PLANT EVOLUTION & PHYLOGENETIC TREE

PROKARYOTES, ALGAE AND PLANTS

Prokaryotes are the organisms classified as Bacteria and Archaea, and are the most successful & abundant organisms on Earth. In fact they have been THE dominant group on earth since life appeared and for around 2000 million years were the only life form on earth. Prokaryotes as a group have the largest biomass on the planet e.g. in the oceans, prokaryotes make up 90% or greater than the total weight of living things; there may be 2.5 x 109 prokaryote cells in a gram of fertile soil. Prokaryotes are also the most ancient organisms on Earth: the earliest known fossil cells belong to a prokaryote, and come from rocks in Western Australia that date back 3500 million years. All prokaryotes are small cells that lack the complex internal structures, like mitochondria and chloroplasts, found in eukaryotic cells. Also, although prokaryotes possess DNA on a chromosome, it is not enclosed in a nucleus.

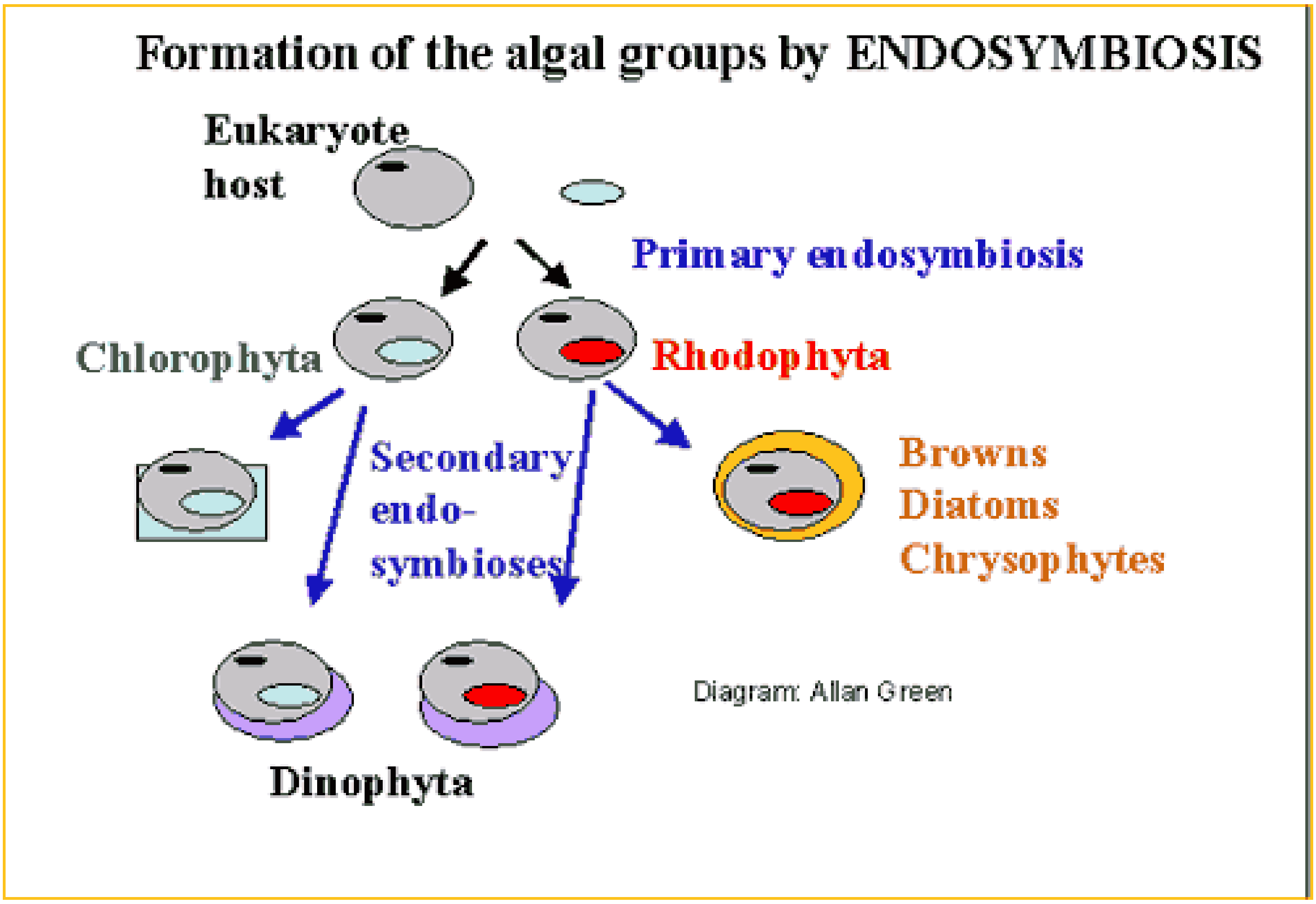
Because prokaryotes are largely invisible to the human eye we tend to forget about them. However, they contributed to the development of an oxygen-rich atmosphere early in Earth's history, and are essential to the processes of decomposition and nutrient cycling, a key role in all ecosystems. They also made a significant contribution to the evolution of the better-known, **eukaryote**, life forms.

Present-day prokaryotes may resemble early fossils, but they are modern organisms that have successfully adapted to modern environmental conditions. They are found in some of the most extreme environments on Earth, including Antarctica, the depths of the oceans and deep in rocks, round deep-sea vents, and in boiling thermal springs and are ever present in our human environments, including cities, homes and the human body.

