scales or spines or other superficial armatures. A polyphyletic group. The **actinophryid** heliozoans (e.g. *Actinophrys*) are possibly related to the chromists.

Phylum: **GRANULORETICULOSA** (= FORAMINIFERA; *forams*, *foraminiferans*):

Most are included in the class **Foraminifera**, predominantly marine planktonic and benthic forms with reticulopodia (long narrow anastomosing pseudopods) provided with a superficial porous skeleton or shell composed of organic material usually reinforced with calcium carbonate. An extremely important group which has given rise to vast fossil deposits (e.g. the Maltese Globigerina Limestone). Representative genera: *Globigerina*, *Nummulites*, *Heterostegina*, *Miniacina*, *Orbitulina*. The class **Reticulomyxia** (= *Athalamea*) includes forms without skeletons such as *Biomyxa* and *Reticulomyxa*.

Phylum: **FILOSEA** (filose amoebas): Amoebas with filopodia (long narrow pseudopods). Include both naked and testate forms (e.g. *Euglypha*). Possibly related to the cercozoans and chlorarachniophytes. Often included within the phylum *Amoebozoa*.

Phylum: **CHLORARACHNIOPHYTA** (= CHLORARACHNIDA):

Only a few species are known. These are net-like amoeboid organisms which are capable of phagotrophic nutrition. Embedded in the cytoplasmic network are numerous chloroplasts, each with four membranes, which contain chlorophylls *a* and *b* and peculiar DNA-containing structures known as a **nucleomorphs** (nucleomorphs also occur in cryptophytes). Produce uniflagellate zoospores, the flagellum being acronematic and bearing tiny hairs (as in some primitive chlorophytes). Probably derived from an association between a protozoan (possibly rhizopodean or foraminiferan) and green algae. Representative genera: *Chlorarachnion*, *Lotharella*, *Gymnochlora*. Sometimes placed close to the *Cryptophyta*, in the *Chromalveolata*, both having 4-membraned chloroplasts with nucleomorph, but they are more probably related to the *Cercozoa*,

c. **Ramicristates**: Amoeboid organisms with branched tubular mitochondrial cristae.

Phylum: **AMOEBOZOA** (=RHIZOPODA; true amoebas):

A paraphyletic assemblage of amoeboid forms occurring in a variety of habitats. The slime mould phyla may also be included here.

Class: **Lobosea** (lobose amoebas): Amoebas which use indeterminate pseudopods (lobopodia) for locomotion. Include naked forms such as the uninucleate *Amoeba* and the large multinucleate *Chaos* and the potentially pathogenic *Acanthamoeba*. Also testate forms in which the amoebas are protected by a shell such as *Arcella*, *Diffugia* and *Centropyxis*. Probably close to the myxomycetes.

Class: **Acarpomyxea**: Possibly artificial group of amoebae with filose pseudopods. Examples are the soil organism *Leptomyxa* with multinucleate cells and the uninucleate marine benthic *Stereomyxa* which produces long hypha like pseudopods.

Class: **Entamoebida**: Anaerobic, endobiotic, sometimes pathogenic amoebas lacking mitochondria. Well known types include *Entamoeba gingivalis* which dwells in the human mouth and *Entamoeba histolytica* which causes amoebic dysentery.

Class: **Archamoebae**: Anaerobic free-living amoebas lacking mitochondria. Includes the sub-class **Pelobionta** (= *Karyoblastea*), sometimes regarded as a separate phylum, which are large amoeboid organisms living in mud in the bottom of freshwater ponds. Lack mitochondria, ER and Golgi apparatus, although they were recently discovered to have some microtubules and a kinetosome (which suggests that they are related to flagellate forms). Also characterized by the large number of symbiotic bacteria which dwell within the cytoplasm. The endobiotic bacteria belong to three species (two of which are methanogenic archaeans) one of which forms a perinuclear zone. Only one species, *Pelomyxa palustris* is so far known. The sub-class **Mastigamoebae** includes forms with flagella such as *Mastigamoeba*. The group may be related to the *Entamoebida*. According to some authorities, can be united with the slime moulds to form the **Conosa**.

"Slime Moulds":

The two ramicristate amoeboid phyla which follow have traditionally been included with the fungi, being collectively known as slime moulds (together with the acrasid cellular slime moulds of the phylum *Discicristata*; the phylum *Plasmodiophoromycota* and the chromist phylum *Labyrinthulomycota*).

Phylum: **DICTYOSTELIOMYCOTA** (Cellular Slime Moulds):

Vegetative stage consisting of phagotrophic uninucleate amoebae. These aggregate (usually as a result of the secretion of cAMP which acts as an attractant) to form a **pseudoplasmodium**. The pseudoplasmodium eventually metamorphoses into a usually stalked sporangium reinforced with cellulose. The spores "hatch" into uninucleate amoebae. Includes one class, the **Dictyosteliomycetes**. The best known genus is *Dictyostelium*. Until recently included also the acrasid slime moulds, now transferred to the discicristate class *Heterolobosea*.

Phylum: **MYXOMYCOTA** (= MYCETOZOA; true slime moulds):

The vegetative phase is usually a large multinucleate **plasmodium** (i.e. large multinucleate amoeba) which feeds phagotrophically or osmotrophically. The plasmodium eventually gives rise to fungus-like reproductive bodies which are typically from 1mm to several millimetres in length. The spores germinate (hatch?!) into uninucleate amoebae which may change into biflagellate cells. Both amoebae and biflagellate cells may act as gametes. The zygotes then grow into the typical multinucleate plasmodium. The recently discovered

Protostelids have a minute plasmodium and sporangium. Includes three classes: **Protosteliomycetes** for the microscopic protostelids; **Ceratiomyxomycetes** with spores not enclosed in sporangia, sometimes considered as monosporic sporangia (e.g. *Ceratiomyxa*), and the **Myxomycetes** for all the rest. Typical genera: *Physarum*, *Arcyria*, *Stemonitis*.

Phylum: **MYXOZOA** (= MYXOSPORIDIA, CNIDOSPORIDIA):

Obligate parasites, formerly regarded as sporozoans, having spores with eversible adhesive filaments and a large amoeboid feeding stage. Mainly parasites on fish. These have been shown to belong to the kingdom **Animalia**, being derived, through degeneration and adaptation to parasitism, from cnidarian ancestors

Phylum: **MICROSPORIDIA**:

Somewhat similar to the *Myxozoa* but which have now been shown to be related to the **Fungi**, being probably derived from the **Zygomycota**.

Kingdom: **CHROMALVEOLATA**
(Chromists and Alveolates)

Both groups were included in this kingdom on the basis of nucleic acid analysis.

a. **Alveolates**

Sub-Kingdom: **ALVEOLATA**

Microorganisms characterized by the presence of sacs (alveoli) associated with the plasmalemma.

Phylum: **CILIOPHORA** (= CILIATA, ciliates):

Characterized by the possession of two different nuclei (meganucleus & micronucleus), the complex exchange of genetic material during a process of conjugation which can be likened to a form of sexual reproduction and typically by the possession of numerous cilia, which are short undulipodia. A large and diverse group which is almost certainly monophyletic. The **Ciliophora** may be divided into a number of sub-phyla and classes. The neat division into a number of classes which was widely accepted until about 1980 has been revised in view of ultrastructural investigations. Several species associate with zooxanthellae or zoochlorellae, thus becoming secondarily phototrophic. Representative genera: *Paramecium*, *Didinium*, *Tetrahymena*, *Vorticella*, *Stentor*, *Euplotes*, *Spirostomum*, *Tokophrya*.

Phylum: **APICOMPLEXA** (= SPOROZOA p.p.):

Obligate parasites in a variety of animals. Have a complex life cycle and typically produce spores. Their main distinguishing characteristic is an **apical complex** of microtubules, fibrils and other organelles at the apical end of the cell which is used in the infection of host cells.

Many apicomplexans also have a vestigial 4-membraned plastid, known as an **apicoplast**, which is of uncertain function but which may indicate their origin from free-living phototrophic ancestors. Best known are the malaria parasites (*Plasmodium* spp.), *Eimeria* which keleton io several domestic animals and birds and *Babesia* from cattle. *Monocystis* and/or *Rhynchocystis* are invariably present in the seminal vesicles of earthworms. Includes some free-living flagellated forms such as *Colpodella* (formerly considered to be a kinetoplastid flagellate) as well as forms, such as *Perkinsus* and *Parvilucifera*, which parasitise dinoflagellates and which seem to be genetically intermediate between the apicomplexans and the dinoflagellates. These two genera have recently been included in a new alveolate phylum, the **Perkinsozoa**. The *Perkinsozoa* together with *Colpodella* are sometimes united as the class **Protoalveolata** within the phylum *Pyrrhophyta*.

Phylum: **HAPLOSPORA** (= HAPLOSPORIDIA): A small group (three known genera: *Haplosporidium*, *Minchina*, *Urosporidium*) of parasites of polychaetes, oysters, nematodes and trematodes. The mono- or multinucleate vegetative cells are intimately connected to the host tissue and have organelles of unknown function known as **haplosporosomes**. Produce spores with an orifice at one pole which may be covered by a hinged lid or by a diaphragm. Sometimes included with the *Apicomplexa* or combined with the *Paramyxea* to form the phylum **Ascetospora**.

Phylum: **PARAMYXEA**: A small group with three known genera (*Marteilia*, *Paramarteilia*, *Paramyxa*) parasitic on marine annelids, mollusca and crustaceans. Like the haplosporidians, they have **haplosporosomes**. Their most notable characteristic is their production of spores which contain several cells nested in each other like Russian dolls.

The old group “**Sporozoa**” has been split into a number of completely unrelated phyla in different kingdoms, the **Apicomplexa** being the most numerous, others being the *Haplospora*, *Paramyxea*, *Myxozoa* and *Microspora*.

Phylum: **PYRRHOPHYTA** (= DINOMASTIGOTA, DINOZOA, DINOFLAGELLATA, DINOPHYTA; dinoflagellates):

This is a very large and diverse group which includes mainly planktonic unicellular forms characteristic mainly of the marine plankton but quite common also in the freshwater plankton. They have a peculiar nuclear structure wherein the chromosomes are permanently condensed, attached to the nuclear membrane, and are not accompanied by histones as in all other eukaryotes. This type of keleton ion has been described as **mesokaryotic**. They have two flagella one of which is acronematic while the other is ribbon-like. There is no fucoxanthin but there may be an assortment of carotenoids and xanthophylls such as peridinin, dinoxanthin, diadinoxanthin. The main reserve is starch. Main chlorophylls, when present, are **chlorophyll a & c**, though species with **chlorophyll b** and with **phycobilins** also exist, indicating various episodes of secondary endosymbiosis. The alveolar apparatus, beneath the plasmalemma, is known as the **amphiesma**; in many species the amphiesmal vesicles contain plates of cellulose which function as a cell wall. Chloroplasts usually have three membranes. Often occur abundantly to produce blooms, e.g. **red tides**, which may be toxic.

Class: **Dinophyceae** (true dinoflagellates): These are characterized by having a transverse furrow round the equator of the cell and a longitudinal furrow on one side. The transverse furrow accommodates the ribbon-like flagellum while the trailing acronematic flagellum is partly housed in the longitudinal furrow. The wall, when present, is typically made up of numerous plates which are elaborately sculptured. Some species (e.g. *Gonyaulax*) produce

toxins which can cause fish mortalities. Others associate with corals and other marine organisms as **zooxanthellae**, a relationship which is very important in the productivity of tropical seas. Some species are phagotrophic (e.g. the luminescent *Noctiluca*); a few are filamentous (e.g. *Dinothrix*). Non-flagellate forms usually produce reproductive stages (**dinospores**) with typical dinoflagellate flagella. The Order **Syndinida** (e.g. *Syndinium*, *Hematodinium*) are endoparasites of crustaceans; sometimes segregated into a separate class, the **Syndiniophyceae**.

Class: **Desmophyceae** (desmoflagellates): A rather small group of mainly estuarine brackish water forms in which the flagella are apical with the acronematic flagellum directed forwards and the ribbon-like flagellum circling its base. The cell walls are simple, being made up of two valves. Typical genera are *Prorocentrum* and *Exuviaella*.

The **ellobiopsids**, a group of endoparasites on crustaceans, with multinucleate hypha-like absorptive filaments (e.g. *Thalassomyces*), and the predatory flagellated **ebriids** (e.g. *Ebria*), with a skeleton resembling that of silicoflagellates, may belong in this phylum.

b. Chromists

:(= CHROMISTA, CHROMOPHYTA, STRAMENOPILA)

Mainly algae with chlorophylls **a** and **c** and a variety of xanthophylls pigments carried in four-membraned chloroplasts.

Sub-kingdom: CHROMOBIONTA

Mainly algal groups with **chlorophyll a** and **c**. Most have dissimilar flagella (one pleuronematic and one acronematic). The pleuronematic flagella bear tubular tripartite mastigonemes. Often use oils as main reserve. Principal carbohydrate reserve is most often **chrysolaminarin**. Chlorophylls often masked by a variety of xanthophyll pigments.. Mastigonemes of pleuronematic flagella typically rigid and tubular. Mitochondrial cristae tubular. Chloroplasts originating from secondary endosymbiosis, i.e. by the incorporation of a photosynthetic eukaryote, and typically have four membranes and a girdle lamella; the original symbiont was probably a red alga. Also includes some organisms traditionally classified as fungi and protozoa.

Phylum: **HETEROKONTOPHYTA** (= CHRYSOPHYTA CHRYSOMONADA; golden algae):

Predominantly unicellular or colonial. Flagella usually two, one pleuronematic and one acronematic. Main accessory pigment is **fucoxanthin**. Cells usually with a large anterior nucleus. The classes *Chrysophyceae*, *Fucophyceae*, *Tribophyceae*, *Eustigmatophyceae*, *Oömycetes* and *Hyphochytriomycetes* are often treated at phylum rank.

Class: **Chrysophyceae**: Very diverse group with unicellular motile or non-motile types. Most are motile unicells (*Ochromonas*). Some are amoeboid (*Chrysamoeba*). Many are colonial, branched (*Dinobryon*). *Hydrurus* is a large branched palmelloid (gelatinous) colony several centimeters long and with a fixed shape.

Class: **Synurophyceae**: Unicellular or colonial forms such as the sphaerical *Synura* or the oval *Mallomonas*; differ from other chrysophytes because the cells are covered with silica scales and by the presence of chlorophyll c_1 (rather than c_2 as in other chrysophytes).

Class: **Pedinellophyceae**: These are radially symmetrical unicellular forms (e.g. *Pedinella*) related to the silicoflagellates.

Class: **Parmophyceae**: Marine non-motile unicells characterised by the possession of walls made up of interlocking silica plates (e.g. *Pentalamina*).

Class: **Pelagophyceae**: Simple unicellular to multicellular marine algae, filamentous or thalloid, benthic or planktonic. Share some characteristics with the brown algae such as the presence of cellulose in the cell walls and laterally inserted flagella. Chloroplast DNA scattered. Motile cells without an eye-spot. They may be related to the ancestors of the brown algae. Representative genera: *Pelagococcus*, *Pelagomonas*, *Aureoumbria*. The predominantly benthic, usually multicellular order: **Sarcinochrysidales** such as *Sarcinochrysis*, *Ankylochrysis* and *Chrysocystis* are sometimes segregated as the class: **Sarcinochrysidophyceae**. Some of these occur as large seaweed-like colonies.

Class: **Chrysomeridophyceae**: A small group of small marine filamentous algae with naked zoospores; similar to the brown algae in some respects, but lack alginates in cell wall and possess violaxanthin. (e.g. *Phaeosaccion*, *Chrysomeris*, *Giraudyopsis*).

Class: **Dictyochoephyceae**: The marine silicoflagellates. Have an internal siliceous skeleton reminiscent of that of the radiolarians; only a few living species (e.g. *Dictyocha*) but they are abundant as fossils. The amoeboid *Rhizochromulina* may belong here or in the related *Pedinellophyceae*.

Class: **Bolidophyceae**: Recently described group, so far represented by three marine planktonic taxa. Very small fast moving cells. Possibly related to the diatoms (e.g. *Bolidomonas*).

Class: **Pinguiphyceae**: A newly established taxon which, so far, includes two genera of marine microorganisms: *Pinguicoccus* being unicellular while *Glossomastix* is colonial.

Class: **Bacillariophyceae** (= *Diatophyceae*; diatoms):

The diatoms are a very distinctive group. They are abundant in all kinds of aquatic media and are especially important constituents of both marine and freshwater plankton, though benthic forms are also very common. Characterized by the possession of a sculptured siliceous cell wall (the **frustule**) which is made up of two halves (**valves**) which fit into each other like a box with a lid. The main accessory pigment is fucoxanthin.

Sub-class: **Pennatophycidae** (*Bacillariophycidae* p.p.; pennate diatoms): Frustules usually bilaterally or biradially symmetrical. Often motile by the extrusion of mucilage through slits (**raphes**) in the frustules. With two chloroplasts. No flagellated stages ever produced. Representative genera: *Navicula*, *Amphora*, *Achnantes*, *Nitzschia*, *Synedra*. Sometimes split into two sub-classes: the **Bacillariophycidae** which have raphes; and the **Fragilariophycidae** which have no raphe.

Sub-class: **Centricophycidae** (*Coscinodiscophyceae*, *Coscinophyceae*; centric diatoms): Frustules often radially symmetrical. Mostly marine. Numerous chloroplasts. Some species produce flagellated male gametes bearing a single (rarely two) pleuronematic flagellum. Representative genera: *Biddulphia*, *Melosira*, *Coscinodiscus*, *Skeletonema*, *Triceratium*. A paraphyletic taxon from which the pennate diatoms arose.

Class: **Fucophyceae** (= *Phaeophyceae*; brown algae):

This is the only grouping within the **Chromista** to include predominantly macroscopic forms. In fact the fucophytes include the largest of all algae. Biochemically and ultrastructurally they tend to conform with other chromist groups. Motile cells have two unequal flagella (one pleuronematic and one acronematic). The main accessory pigment is fucoxanthin while the chief polysaccharide reserve is **laminarin**, carbohydrates being translocated mainly as mannitol. Chloroplasts one to many. An important group of benthic seaweeds. Simple forms are filamentous (*Ectocarpus*), the filaments may be aggregated in such a way as to form a pseudoparenchymatous thallus (*Chordaria*, *Mesogloia*, *Liebmannia*) or may be encrusting (*Ralfsia*). Most brown algae are parenchymatous with a definite tissue organization. These can be relatively simple sheet-like forms (*Punctaria*, *Petalonia*), hollow tubes (*Scytosiphon*), bag-like forms (*Colpomenia*). The more robust forms are the **kelps** (order: **Laminariales**) which are mainly restricted to cool oceanic coasts and include the largest seaweeds, such as *Macrocystis* which may exceed 60 metres; and the **fucoids** (order: **Fucales**) which include forms such as *Fucus*, as well as *Cystoseira* and *Sargassum* which are abundant in the Mediterranean. The seaweeds in the order **Dictyotales** are unusual in having male gametes with a single anterior pantonematic flagellum; this group includes seaweeds with a flattened, more or less branched thallus such as *Dictyota*, *Padina* and *Dictyopteris*.

Class: **Phaeothamniophyceae**: Small branched multicellular filamentous freshwater algae (e.g. *Phaeothamnion*, *Phaeobotrys*, *Chrysodictyon*). Traditionally included in the *Chrysophyceae* but actually more closely related to the *Tribophyceae* and *Fucophyceae*.

Class: **Tribophyceae** (= *Xanthophyceae*; yellow-green algae):

A large group of algae common in all aquatic habitats. The two flagella are typically very unequal in length and are usually more or less laterally inserted. The cells contain numerous chloroplasts. They are unusual in having no fucoxanthin, this being replaced by other xanthophylls such as **vaucherixanthin** and **cryptoxanthin**. **Chlorophyll e** may replace chlorophyll c in some of the species. A very diverse group dominated by unicellular types (e.g. *Ophiocystis*). There are also more complex forms such as the multicellular filaments *Tribonema* and *Bumillera*, the vesicular *Botrydium*, an aerial genus of compact muds, and the oogamous non-septate *Vaucheria* which is common in all aquatic habitats. They are probably closely related to the Oömycetes.

Class: **Eustigmatophyceae** (eustigs):

A group which accommodates organisms previously included in the **Tribophyta**, which they resemble in lacking fucoxanthin which, at least in some forms, is replaced by **violaxanthin**; in the absence of chlorophyll c and the presence, in some species, of **chlorophyll e**. They differ in having a single large chloroplast and in having a large anterior eyespot (**eustigma**). There is typically a single pleuronematic flagellum (with evidence of a second degenerate flagellum) with a characteristic basal swelling closely associated with the eyespot. The reserve product is a still uncharacterized glucan (i.e. not chrysolaminarin). Representative genera: *Nannochloropsis*, *Eustigmatos*, *Vischeria*.

Phylum: **Hyphochytriomycetes** (hyphochytrids):

A small group (less than 20 species) of aquatic or parasitic fungi. Superficially very similar to the chytrids but clearly separated from these by their single anterior pleuronematic flagellum. Cell walls are chitinous. Representative genera: *Rhizidiomyces* and *Hyphochytrium*.

Phylum: **Oömycetes** (oömycetes):

A large group of parasitic or saprotrophic fungi characterized by their oögamous fertilization and by the possession of **biflagellate** motile cells (these being equipped with one pleuronematic and one acronematic flagellum). The food reserve is **mycolaminarin** while cell walls are composed of β -glucan and cellulose. The best known oömycetes are the aquatic water moulds such as *Saprolegnia* and *Achlya*, some of which are facultatively parasitic on fish. Various types are serious phytopathogens such as *Phytophthora* which causes **potato blight**, *Plasmopara* which causes **mildew** on vines, *Pythium* which causes **damping-off** in seedlings, and *Peronospora* the many species of which cause mildews in various plants. Two sub-classes may be recognized; the ***Saprolegniomycetidae*** to accommodate the free living water moulds, and the ***Peronosporomycetidae*** for the specialised conidia-producing parasitic forms. There is evidence that the oömycetes are closely related to the algal class ***Tribophyceae***, particularly to the order ***Vaucheriales***. The *Oömycota* and *Hyphochytriomycota* are sometime combined into the phylum ***Pseudofungi***.

The photosynthetic classes of the *Heterokontophyta* are sometimes grouped in the phylum ***Ochromphyta***; such a group, however, is paraphyletic since it excludes organisms which are clearly related to those which it includes.

Phylum: **RAPHIDOPHYTA** (= CHLOROMONADOPHYTA):

A small group of anomalous flagellates with possible relationships to the ***Chrysophyceae***, or ***Cryptophyceae***. They have a large anterior nucleus (like the chrysophytes) and two unequal flagella. Their cell contains many chloroplasts - without any xanthophylls. A feature common to most is the presence of **ejectosomes** which discharge when the organism is irritated. Typical genera are *Vacuolaria* and *Raphidomonas*. There is only one class, the ***Raphidophyceae***.

Phylum: **LABYRINTHULOMYCOTA** (slime nets, labyrinthulids):

A small group of organisms with no clear relationship to any other group. Traditionally classified with the fungi and slime moulds. The best known types are marine, but some also occur in other habitats. Mainly osmotrophic and/or parasitic. The vegetative stage is a more or less extensive mobile network which contains spindle-shaped cells. The strands of the net are contractile and are probably responsible for the movement of the cells within. This ectoplasmic network is secreted by structures called **bothrosomes**, which are peculiar to this group. Species of *Labyrinthula* have been implicated in causing disease in sea-grasses, but their exact role is still unexplained. Possibly includes two classes: ***Labyrinthulea*** to accommodate typical labyrinthulids and the ***Thraustochytridea*** to accommodate *Thraustochytria* and related forms which have been transferred to this group from the *Chytriomycota*. Often included with the slime moulds.

Phylum: **BICOSOECIDA** (= BICOECIDA):

Often included in the ***Zoomastigina***. These marine heterotrophic flagellates are actually very similar to simple chrysophytes. Most species are housed in a chitinous **lorica** (cup-shaped envelope) with the pleuronematic flagellum extending outwards and serving to create a current to bring food towards the organisms, while the acronematic flagellum attaches the cell to the inside of the lorica. Examples are *Cafeteria*, *Pseudobodo*, *Bicoeca*. These are sometimes combined with the *Labyrinthulomycota* to form the phylum ***Sagenidia***.

Sub-kingdom: **HAPTOBIONTA**

Flagella acronematic and similar; presence of a haptonema between the flagella.

Phylum: **HAPTOPHYTA** (=HAPTOMONADA, PRYMNESIOPHYTA):

Traditionally considered as related to the *Chrysophyta* but ultrastructural studies suggest that they are not. They are characterized by the possession of two, normally apical, acronematic flagella. Between the flagella there is a thread-like structure, the **haptonema**, which is an attachment organelle. There is no real cell-wall but the cell-surface is often scaly. They are biochemically peculiar in that they store **paramylon** (as in the *Euglenophyta*) and may possess both α - and γ -carotene in addition to the ubiquitous β -carotene. The main accessory pigment is **fucoxanthin**. Prymnesiophytes are predominantly marine. Many species have resting stages which are covered in calcareous plates known as **coccoliths**. These coccolith bearers are known as **coccolithophorids** (e.g. *Emiliana*). Their abundant fossil remains make them ideal markers in stratigraphy. *Chrysochromulina*, a simple type, may produce toxins such that unusually dense blooms may affect fisheries. *Phaeocystis* is a palmelloid form. There is a single class, the **Haptophyceae** (=Prymnesiophyceae).

Sub-kingdom: **CRYPTOBIONTA**

Flagella both pleuronematic, with bipartite mastigonemes, chloroplast with nucleomorph.

Phylum: **CRYPTOPHYTA** (= CRYPTOMONADA, CRYPTOZOA; cryptoflagellates, cryptomonads):

Predominantly unicellular motile forms from both marine and freshwater habitats, phototrophic or heterotrophic. They resemble the *Euglenophyta* by possessing a pair of flagella arising out of a gullet (**crypt**) and in the permanently condensed chromosomes. The two flagella are pleuronematic and of unequal length, bearing bipartite mastigonemes: two rows in one and one row in the second. The food reserve is starch and the chlorophylls (**a** & **c₂**) are accompanied by **biloprotein** pigments (as in the *Cyanophyta* and *Rhodophyta* but, unlike these, without phycobilisomes, thus resulting in stacked thylakoids). No β -carotene is present, it being replaced by α -carotene. There is also no fucoxanthin, which is replaced by an assortment of xanthophylls such as **cryptoxanthin** and **alloxanthin**. The chloroplasts, which are bounded by four membranes, carry a peculiar body, the **nucleomorph**, representing a rudimentary nucleus, between the outer and inner pairs of membranes. This indicates that the chloroplasts were, in origin, endosymbiotic (probably red) algae. Many species have ejectosomes (as in the *Raphidophyta* and some *Pyrrhophyta*). Apart from the typical motile forms (e.g. *Chilomonas*, *Chroomonas*, *Cryptomonas*) there are some non-motile benthic unicells (*Tetragonidium*) and a rudimentary filamentous form (*Bjornbergiella*). Includes a single class, the **Cryptophyceae**, probably the most primitive clade within the *Chromista*.

Phylum: **SLOPALINIDA** (=OPALINATA):

An anomalous group of endocommensals from the colon and rectum of a variety of vertebrates. Until recently included among the protozoa.

Class: **Proteromonada**: A small group of biflagellate uninucleate organisms. Only two genera: *Proteromonas*, *Karatomorpha*.

Class: **Opalinida**: Large forms with two to numerous nuclei and a ciliated surface. The cilia arise from the dense rows of kinetosomes forming what is known as a **falx**. Occur mainly in amphibians. e.g. *Opalina*, *Protoopalina*, *Cepedea*.

Kingdom: **FUNGI**
(= MYCOPHYTA, MYCOTA, MYCOBIONTA)

Heterotrophic, typically saprotrophic or parasitic. Typically non-flagellated (with the exception of the chytrids). Mostly non-aquatic. Cell walls typically chitinous. Normally filamentous, rarely unicellular. Mitochondrial cristae flattened (tubular in the **Protozoa** and **Chromista**).

Phylum: **MICROSPORA** (Microsporidians)

This group of obligate parasites of insects and vertebrates has traditionally been regarded as sporozoan protozoa. When the sporozoa were fragmented, the microsporidians were placed close to, or within, the *Myxozoa*. However recent macromolecular analysis has shown that their proper place is with the fungi, being possibly derived from the Zygomycota. They are anaerobic, lacking mitochondria, peroxisomes and Golgi bodies; cells often dikaryotic; their chief diagnostic feature is a coiled **polar filament**, rather similar to that of the myxozoans which, when everted, serves to inject the sporoplasm into a host cell. Examples are *Glugea*, which causes tumours in fish; and *Nosema* which parasitises bees.

Phylum: **CHYTRIOMYCOTA** (chytrids):

A large group of parasitic or saprotrophic forms. Free-living types are usually aquatic (especially in freshwater). The main characteristic is the motile cell bearing a single posterior acronematic flagellum. Cell wall usually chitinous (cellulose in the order **Monoblepharidales** which are also characterized by being oögamous). Some have alternation of generations. Hyphae coenocytic or pseudoseptate (having false septa). Food reserve is usually glycogen. Some species cause disease in cultivated plants e.g. *Synchytrium* causing "**black wart**" disease on potato tubers. Other common genera are the parasitic *Ospidium* and the free-living *Allomyces*, which has pseudoseptate hyphae, and *Monoblepharis* with aseptate hyphae. A single class, **Chytriomycetes**, is recognized though the three evolutionary lines in this group may warrant elevation to class status.

Phylum: **ZYGOMYCOTA** (conjugating fungi):

Fungi with aseptate hyphae and structurally simple reproductive bodies typically consisting of a sporangium carried on a single hypha, the sporangiophore. Karyogamy (nuclear fusion) carried out at the time of fertilization.

Class: **Zygomycetes**: Saprotrophic forms which include the familiar **pin-moulds** such as *Mucor*, *Rhizopus* and *Phycomyces* wherein a black sphaerical sporangium is subtended by a long hypha, the sporangiophore. *Pilobolus* is a specialized coprophilic (dung-dwelling) species which can forcibly eject a spore mass. The order **Entomophthorales** includes species which are mostly parasitic on insects or, more rarely, on plants or saprotrophic. *Entomophthora* (*Empusa*) is a common parasite of flies. The order **Zoopagales** includes

microscopic fungi most of which are either predaceous or parasitic on amoebae and nematodes. In the predaceous species, the prey adheres to the fungal hyphae as a result of the secretion of sticky substances by the latter.

Class: **Trichomycetes**: Microscopic fungi which are obligate symbionts or commensals in a variety of arthropods. Zygosporangia usually biconical. Some species produce appendaged spores called **trichospores** while species of the order **Amoebidiales** produce amoeboid spores. Only a few species are known. Representative genera: *Harpella*, *Asellaria*, *Amoebidium*. Hyphae are sometimes septate.

Phylum: **GLOMEROMYCOTA**: This recently instituted phylum includes the mycobionts of the vesicular-arbuscular mycorrhizae (VAMs), such as *Gigaspora* and *Glomus*, which are intimately associated with the roots of a wide range of plants. Also included here is the unusual vesicle-shaped *Geosiphon* which contains intracellular filaments of the cyanobacterium *Nostoc*. It is the only non-endophytic member of this class so far known. Have large multinucleate spores with layered walls often grouped in sporocarps. Includes the single class **Glomeromycetes**. Due to their aseptate hyphae they were formerly included in the phylum Zygomycota.

The following two phyla: **Ascomycota** and **Basidiomycota**, which comprise the "higher fungi" probably share a common ancestry and in many classifications are regarded - with some justification - as a single phylum, the **EUMYCOTA**.

Phylum: **ASCOMYCOTA** (bag fungi, ascomycetes):

Fungi with septate hyphae provided with large septal pores. Karyogamy is delayed, occurring just prior to spore formation so that conjugation leads to formation of **dikaryotic** (binucleate) bodies. The spores (**ascospores**) are enclosed in sporangia called **asci** (ascosporangia). Each ascus typically contains **eight** (occasionally four) spores. Asci are usually carried by fruiting bodies termed **ascocarps**. Many forms also reproduce vegetatively by means of spore-like bodies termed **conidia** which are sometimes multicellular and are typically carried on **conidiophores**. The systematics of the ascomycetes is currently in a state of flux and the classification given here is a provisional one.

a. **"Hemiascomycetes"**: (subphyla: **Saccharomycotina** and **Taphrinomycotina**):

Ascomycetes without ascocarps. Formerly regarded as a single class. Includes the yeasts (e.g. *Saccharomyces*) which have lost their mycelial organization, becoming unicellular, and plant-parasitic forms such as the order **Taphrinales**, many of which cause diseases in economic plants usually marked by spectacular symptoms such as galls and/or colour changes. *Taphrina deformans* is a common parasite of the almond tree. Several classes are now recognized:

Sub-phylum: Saccharomycotina:

Class: **Saccharomycetes**

Sub-phylum: Taphrinomycotina:

Class: **Neoelectromycetes**

Class: ***Pneumocystidomycetes***

Class: ***Schizosaccharomycetes***

Class: ***Taphrinomycetes***

The remaining ascomycetes belong to the sub-phylum: **Pezizomycotina**.

b. “***Plectomycetes***”: Formerly regarded as a Class.

Class: **Eurotiomycetes**: Most members of this group are moulds with dominant conidial stages. Ascocarps are **cleistothecia**. Many plectomycetes are better known by the names of their “**imperfect**” (i.e. conidial) stages. Ascocarps are **cleistothecia** which are usually more or less sphaerical. Representative genera: *Eurotium* (imperfect state: *Aspergillus*); *Talaromyces* (imperfect state: *Penicillium*).

c. “***Pyrenomycetes***”: Formerly regarded as a class. Large group of fungi many of which are wood-dwelling or develop on dead vegetable matter. Several aquatic, including marine, species also exist. The ascocarp is a **perithecium**. In some forms the perithecia may be united into large bodies known as **stromata** (sing. stroma). Most non-lichenised forms are now included in the class: **Sordariomycetes** (e.g. *Erysiphe*, *Cordyceps*, *Hypocrea*, *Xylaria*, *Daldinia*). The “***Laboulbeniomycetes***”, formerly regarded as a separate class, may be related to these groups; their taxonomic position is still unclear. They are a rather obscure (though quite large) group of fungi which are obligate ectoparasites of insects (especially Coleoptera) and occasionally other arthropods. Exhibit a very high degree of host specificity which may also include gender specificity. Attached to external surface of host by means of a “foot”. The ascocarp is typically perithecial. Although described as parasites, they seem to cause little or no harm to the host. Representative genera: *Laboulbenia*, *Rickia*.

d. “***Loculoascomycetes***”: Formerly regarded as a class.

Superficially rather similar to the **pyrenomycetes** but the asci are **bitunicate** (with a double wall). The superficially perithecioid ascocarps are **ascostromata** wherein the asci are embedded in locules within a stroma. Most non-lichenised genera belong in the class: **Dothideomycetes**: (e.g. *Venturia*, *Sphaerella*, *Metasphaeria*). Also several lichen fungi, mostly belonging in the class: **Arthoniomycetes** (e.g. *Roccella*, *Arthonia*, *Opegrapha*, *Dirina*). Apart from saprotrophic and parasitic species, the class: **Chaetothyriomycetes** also includes several genera of lichen fungi (e.g. *Dermatocarpon*, *Verrucaria*).

e. “***Discomycetes***”: Formerly regarded as a class. A large group of fungi occurring in a variety of habitats. Mainly saprophytes. Ascocarps are typically cup-shaped **apothecia** but may also assume other shapes. Some species are characterized by large fleshy apothecia. Most non-lichenised genera belong to the class: **Leotiomycetes** (e.g. *Geoglossum*, *Helotium*, *Sclerotinia*) and to the class: **Pezizomycetes** (e.g. *Ascobolus*, *Peziza*, *Morchella*, *Aleura*, *Helvella*, *Tuber*, this last being a truffle, with subterranean apothecia). A large proportion of the lichen fungi belong to the class: **Lecanoromycetes** (e.g. *Lecanora*, *Xanthoria*, *Ramalina*, *Cladonia*, *Peltigera*).

Phylum: **BASIDIOMYCOTA** (club fungi, basidiomycetes):

Fungi with spores carried on sporangia called **basidia** (basidiosporangia) typically carried by fruiting bodies called **basidiocarps**. Each basidium typically carries four basidiospores (occasionally two). A basidium may be unicellular (**holobasidium**) or septate (**phragmobasidium**). Sexual reproductive structures often reduced. As in the ascomycetes,

karyogamy is delayed and a dikaryotic thallus is produced. Dikaryotic hyphae are typically equipped with **clamp connections**.

Class: **Agaricomycetes** (= *Hymenomycetes*): Fungi with well developed, often large basidiocarps. Basidia carried on a **hymenium** which is exposed to the air. Basidiospores usually forcibly ejected. Most "*mushrooms*" belong to this class. The basidiocarp generally consists of a **cap** or **pileus** subtended by a stalk-like **stipe**, though the latter is often absent.

Sub-class: **Agaricomycetidae**: The hymenium typically covers "**gills**" or **tubes**. Basidia are non-septate. Includes most typical mushrooms. Typical genera: *Tricholoma*, *Agaricus* (= *Psalliota*), *Pleurotus*, *Russula*, *Boletus*, *Coprinus*. The **gasteromycetes**, formerly regarded as a class, are specialized fungi with well developed basidiocarps. Their basidiospores are not forcibly discharged from basidia. Basidia enclosed within basidiocarp and spores are released as a dry dust by being "puffed" out (as in *Lycoperdon*, *Geaster*, *Tulostoma*, *Scleroderma*) or by emerging as a sticky mass and attracting flies which disperse them (e.g. *Phallus*, *Clathrus*, *Aseroë*).

Sub-class: **Aphyllorphormycetidae**: Includes fungi without "gills" or tubes (although many have tube-like pores which, however, are not separable from the flesh of the pileus). Typical genera are *Polyporus*, *Ganoderma*, *Cantharellus*, *Hydnum*, *Clavaria*.

Class: **Tremellomycetes** (= *Phragmobasidiomycetes*): Fungi with gelatinous basidiocarp and septate basidia. Mostly on dead wood. Typical genera: *Auricularia*, *Tremella*, *Hirneola*, *Exidia*.

Class: **Uredinomycetes** (= *Teliomycetes*): Obligate parasites on plants; many are of considerable economic importance. No basidiocarp is produced and the basidia are septate. Life cycle is usually very complex and may involve an alternation of hosts. The life cycle is basically a trigenetic one. Includes the **rusts** (e.g. *Puccinia*, *Uredo*, *Uromyces*)

Class: **Ustomycetes** (= *Ustilaginomycetes*): Like the **Teliomycetes** but with simpler life cycle. Includes the **smuts** which are parasites on various plants. Typical genera: *Ustilago*, *Tilletia*.

The following two groups are artificial, their members being distributed among other fungal phyla, particularly **Ascomycota** and, to a lesser extent, **Basidiomycota**. They are still often used as a matter of convenience.

Form-phylum: **DEUTEROMYCOTA**

(= FUNGI IMPERFECTI; imperfect fungi, deuteromycetes, mitosporic fungi):

This artificial assemblage is used to include those fungi in which the "**perfect**" or **teleomorph** phase (i.e. ascus-bearing or, less frequently, basidium-bearing) is unknown. The "**imperfect**" stage is the **anamorph**. In several cases imperfect fungi have been assigned to their proper perfect stage, many turning out to be **plectomycetes**, **pyrenomycetes** and **loculoascomycetes**. Deuteromycete names such as *Penicillium* and *Aspergillus* are still often used despite many of the species having known perfect stages. Divided into three form-classes: **Blastomycetes** for the yeast-like forms;

Hyphomycetes for the forms with exposed conidia (e.g. *Botryosporium*, *Torula*) and **Coelomycetes** for forms with conidia enclosed in fruiting bodies (e.g. *Phoma*, *Melanconia*).

Form-phylum: **LICHENES** (= MYCOPHYCOPHYTA; lichens):

Large assemblage of composite organisms consisting of fungi with endosymbiotic green or blue-green algae. The association profoundly modifies the fungal component so that most lichenised fungi can be recognised as such with comparative ease. Most lichen fungi are ascomycetes though some are basidiomycetes and deuteromycetes. The fungi can be assigned with ease to their relative fungal group since they produce normal fungal fructifications. This form-phylum is only used when lichens are being dealt with separately. May be grouped into three form-classes: The **Ascolichenes** (e.g. *Xanthoria*, *Verrucaria*, *Caloplaca*, *Cladonia*, *Rocella*, *Ramalina*, *Usnea*); **Basidiolichenes** (e.g. *Cora*, *Botrydina*) and **Deuterolichenes** (e.g. *Lepraria*). The scientific name of the lichen is also the name of the fungal component.

The Fungi, together with the Animalia and Choanoflagellata, form a monophyletic clade known as the **Opisthokonts** because of the single posterior acronematic flagellum of their motile cells.

Kingdom unknown

Form-phylum: **NEMATOPHYTA** (EXTINCT):

These enigmatic fossils from the early Devonian belong to freshwater or subaerial, possibly terrestrial organisms. Remains include trunklike structures about 1m in diameter and 2m long traversed by tube-like cells embedded in a matrix of smaller cells (*Prototaxites*) and flat sheets with a somewhat fungoid internal organisation (*Nematothallus*). It is possible that the two forms may be different parts of the same plant. Their relationships are so far totally unknown. They have been compared with kelp-like algae, green algae, fungi and lichens. They seem to be an early experiment at terrestrial life which eventually lost out to the emerging vascular plants. Recent evidence suggests that at least some "nematophyte" fossils may actually be remains of ancient bryophytes.

Kingdom: **PLANTAE**
(=EUPHYTA)

Photosynthetic organisms with chloroplasts bounded by two membranes and thus originating by means of primary endosymbiosis. Mitochondrial cristae are flattened.

Sub - Kingdom: **RHODOPHYCOTA**
(= RHODOBIONTA, AKONTA, RHODISTA)

Except for some of the **Glaucophyta**, characterized by the total absence of flagellation and the presence, in the two-membraned chloroplasts, of phycobiloprotein pigments, phycoerythrin and phycocyanin, which occur within phycobilisomes, because of which the thylakoid lamellae are unstacked.

Phylum: **GLAUCOPHYTA** (= GLAUCOCYSTOPHYTA):

A small anomalous phylum characterised by chloroplasts (**cyanelles**) which resemble whole cyanophytes, complete with a thin peptidoglycan wall and with pigments and thylakoids similar to those of cyanophytes. May bear two flagella of unequal length which carry rows of delicate hairs similar to those of some primitive chlorophytes. The cyanelles are so similar to cyanophytes that until recently it was held that glaucophytes represent a composite organism involving an association between a heterotrophic unicells and cyanophytes. But it has since been shown that the genome of the cyanelles is similar to that of typical chloroplasts rather than to that of free-living cyanophytes. Glaucophytes may represent an early stage in eukaryote evolution. Their exact systematic position is debatable and they have been accommodated in the Rhodophycota mainly because of the nature of chloroplast pigmentation. They may be close to the common ancestors of the Rhodophycota and the green plants. Representative genera are *Glaucocystis*, *Gloeochaete*, *Peliana* and *Cyanophora*.

Phylum: **RHODOPHYTA** (red algae):

Predominantly marine, macroscopic algae. The food reserve is usually **floridean starch**, which is rather similar to glycogen. Some species contain the additional chlorophyll *d*.

Class: **Cyandiophyceae**: Includes a single microscopic species from thermal waters, *Cyanidium caldarium*, with a very primitive cell structure. It carries a single chromatophore with chlorophyll *a*, allophycocyanin and c-phycocyanin (i.e. as in the blue-green algae). Sometimes included in the following class and sometimes treated as an independent phylum.

Class: **Bangiophyceae**: The lower red algae characterized by their simple morphology. Chloroplasts often stellate and often with pyrenoids. Primary pit connections between cells are rare. Reproduction simple or involving an alternation of two generations. Asexual spores not in fours. May be unicellular (*Porphyridium*), filamentous (*Bangia*, *Chroodactylon*, *Erythrotrichia*, *Stylonema*), sheet-like (*Porphyra*) or pseudoparenchymatous (*Compsopogon*). About ¼ of the species occur in freshwater.

Class: **Florideophyceae**: The higher red algae which are invariably multicellular. Chloroplasts various, not stellate and rarely with pyrenoids. Pit connections always present. Life cycle complex, most often involving an alternation of three generations: gametophyte, carposporophyte and tetrasporophyte. Asexual spores usually produced in fours and hence known as **tetraspores**. The group includes several thousand predominantly marine species. Mainly filamentous or pseudoparenchymatous. The Order **Corallinales** (Coralline algae) includes heavily calcified forms many of which are important reef builders. The Coralline Limestones of the Maltese islands are composed largely of the remains of these algae. Representative genera: *Ceramium*, *Polysiphonia*, *Gelidium*, *Nemalion*, *Delesseria*, *Nitophyllum*; coralline genera: *Corallina*, *Jania*, *Halptilon*, *Amphiroa*, *Lithothamnion*, *Phymatolithon*, *Lithophyllum*.

GREEN PLANTS

(= CHLOROBIONTA, VIRIDIPLANTAE)

Includes the green algae and the "higher plants" (embryophytes). Characterised by the presence of chlorophylls *a* and *b*. Flagella, when present, acronematic. Food reserve typically starch. Cell wall mainly based on cellulose.

Sub-Kingdom: **CHLOROPHYCOTA**

Green algae characterised by symmetrically inserted apical flagella and, usually, phycoplastic cell division.

Phylum: **CHLOROPHYTA** s.s. (green algae):

Investigation of the ultrastructure of the flagellar complex and dividing cells has necessitated a revision of the group. The classification adopted below is a provisional one which attempts to give an approximation of the relative status and relationship of the various groups.

Sub-phylum: **PRASINOPHYTINA**:

Artificial assemblage of presumably primitive forms with more or less clear affinity to the other chlorophyte groupings. Cells naked or covered with scales; flagella also scaly. The cell-body scales may be the precursors of true cell walls. Presumably a paraphyletic group from which both chlorophytes and streptophytes arose. Predominantly marine.

Class: **Prasinophyceae** (= *Micromonadophyceae*): Mainly planktonic (e.g. *Halosphaeria*, *Pyramimonas*), occasionally benthic (*Prasinocladus*) or endozoic (e.g. *Tetraselmis convolutae* in the turbellarian *Convoluta roscoffensis*).

Class: **Pedinophyceae** (= *Loxophyceae*): Very simple forms such as *Pedinomonas*, with a single flagellum and lacking body scales.

Class **Picocystophyceae**: It is a recently erected taxon is provisionally placed here. It was created to house the newly described picoplankter, *Picocystis salinarum*, from a saline lake in California; it is a minute flagellate with a polyarabinose cell wall and an unusual mixture of xanthophylls.

Sub-phylum: **CHLOROPHYTINA**:

Cells divide by means of a **phycoplast** which forms between the daughter nuclei. Spindle closed; spindle fibres not persistent. Motile cells are symmetrical with apical flagella. Unicellular, colonial, filamentous. Mainly in freshwater but also common in sea water.

Class: **Chlorophyceae**: A diverse group of mainly non-motile algae with naked zooids. Includes unicells (e.g. *Oöcystis*), non-motile colonies (e.g. *Scenedesmus*, *Pediastrum*, *Hydrodictyon*), palmelloid (gelatinous colonies e.g. *Palmella*, *Tetraspora*), simple filaments (e.g. *Microspora*). Further study may see the transfer of several types to the newly erected class **Chlamydomphyceae**.

Class: **Chlamydomphyceae**: A newly established group to accommodate forms, similar to the **Chlorophyceae** but with walled zooids as well as differences in mode of cleavage and other features. Includes motile unicells (e.g. *Chlamydomonas*), non-motile unicells (e.g. *Chlorococcum*), motile colonies (e.g. *Volvox*, *Pandorina*, *Eudorina*, *Gonium*) as well as the

order: **Chaetophorales** which bears branched pointed filaments (e.g. *Draparnaldia*, *Stigeoclonium*).

Class: **Oedogoniophyceae**: Exclusively freshwater filamentous forms; oogamous, with a complex life cycle and peculiar mode of cell division, motile cells multiflagellate. At least some forms have an outer cell-wall containing chitin. Only three genera: *Oedogonium*, with simple filaments includes the bulk of the species. *Bulbochaete* and *Oedocladium* have branched filaments.

Class: **Trebouxiophyceae** (= *Pleurastrorphyceae*): Unicellular, colonial to filamentous and thalloid forms. Intermediate in a number of characters between the **Chlorophyceae** and the **Ulvophyceae**. Mainly freshwater or terrestrial. Includes *Trebouxia*, a common symbiont in lichens; the similar *Chlorella*, a common genus with free-living or symbiotic species; and the filamentous *Microthamnion*. . The order: **Prasiolales** (e.g. *Prasiola*) with a small foliose thallus is provisionally included here. Includes aerial and subaerial forms, occasionally coastal.

Sub-phylum: **ULVOPHYTINA**:

Mainly macroscopic, predominantly marine forms. Spindle closed but spindle fibres rather persistent. No phycoplast or phragmoplast is formed. Gametes symmetrical.

Class: **Ulvophyceae**: Cells typically uninucleate. Plants unicellular (e.g. *Chlorocystis*), filamentous (e.g. *Ulothrix*, *Percursaria*), tubular (e.g. *Ulva* subgenus *Enteromorpha*, *Blidingia*), monostromatic sheets (e.g. *Monostroma*, some species of which occur in freshwater), distromatic sheets (e.g. *Ulva*).

Class: **Cladophorophyceae**: Multicellular, predominantly marine, algae with multinucleate cells. Simplest forms are filamentous, simple (e.g. *Chaetomorpha*, *Rhizoclonium*) or branched (e.g. *Cladophora*). More complex forms are those with interlocking filaments (e.g. *Microdictyon*, *Anadyomene*) while the more specialised have few large cells (e.g. *Valonia*).

Class: **Bryopsidophyceae**: Siphonaceous algae, characterized by a thallus consisting of large cells containing numerous nuclei. Contain α -carotene (rather than β -carotene usually found in other chlorophytes). Cell walls usually contain polysaccharides such as mannans and xylans instead of, or in addition to, cellulose. Examples include *Bryopsis* and *Derbesia* with branched filamentous structure; *Codium* and *Halimeda* with spongy thally, the latter segmented and calcified; and *Caulerpa*, *Udotea* and *Flabellia* with flattened thalli. Exclusively marine.

Class: **Dasycladophyceae**: Calcified siphonaceous algae wherein most species have a central axis with whorled lateral branches. Multinucleate or with a single basal nucleus. Exclusively marine algae occurring mainly in tropical and subtropical seas. Due to their strong calcification, they have left a rich fossil record, some dating back to the Precambrian. Examples are *Dasycladus*, *Acetabularia*, *Neomeris*, *Cympolia*.

The **Cladophorophyceae**, **Bryopsidophyceae**, and **Dasycladophyceae** are often united in a single class, as **Bryopsidophyceae**, due to their multinucleate cells and biochemical features; they are also often included in the **Ulvophyceae**.

Class: **Trentepohliophyceae**: An odd group of small subaerial algae. Multicellular, with branched filaments. Placed here only tentatively since they share characteristics with the various other subphyla (e.g. their cells divide through the formation of a **phragmoplast**). Separated due to peculiarities in their flagellar apparatus. *Trentepohlia* occurs on damp soil and rocks and on the bark of trees; it may also occur as the algal component in lichens. *Phycopeltis* is a tropical or subtropical epiphyte. *Cephaleuros*, a tropical genus, may grow parasitically on the leaves of various plants.

Sub-kingdom: **STREPTOPHYCOTA**
(charophytes and embryophytes)

Green plants with phragmoplastic cell division and flagella, when present, inserted asymmetrically.

a. **green algal streptophytes**

Phylum: **CHAROPHYTA** (charophytes):

Microscopic to macroscopic forms. Cells divide by means of a **phragmoplast**. Spindle open and spindle fibres persistent. Motile cells, when present, asymmetrical with only two flagella inserted askew. The "higher" plants have evolved within this group. In freshwater, occasionally in brackish water.

Class: **Mesostigmatophyceae** (= *Chaetosphaeridiophyceae*): A newly erected class to accommodate, so far, the unicellular flagellate *Mesostigma* (formerly included in the *Prasinophyceae* because of its prominently scaly flagella) and the multicellular filamentous *Chaetosphaeridium* (often included in the *Coleochaetophyceae* due to its sheathed hairs). The relationship between the two genera is based on SSU rRNA sequencing. Morphologically they are united by the presence of scaly flagella. *Conochaete*, usually included in the family *Chaetosphaeridiaceae*, probably belongs here.

Class: **Klebsormidiophyceae**: Includes simple forms such as the colonial *Chlorokybus* (sometimes included in its own class: **Chlorokybophyceae**) and the filamentous *Klebsormidium*. Mainly subaerial and freshwater species with motile reproductive cells.

Class: **Zygophyceae** (= *Gamophyceae*, *Conjugatophyceae*, *Zygnematophyceae*; conjugating algae): Unicellular (the **desmids**, e.g. *Cosmarium*, *Staurostrum*, *Closterium*, *Micrasterias*), or simple filaments (*Zygnema*, *Mougeotia*, *Spirogyra*, *Debarya*). No motile cells. Gametes amoeboid. The desmids are an important component of freshwater plankton.

Class: **Charophyceae** (Stoneworts): These are the most structurally complex green algae. Reproductive bodies highly specialized. Oögamous. Characteristic whorled branching and large multinucleate cells. Main genera: *Chara*, *Nitella*, *Tolypella*, *Lamprothamnium*.

Class: **Coleochaetophyceae**: Formerly included in the Order **Chaetophorales** (*Chlamytophyceae*) but phragmoplastic and has all the other features characteristic of the **Charophyta**. Distinguished by the presence of sheathed hairs. The oogamous genus *Coleochaete* is particularly interesting since it may be quite similar to the ancestral forms from which higher plants evolved. The fossil *Parka* (Upper Silurian - Lower Devonian) may be related to *Coleochaete*.

b. **Higher plants**

The so-called "higher plants" (**EMBRYOPHYTA, METAPHYTA**) are clearly derived from the green algae of the phylum **Charophyta** with which they share the most basic features:- open spindles, formation of phragmoplast, asymmetrical male gametes with the flagella inserted askew. They also possess typical green-algal chemistry:- presence of chlorophylls *a* and *b*, starch as main carbohydrate reserve, predominance of **cellulose** in cell wall.

The "higher plants" differ from the algae in that reproductive organs (male & female gametangia, sporangia) are surrounded by a jacket of sterile cells - though this might be reduced or lost to a greater or lesser extent in the gametangia of the more advanced groups. All "higher plants" have a digenetic life cycle with an alternation between a haploid gametophyte which produces the gametes and a diploid sporophyte which produces spores. The zygote develops into a sporophyte embryo which remains dependent on the parental gametophyte for a significant period. There is a progressive tendency to reduce dependence on water (special features which separate higher plants from charophytes and chlorophytes are mainly related to adaptation to an extra-aquatic existence) thus, advanced groups have lost the male gamete flagella; there is also a tendency towards the reduction of the gametophytic stage in both complexity/size and duration (the gametophyte is the stage which is most dependent on water) and on increase in size, complexity and duration of the sporophytic stage.

a. **Bryophytes**

Apart from the lack (with few exceptions) of vascularity, bryophytes are characterized by the relative dominance, in most species, of the gametophytic stage, the sporophyte being typically transient and more or less parasitic on the gametophyte. Typically small plants which are tied to humid conditions, at least during the active growth / reproduction stage although many species are capable of tiding over dry seasons by suspending activity. The male gametangia (**antheridia**) and the female gametangia (**archegonia**) are equipped with well developed walls. Male gametes (**antherozoids**) have two anterior flagella. Was considered to be a natural group but recent studies suggest that the three bryophyte groups may have had separate origins and, in some modern classifications, each has been elevated to phylum rank.

Phylum: **MARCHANTIOPHYTA** (= *Hepaticophyta*, *Hepaticae*; liverworts, hepatics): Most liverworts have a dorsiventral organization. The gametophyte may be thalloid or leafy in which case the leaves are usually distichous (in one plane) and typically without midrib. The main difference between the liverworts and the other bryophytes is in the structure and contents of the **sporogonium** (i.e. sporangium, capsule) which typically opens by a number of sutures. Apart from the spore mass, the sporogonium also contains filamentous cells with

spirally thickened walls which are known as **elaters**. These are hygroscopic and their movements, when the sporogonium opens, help to ruffle up the spores making it easier for these to be caught up by air currents.

Class: **Marchantiopsida**: Exclusively thalloid liverworts with thallus often equipped with large complex pores to allow gaseous exchange. Antheridia and archegonia often raised on stalk-like **antheridiophores** and **archegoniophores** respectively (e.g. *Marchantia*, *Lunularia*). In others gametangia are borne directly on the thallus (e.g. *Riccia*, *Sphaerocarpus*). *Riella* is a submerged aquatic while *Ricciocarpus* and a few species of *Riccia* float on the water surface.

Class: **Jungermannniopsida**: Predominantly leafy liverworts (e.g. *Lophozia*, *Cephalozia*, *Frullania*, *Plagiochila*) but also including some thalloid forms (e.g. *Pellia*, *Petalophyllum*) as well as intermediate types (e.g. *Fossombronina*). Sporogonium typically raised on a seta.

Phylum: **BRYOPHYTA** s.s. (= *Musci*; mosses): Mosses are the most familiar and numerous of all the bryophyte groups. The gametophytes are leafy, the leaves being usually arranged spirally around the central axis (although a few distichous species also exist e.g. *Fissidens*) and equipped with a distinct midrib. The sporophyte is usually photosynthetic and carries stomata on the sporogonium. Moss spores typically germinate into a filamentous **protonema** out of which several leafy gametophytes emerge; in the andreaeid and sphagnum mosses the protonema is thalloid.

Class: **Bryopsida**: By far the largest class. The sporogonium is equipped with a complex opening mechanism. This consists of a series of hygroscopic **peristome** teeth (usually in multiples of eight) which are provided with thickenings in such a way that their movements in dry air cause the sporogonium to open while in moist air they cause it to close. A **columella** is present in the middle of the sporogonium and elaters are absent. A few mosses have become adapted to an aquatic mode of life (e.g. *Fontinalis*). Typical mosses are *Bryum*, *Funaria*, *Tortula* and *Barbula* with short erect branches. Genera such as *Thamnum*, *Thuidium*, *Rhynchostegiella* and *Scorpiurium* have long creeping or erect profusely branched gametophytes. Most typical mosses are in the sub-class **Bryiidae**. The sub-class: **Buxbaumiidae** includes mosses with a reduced, partly saprophytic, gametophyte while the sporophyte bears a large asymmetrical capsule with one row of peristome teeth (e.g. *Buxbaumia*, *Diphyscium*).

Class: **Tetraphidopsida**: Superficially similar, though not closely related, to the *Bryiidae* but capsule with four rigid peristome teeth. E.g. *Tetraphis*.

Class **Polytrichopsida** (cord-mosses): Large erect mosses with the sporogonium shedding the spores through pores. These have vascular tissues consisting of water-conducting cells, the **hydroids** forming the **hadrom**, similar to tracheary elements of vascular plants but usually lacking lignified secondary cell walls, and sugar-conducting cells, the **leptoids** forming the **leptom**, which are akin to sieve elements of tracheophytes; the vascular cylinder is strengthened by supporting cells, the **sterids**. E.g. *Polytrichum*, *Atrichum*.

Class **Sphagnopsida** (bog-mosses): Large amphibious mosses which occur in bogs, their dead foliage providing peat. Their sporogonia, which shed their spores explosively, lack a

seta and are raised on a stalk of gametophytic tissue known as a **pseudopodium**. Protonema thalloid. Only one genus: *Sphagnum*.

Class: **Andreaeopsida** (granite-mosses): which inhabit alpine environments, also have sporogonia supported on a pseudopodium; these open by means of longitudinal slits. E.g. *Andreaea*. An unusual bryophyte, *Takakia*, with leaves divided into two filiform segments and capsules opening by a single oblique slit, is sometimes segregated into a separate class, the **Takakiopsida**.

Phylum: **ANTHOCEROTOPHYTA** (hornworts): These are thalloid bryophytes which have traditionally been included among the liverworts from which they differ, however, in several important respects. The gametophyte is typically a simple thin thallus while the sporophyte has a remarkable structure. This is a long tapering cylindrical structure which is photosynthetic, equipped with stomata similar to those of vascular plants and elongating by means of a **basal meristem**. The sporogonium is not distinct and in fact all parts of the growing sporophyte can develop sporogonial activity. The spore-carrying portion splits lengthwise by means of two sutures to liberate the spores which are accompanied by elater-like multicellular filaments known as **pseudoelaters**. A central strand, the columella, occurs in the middle of the sporophyte. In *Dendroceros* this columella contains lignin. The cells of hornwort gametophytes usually have a single chloroplast equipped with a pyrenoid - the only case among the higher plants, suggesting that hornworts may be rather primitive. Representative genera: *Anthoceros*, *Phaeoceros*, *Dendroceros*, *Notothylas*. Possibly unrelated to other bryophytes. One class, the **Anthocerotopsida**.

Note: The fossil *Protosalvinia* from the Upper Devonian, probably adapted to alternating submergence and emergence, is an enigmatic taxon which may possibly have some affinity with bryophytes.

b. **Tracheophytes** (vascular plants)

This includes the great majority of the land plants wherein the sporophyte is the dominant stage in the life cycle and is provided with **vascular** tissues: **xylem** for water conduction and **phloem** for conduction of photosynthates. The presence of **lignin** in the xylem, originally meant to ensure the maintenance of open tracheary conduits, has enabled many of these plants to accumulate large amounts of wood thus making it possible to produce large free-standing plants: trees and shrubs. Vascular plants may be considered, very legitimately, as constituting a single phylum, the **TRACHEOPHYTA**. In this classification, however, the tracheophytes have been split into a number of distinct phyla in order to highlight the various evolutionary lines, and to avoid the proliferation of intermediate ranks. It should be borne in mind, however, that vascular plants are very probably monophyletic and quite clearly derived from the charophytine line.

a. ***Pteridophytes***:

Free-sporing vascular plants which do not produce seed, typically having multiflagellate male gametes.

Phylum: **RHYNIOPHYTA** (EXTINCT):

These are the earliest vascular plants, appearing in the fossil record in the Silurian (about 400 million years ago) and becoming extinct about 345 million years ago towards the end of the Devonian. They were mainly small simple swamp plants lacking roots and leaves, the vascular system was **protostelic** (i.e. with one central vascular cylinder). Sporangia, which are carried singly, typically at the tip of main or lateral axes, are simple in organization and produce one kind of spore (homosporous). At least some species had an alternation of isomorphic generations. Typical genera are *Cooksonia*, *Rhynia* and *Horneophyton*. *Taenioocradia* was unusual in that it had flattened axes, possibly indicative of a submerged aquatic habit.

Phylum: **ZOSTEROPHYLLOPHYTA** (EXTINCT):

A fossil group restricted to the Devonian period. Rather similar to the rhyniophytes but the sporangia were carried in terminal groups on small stalks. They often had short branches of limited growth called **enations** which some believe to be ancestral to true leaves. Most zosterophyllophytes were probably emergent aquatics. Typical genera are *Zosterophyllum*, *Hicklingia* and *Sawdonia*. *Asteroxylon* represents a more robust growth form with the aerial axes covered with scale-like enations. They are probably ancestral to the **Lycopodiophyta**.

Phylum: **TRIMEROPHYTA** (EXTINCT):

This group of plants is rather similar to the rhyniophytes, but trimerophytes tend to be larger and have more complex branching patterns. The sporangia were in clusters in the apices of branches. Some species had spine-like appendages along their axes. They flourished from the beginning to the middle of the Devonian period. Typical genera are *Psilophyton*, *Trimerophyton* and *Pertica*. Ancestral to ferns and horsetails.

Phylum: **PSILOTOPHYTA** (psilotes, whisk ferns):

The psilotes show some remarkable similarities to the rhyniophytes with which they were often united. These similarities include the protostelic vascular tissue, lack of roots and true leaves and the simple organization of the sporangia. These last, however, are always axillary, being subtended by an enation or leaf-like appendage and are differently organized from those of the rhyniophytes. It is therefore likely that similarities to the extinct rhyniophytes are a matter of convergence. A recent view is that psilotes are not a primitive group but that they owe their simplicity to reduction, they being possibly derived from a primitive fern (possibly close to the fern family **Stromatopteridaceae**). This view, however, has not gained wide currency. There are only two genera with very few species, *Psilotum* with narrow dichotomous branches and *Tmesipteris* with flattened leaf-like appendages. There is no definite fossil record!

Phylum: **LYCOPODIOPHYTA** (=LYCOPHYTA, LEPIDOPHYTA; club-mosses):

Club mosses made their appearance in the early Devonian - probably evolving from zosterophyllophyte ancestors. In the Carboniferous they were the dominant plants when great tracts were covered by lycopsid forests, these trees often being some 30m high. All modern lycophytes are rather low growing, usually creeping, herbs. Modern lycophytes include both **homosporous** and **heterosporous** forms. The heterosporous forms produce **megaspores** which give rise to female gametophytes and **microspores** which give rise to

male gametophytes. The gametophytes of heterosporous forms are typically **endosporic** (i.e. remain within the spore walls). They are also very highly reduced. The fertilized female gametophyte with sporophyte embryo and enclosed in the megaspore wall is very similar to a seed but it should be emphasized that there is no direct relationship between the lycophytes and the seed plants. Lycopodiophytes typically have numerous scale-like, needle-shaped or strap-shaped (the latter in some fossil species) leaves which cloth much or all of the stem. In the arborescent fossil forms, the leaves used to be progressively shed leaving characteristic rhomboidal leaf-scars. The sporangia are typically produced in compact structures called **strobili** ("cones") usually at branch apices. Each sporangium is subtended by a **sporophyll**.

Class: **Lycopodiopsida**: Typically forms with scale-like to strap-shaped leaves and well developed branching. Includes the modern homosporous lycophytes *Lycopodium* (together with its segregates: *Huperzia*, *Phlegmariurus*, *Diplazium*, *Lycopodiella* and *Diplazium*) and *Phylloglossum*. The heterosporous forms include the large genus *Selaginella*. Also includes large fossil trees such as *Lepidodendron* and *Sigillaria*. The heterosporous forms are sometimes included in the following class.

Class: **Isoëtopsida**: Includes the modern heterosporous Quill-worts, *Isoetes* and *Stylites* which have long pointed leaves and a contracted axis which, in *Isoetes* is often embedded in the substrate. *Isoetes* species are aquatic or tied to wet substrates while *Stylites* can grow in drier conditions. The fossil genera *Pleuromeia*, *Nathorstiana* and *Chalonera* were small trees possibly related to the ancestors of *Isoetes* and *Stylites*.

Phylum: **EQUISETOPHYTA** (= SPHENOPHYTA, CALAMOPHYTA; horsetails):

The horsetails are a very distinct group which made its appearance in the late Devonian. They are characterized by their jointed ribbed stems, leaves appearing in whorls at the nodes, and terminal strobili. They are all homosporous.

Class: **Hyeniodonta** (EXTINCT): This is the most primitive group attributed to the *Equisetophyta* and has affinities with the ancestral *Trimerophyta* as well as with the extinct fern class *Cladoxylopsida*. Much of the branching was dichotomous and sporangia were not in compact strobili. Representative genera: *Hyenia*, *Calamophyton*.

Class: **Pseudoborniodonta** (EXTINCT): Represented by a single genus, *Pseudobornia*, a tree-like form from the Upper Devonian which grew some 20 metres high. It had dichotomously branched leaves with feather-like appendages.

Class: **Equisetopsida**: These are represented by the single modern genus *Equisetum* and several fossil genera. In *Equisetum*, a genus of about twenty-five species, the axes are impregnated with silica. The spores contain chlorophyll and are equipped with four hygroscopic **elaters** which unfold in dry air aiding in the spores' buoyancy and release. The sporophylls are **peltate** (i.e. umbrella shaped). Fossil horsetails included plants several metres in height which were abundant in swampy areas during the Carboniferous period. Examples of fossil genera are *Calamites*, *Schizoneura*.

Class: **Sphenophyllopsida** (EXTINCT): This fossil group persisted between the Devonian and the Triassic and consisted of creeping and/or scrambling plants with rather large whorled leaves (the leaves of the equisetopsids, in contrast, tend to be minute) and rather

loose strobili. Several species were possibly semi-aquatic. Typical genera: *Sphenophyllum*, *Bowmanites*.

Phylum: **POLYPODIOPHYTA** (=FILICOPHYTA, PTEROPHYTA; ferns):

Ferns are the most abundant and best known of the modern pteridophytes. They differ from other pteridophytic groups in being macrophyllous (i.e. with large multi-veined leaves) and in that they do not form strobili. The ferns appear on the fossil record in the mid-Devonian and have been important components of the vegetation ever since. Modern ferns include small herbaceous species as well as large palm-like tree ferns.

Class: **Cladoxylopsida** (EXTINCT): These early fern-like plants tend to have rather small, dissected whorled leaves and a complex much-divided vascular cylinder. Sporophylls are dichotomously branched having sporangia at the tips. Representative genera: *Pseudosporochnus*, *Cladoxylon*. Possibly related to the *Hyeniopsida* of the phylum *Equisetophyta*.

Class: **Coenopteridopsida** (EXTINCT): A rather large array of extinct ferns spanning from the late Devonian to the Permian. They are typically protostelic and rarely produce secondary xylem. Representative genera are: *Stauropteris*, *Zygopteris* and *Rhacophyton*. Probably polyphyletic.

Class: **Marattiopsida**: This primitive group of ferns, with a fossil record extending back to the Carboniferous period is now represented by about five living genera. Like the ophioglossopsids their sporangia are "**eusporangiate**" (developing from a group of cells and with a wall made up of more than one layer of cells) and are typically fused into **synangia**. They usually bear large pinnately compound leaves. Representative living genera are *Marattia* and *Angiopteris* while the best known fossil genus is the tree-fern *Psaronius*.

Class: **Ophioglossopsida** (adderstongue and moonwort ferns): This small group of structurally primitive ferns has left only a scant fossil record, all from the Cenozoic, and is represented mainly by the living genera *Botrychium*, *Helminthostachys* and *Ophioglossum*, plus a few related genera. All ophioglossopsids are rather small herbaceous ferns typically carrying a single leaf (entire in *Ophioglossum* but variously divided in the others) and a sporangium-bearing branch, the **sporangiophore**. It has recently been suggested that the ophioglossopsids may not be true ferns but may be more closely related to the extinct progymnosperms.

Class: **Osmundopsida**: A primitive group in which the sporangia are intermediate between the eusporangiate and leptosporangiate conditions. Fertile fronds are very distinct from sterile fronds. The osmundids date back to the Permian period; the best known genera are *Osmunda* and *Todea*.

Class: **Gleicheniopsida**: Group of leptosporangiate ferns with sporangia having an oblique annulus. Mainly from the tropics and subtropics of the southern hemisphere. Examples are *Hymenophyllum*, *trichomanes* and *Gleichenia*.

Class: **Polypodiopsida** (= *Filicopsida*): This group includes the great majority of living ferns. These ferns are **leptosporangiate** (having sporangia developing from a single cell and with

a wall having one layer of cells). In most cases the sporangia occur in groups known as **sori**, typically on the underside of the leaves. Most modern ferns are more or less herbaceous but some can attain considerable heights such as the tree-ferns *Alsophila*, *Cyathea* and *Dicksonia*. The sporangia typically open as a result of the shrinkage of a band of cells surrounding part of the sporangium forming the so-called **annulus**. As a result of the way in which the annulus cells are thickened, when this shrinks it causes the sporangium to split open along a line of low resistance (the **stomium**) thus dispersing the spores. The great majority of ferns are homosporous but the aquatic genera *Marsilea*, *Pilularia*, *Regnellidium*, *Salvinia* and *Azolla* are heterosporous. These aquatic ferns are generally placed in two distinct sub-classes (**Marsileidae** and **Salviniidae**); the great majority of filicopsids belong in the sub-class: **Polypodiidae** (= *Filicidae*), representative genera of which include: *Pteris*, *Polypodium*, *Davallia*, *Adiantum*, *Asplenium*, *Nephrolepis*, *Pteridium*, *Blechnum* as well as the tree-ferns noted above.

b. Gymnosperms:

Heterosporous vascular plants, typically woody and bearing **seeds** which are sporophyte embryos enclosed in female gametophytic tissue and in turn surrounded by a protective wall derived from the megasporangial wall (**nucellus**) and megasporophyll-derived **integuments**. The **ovules** (integuments + nucellus + female gametophyte) are not totally enclosed so that in order to effect fertilization the **pollen grains** (microspores containing an endosporic male gametophyte) can land directly on the ovule - hence the term *gymnosperm* (i.e. with naked seed).

Phylum: **PROGYMNOSPERMOPHYTA** (EXTINCT):

This group of trees which existed during the late middle and the upper Devonian combine typical gymnosperm with filicophyte characters. Thus the type of wood is characteristic of the gymnosperms as well as the fact that, like woody seed-plants, they developed a periderm. However many of them were apparently still homosporous although there is also evidence of heterosporous forms. Thus not all progymnosperms produced seeds. Of the most important genera, *Aneurophyton*, which is the more primitive, seems to have been homosporous and did not produce true seed while *Archaeopteris* and *Callixylon* seem to have produced true seeds and to have been heterosporous.

Phylum: **PTERIDOSPERMOPHYTA** (EXTINCT - pteridosperms, seed ferns):

The seed ferns are a large and diverse group of plants with a fossil record extending from the Carboniferous period and throughout most of the Mesozoic era. They were mainly fern-like shrubs and small trees - others may have been creepers and lianas. The sporangia were borne on their fronds and did not form strobili. The ovule was typically surrounded by a cup-like structure referred to as a **cupule**.

Class: **Lyginopteridopsida**: Large assemblage of pteridosperms belonging mainly to the Palaeozoic; presumably polyphyletic. Ovules not enclosed. Typical genera are *Calamopitys*, *Lyginopteris*, *Medullosa* and *Callistophyton*.

Class: **Caytoniopsida**: Mesozoic pteridosperms in which the ovules were enclosed in ovary-like structures suggesting that they may have been somewhat angiospermous - however this group does not seem to be ancestral to the true flowering-plants. Includes three known evolutionary lines: the order **Caytoniales** (e.g. *Caytonia*), the order

Corytospermales (e.g. *Pteruchus*, *Rauflorinia*, *Kachchhia*) and the order **Peltaspermales** (e.g. *Lepidopteris*).

Class: **Glossopteridopsida**: Common in the Permian and early Triassic periods and persisting till the Jurassic, also had angiospermous characters. It is rather anomalous and some authorities think that it might bear some relationship to the **Gnetophyta** or/and to the flowering-plants. Typical genera: *Glossopteris*, *Ottokaria*, *Dankenia*.

Phylum: **CYCADOPHYTA** (cycads):

This group of palm-like gymnosperms has a fossil record extending back into the Carboniferous period and were very abundant throughout the Mesozoic. The sporophylls are typically grouped together to form large strobili. The male gametes (antherozoids) are multiflagellate. Probably polyphyletic.

Class: **Cycadopsida** ("true" cycads): Several genera of cycads still exist and since they still have an organization which is very similar to that of their Palaeozoic and Mesozoic forbears, they must be regarded as "**living fossils**". Cycadopsids are dioecious since megasporangial and microsporangial cones are borne on separate plants. These cones (strobili) are typically borne in the centre of a crown of large palm-like fronds. Representative genera are *Cycas*, *Zamia*, *Macrozamia*, *Ceratozamia*, *Dioön*, *Encephalartos*, *Bowenia* and *Stangeria*.

Class: **Cycadeoidopsida** (= *Benettitopsida*; cycadeoids - EXTINCT): The cycadeoids which evolved in, dominated and became extinct in the Mesozoic era, were cycad-like but often bore "mixed" strobili including both microsporangia and megasporangia in separate whorls of microsporophylls and megasporophylls, often supplemented by whorls of sterile sporophylls so that the strobili were very similar to true flowers. In fact it is very probable that in some types these were brightly coloured and may have been pollinated by insects or other small flying animals. It has been contended that cycadeoids may have been ancestral to the true flowering plants but most probably the similarity between the cycadeoid flower and the true flower was due to convergence. Nonetheless recent cladistic analysis suggests that cycadeoids are close to the angiosperms. Examples of cycadeoids are *Cycadeoidea* (= *Benettites*) and *Williamsonia*.

Class: **Pentoxyllopsida** (EXTINCT): Restricted to the Jurassic period. They had microsporangial and megasporangial strobili, these last somewhat resembling mulberries, but the leaves seem to have been simple. There were five steles and the wood was compact as in the conifers. Their placing in the **Cycadophyta** is tentative. They may be derived from medullosan pteridosperms while recent cladistic analysis suggests that they are close to the angiosperms.

Phylum: **GINKGOPHYTA** (Maidenhair trees):

There is only one surviving species in this division: *Ginkgo biloba* which is a native of China and is widespread in cultivation. It is thus a veritable "**living fossil**". Ginkgophytes flourished from the Permian and throughout the Mesozoic and nearly became extinct at the end of the Cretaceous period, probably victims to the same episode which killed off dinosaurs, cycadeoids and a host of other groups. They are characterised by the non-strobilate megasporangia, multiflagellate antherozoids and rather small, dichotomously veined leaves. Possibly derived from the **Cordaitophyta**. The order **Czekanowskiales** (EXTINCT), Jurassic

and Cretaceous trees with filiform leaves, have traditionally been included with the ginkgos because of superficial resemblances. However, they may be more closely related to the glossopterids and, like them, have rather angiospermous ovules. Typical genus; *Czekanowskia*.

Phylum: **CORDAÏTOPHYTA** (EXTINCT):

This group is almost certainly related to the modern conifers. They were mainly large trees with long strap-shaped leaves and loose compound strobili. They flourished mainly in the Carboniferous period and became extinct by the end of the Palaeozoic. Representative genera: *Cordaïtes*, *Poroxylon*.

Phylum: **PINOPHYTA** (= CONIFEROPHYTA; conifers):

The conifers, still an important component of the vegetation of cool climates, appeared in the late Palaeozoic. They are typically large trees with resin canals in their wood and with compact strobili, the megasporophyllous strobili typically becoming woody. The male gametes are not motile.

Class: **Pinopsida**: This includes the typical conifers with characters as noted above. Representative genera are *Pinus* (pines), *Abies* (firs), *Picea* (spruce), *Larix* (larch), *Araucaria*, *Agathis*, *Thuya*, *Cupressus* (cypress), *Cedrus* (cedar), *Juniperus* (juniper), *Tetraclinis* (sandarac), *Sequoia* and *Sequoiadendron* (which are the largest trees ever to have existed) and *Podocarpus*. The Bristlecone pine (*Pinus aristata*) includes live specimens which have been dated at 4,500 years while it is estimated that sequoias may have a life expectancy of 7000 years. The fossil record goes back to the late Carboniferous.

Class: **Taxopsida** (yews): The taxads differ from the other conifers in that they lack resin canals while the ovules are solitary and often surrounded by a fleshy aril. Typical genera are *Taxus* and *Torreya*. Their fossil record extends back to the Triassic.

Phylum: **GNETOPHYTA** (gnetads):

This anomalous group includes just three living genera: *Ephedra*, *Welwitschia* and *Gnetum* which are morphologically completely different from each other and from other gymnosperms. They are placed together because they all have vessels (as opposed to tracheids, typical of other gymnosperms), compound strobili and opposite or whorled leaves. *Ephedra* includes shrubs with leaves reduced to scales; details of the strobili have suggested a relationship to the cordaïtophytes. *Welwitschia* is a very unusual genus with just one Namibian species. It has just two enormous leaves each with a basal meristem so that they grow continuously. Specimens over 2000 years old are known. *Gnetum* is a genus of lianas, trees and shrubs which have leaves similar to those of angiosperms. Some authorities believe that *Gnetum* may have evolved from angiospermous ancestors. Double fertilisation, otherwise confined to the angiosperms, has recently been discovered in *Ephedra* and *Gnetum*. Recent cladistic analysis suggests that the gnetads are a natural group related to the angiosperms, cycadeoids and pentoxylsids. The fossil record is rather scant although pollen similar to that of *Ephedra* and *Welwitschia* has been dated back to the Permian period. *Dechellya* from the Triassic and *Drewria* from the Cretaceous are believed to be gnetads. The unusual fossil *Sanmiguelia* from the Triassic possesses both gnetalean and angiosperm characters.

c. **Angiosperms:**

The flowering plants include just one division described below.

Phylum: **MAGNOLIOPHYTA** (= ANTHOPHYTA, ANGIOSPERMOPHYTA; flowering plants):

The flowering plants are characterized by having ovules enclosed in **carpels** (variously folded megasporophylls) so that the pollen grains cannot land directly on the ovules. Instead they land on a **stigma** which is a receptive part of the carpel. Flowering plants are also characterized by the absence of archegonia in their female gametophytes (a characteristic which they share with the genus *Gnetum* within the *Gnetophyta*), vessels in the xylem (which are derived differently from those of the gnetophytes) and, perhaps most significantly, by **double fertilization** wherein one male gamete fuses with the female gamete (**oosphere**) and the second male gamete fuses with a diploid/polyploid nucleus to generate a reserve known as **endosperm**. Double fertilisation has also been noted in the gnetalean genera *Ephedra* and *Gnetum*, further emphasising the relationship between these two groups. The flower is a sort of mixed strobilus with sterile sporophylls (**sepals/petals/tepals**), microsporophylls (**stamens**) and megasporophylls (**carpels**). Until recently, undisputed fossil record for the flowering plants extended to the early Cretaceous but, by the end of the Cretaceous, most existing families had already appeared on the scene. Possibly the most astonishing case of an evolutionary explosion. The rapid evolution of flowering plants probably spelt the doom for the various Mesozoic gymnosperms. Some pre-Cretaceous fossils with angiosperm characteristics are known from the Triassic (e.g. *Sanmiguelia*) and the Jurassic (e.g. *Furcula*). The recently discovered late Jurassic fossil *Archaeofructus* (with two known species), from China, seems to be the earliest authenticated flowering plant; it seems to have been an aquatic herb. The early Cretaceous *Bevhalstia* may also be an early flowering plant, though it also has some gnetalean features. Angiospermous (i.e. enclosed) ovules are known in pteridosperm groups such as the caytoniopsids, glossopterids, pentoxylsids and *Czekanowskia* but pollen grains still had direct access to the ovules. Cycadeoids had flower-like strobili. Recent cladistic analysis suggest an affinity between the angiosperms, gnetads, cycadeoids and pentoxylsids (which are sometimes collectively known as **anthophytes**)

Primitive characteristics of angiosperms include: "hermaphrodite" flowers as opposed to the monoecious or dioecious condition; and monoaperturate (with a single aperture in the walls of the pollen grains) as opposed to triaperturate (with three apertures in the walls of the pollen grains) pollen grains. Two classes, the monocotyledons and the dicotyledons, are traditionally recognized but, recent cladistic analysis based largely on macromolecular investigations, strongly suggest that such a classification is not natural and thus it is a better to recognize, either a single class (Magnoliopsida) with a number of subclasses. Or three classes: Magnoliopsida (primitive dicotyledons), Liliopsida (monocotyledons) and Rosopsida (more advanced dicotyledons).

Dicotyledons:

Equipped with a true **vascular cambium** so that many species are woody trees and shrubs with secondary thickening. Leaves typically with reticulate venation. Floral parts rarely in multiples of three. Dicots are a paraphyletic group since they include the ancestors of the monocots. The more primitive groups have **monoaperturate** (with single slit/pore) pollen grains (as do the monocots)

Class: **Magnoliopsida:**

A paraphyletic group of primitive angiosperms with monoaperturate pollen grains (as in the monocots); include a variety of trees, climbers and herbs. Often bearing numerous stamens and often no clear distinction between sepals and petals. It used to be assumed that the woody forms were the most primitive but the earliest known fossil angiosperms are actually herbaceous. Xylem often with tracheids. Herbaceous groups (known as non-monocot palaeoherbs) include, among others, the orders **Nymphaeales** (water lilies), **Ceratophyllales** (hornworts), **Piperales** (peppers) and **Aristolochiales** (birthworts) which last may be ancestral to the monocots. Woody groups include, among others, the orders **Magnoliales** (magnolias), **Laurales** (bay laurels & avocados) and **Illiciales**.

If included in a single class with the remaining angiosperms they would form the sub-class: **Magnoliidae**:

Class: **Rosopsida** (=Hamamelidopsida; eudicots):

The Eudicots include the great majority of existing vascular plant species. They are characterized by having triaperturate pollen grains (with three apertures in the exine, or often more, but these are derived). Their floral parts are very rarely in multiples of three. They range from huge trees such as eucalypts (*Eucalyptus*) and oaks (*Quercus*) to tiny herbs (e.g. *Sagina*). Some have greatly reduced leaves and fleshy stems such as the cacti (family **Cactaceae**). Several have become aquatic e.g. *Ceratophyllum* and *Nymphaea* (water-lily), while others have adopted a parasitic mode of life (e.g. families **Orobanchaceae** [broomrapes], **Rafflesiaceae** [with the largest known flowers], **Balanophoraceae**). Includes some families of great economic importance such as the **Fabaceae** (= *Leguminosae*; legume family), **Apiaceae** (= *Umbelliferae*; carrot family), **Asteraceae** (= *Compositae*, lettuce family) and **Solanaceae** (potato family). Include several evolutionary lines. The principal lines include the sub-classes **Caryophyllidae**, **Rosidae** and **Asteridae**. The **Caryophyllidae** often have **betalain** pigments rather than the anthocyanins found in other angiosperms; trinucleate pollen and produce perisperm (in the thick nucellus) as a seed food reserve. The **Rosidae** are a large assemblage of mainly polypetalous (with free petals) plants. The **Asteridae** include most gamopetalous (with fused petals) groups. Hereunder is an overview of the angiosperm subclasses:

Sub-class: **Ranunculidae**: A primitive group which includes, among others, the buttercup (*Ranunculaceae*) and the poppy (*Papaveraceae*) families. Usually with numerous stamens

Sub-class: **Hamamelidae**: Rather specialized plants including, among others, the stonecrop (*Crassulaceae*), saxifrage (*Saxifragaceae*), grapevine (*Vitaceae*), walnut (*Juglandaceae*) and oak (*Fagaceae*) families. Flowers generally polypetalous, occasionally sympetalous or, in many of trees, apetalous.

Sub-class: **Caryophyllidae**: Largely polypetalous plants often tied to saline or desert habitats. Includes, among others, the cactus (*Cactaceae*), goosefoot (*Chenopodiaceae*), amaranth (*Amaranthaceae*), carnation (*Caryophyllaceae*), knotgrass (*Polygonaceae*) and tamarisk (*Tamaricaceae*) families.

Sub-class: **Rosidae**: Large assemblage of mainly polypetalous flowering plants. Includes the mallow (*Malvaceae*), rose (*Rosaceae*), pea (*Fabaceae*), stinging-nettle (*Urticaceae*), oxalis (*Oxalidaceae*), cabbage (*Brassicaceae*), citrus (*Rutaceae*), violet (*Violaceae*), spurge (*Euphorbiaceae*) and geranium (*Geraniaceae*) families.

Sub-class: **Asteridae**: Large assemblage of mainly sympetalous angiosperms including heath (*Ericaceae*), honeysuckle (*Caprifoliaceae*), carrot (*Apiaceae*) and daisy (*Asteraceae*) families.

Sub-class: **Lamiidae**: Also largely sympetalous and probably share their origin with the *Asteridae* with which they are sometimes included. Includes the potato (*Solanaceae*), morning glory (*Convolvulaceae*), borage (*Boraginaceae*), madder (*Rubiaceae*), plantain (*Pantaginaceae*), broomrape (*Orobanchaceae*) and mint (*Lamiaceae*) families.

Monocotyledons:

Class: Liliopsida

Lack a vascular cambium so that most monocots are herbaceous. Monocot trees (e.g. palms and dragon trees) have **anomalous secondary thickening** which forms in a different manner from that of dicots. Leaves typically with parallel venation. Floral parts typically in multiples of three; pollen grains are monoaperturate. Includes large trees such as the palms (family **Arecaceae** [= *Palmae*, *Principes*]) down to the tiny floating *Wolffia*, just one millimetre across and the smallest flowering plant. Most are bulbous herbs with strap-shaped leaves. Includes several aquatic species including the marine **seagrasses** (e.g. *Posidonia*, *Cymodocea*, *Zostera*, *Nanozostera*, *Thalassia*, *Phyllospadix*, *Halophila*) which create important marine communities. Also includes plants of great economic importance, notably the grass family **Poaceae** (= *Gramineae*) which includes the cereal species. A monophyletic group derived from dicot ancestors, possibly close to the dicot order **Aristolochiales**.

Sub-class: **Alismatidae**: Minute to large herbs, often hydrophytic (including also all the seagrasses) and with distinct sepals and petals. Includes the arum (*Araceae*), water plantain (*Alismataceae*), pondweed (*Potamogetonaceae*), tapeweed (*Hydrocharitaceae*) and seagrass (*Zosteraceae*, *Posidoniaceae* etc.) families.

Sub-class: **Commelinidae**: Herbs and trees (palms) often with distinct sepals and petals. Includes the palm (*Arecaceae*), spiderwort (*Commelinaceae*), banana (*Musaceae*) bromeliad (*Bromeliaceae*), sedge (*Cyperaceae*), grass (*Poaceae*) and rush (*Juncaceae*) families.

Sub-class: **Liliidae**: Mainly perennial herbs, occasionally trees, with petaloid sepals such that the three sepals and three petals have a similar structure and are thus referred to as tepals; often with underground perennating organs. Includes the lily (*Liliaceae*), hyacinth (*Hyacinthaceae*), asphodel (*Asphodelaceae*), agave (*Agavaceae*), iris (*Iridaceae*), onion (*Alliaceae*), asparagus (*Asparagaceae*), dragon tree (*Dracaenaceae*) and orchid (*Orchidaceae*) families

Note: Ribosomal RNA sequencing suggests that the Kingdoms: **PLANTAE** and **FUNGI**, as well as the **ANIMALIA** may share a common origin, with the fungi being more closely related to the animals.