The Cyanobacteria (blue-green algae) are a group of prokaryotes that are extremely important both ecologically (especially in global carbon and nitrogen cycles) and evolutionary terms. Stromatolites, which are formed by cyanobacteria, provide living and fossil evidence of cyanobacteria going back 2700 million years. Today stromatolites grow only in shallow, salty pools in hot, dry climates (e.g. Shark Bay in Western Australia), and their abundance in ancient rocks implies similar environmental conditions in those times. Stromatolites and other cyanobacteria were the main contributors to the marked increase in atmospheric oxygen concentrations that began around 2000 million years ago. Today, cyanobacteria are found everywhere - in marine, freshwater and terrestrial environments and as symbionts e.g. lichen - and contribute up to 50% of the atmosphere's oxygen.

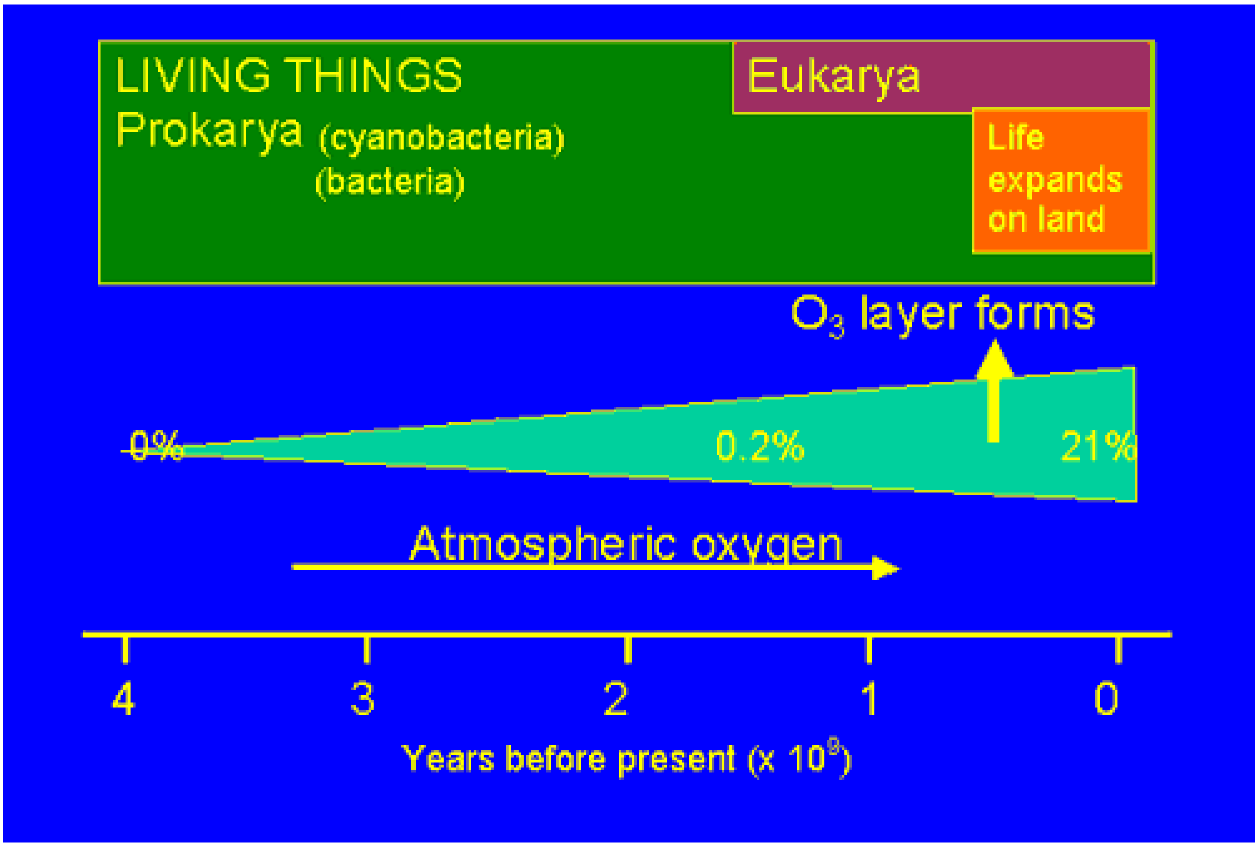
DNA evidence suggests that the first eukaryotes (green plants) evolved from prokaryotes (through endosymbiotic events) between 2500 and 1000 million years ago. Fossils of eukaryotes that resemble living brown algae have been found in sedimentary rocks from China that are 1700 million years old, while possibly the oldest photosynthetic eukaryote, *Grypania*, comes from rocks 2100 million years old. Note that the diversity of modern algal groups, and particularly of their chloroplasts, suggests that these endosymbiotic events were not unusual. Modern algae comprise a range of organisms with very different structures but identical photosynthetic pigments. This suggests that very different host organisms have formed a symbiosis with the same photosynthetic cells. That is, the algal groups must have evolved through separate endosymbiotic events, and the group as a whole is identified on the basis of a similar level of structure, rather than on its evolutionary origins. Such groups, where the members have several different evolutionary origins, are described as **polyphyletic**.

Cyanobacteria have a close evolutionary relationship with eukaryotes. They have the same photosynthetic pigments as the chloroplasts of algae and land plants. Chloroplasts are the right size to be descended from bacteria, reproduce in the same manner, by binary fission, and have their own genome in the form of a single circular DNA molecule. The enzymes and transport systems found on the folded inner membranes of chloroplasts are similar to those found on the cell membranes of modern cyanobacteria, as are their ribosomes. These similarities between cyanobacteria and chloroplasts suggest an evolutionary link between the two, and can be explained by the theory of endosymbiosis.



THE EARLIEST LAND "PLANTS"

For 1500 million years photosynthetic organisms remained in the sea. This is because, in the absence of a protective ozone layer, the land was bathed in lethal levels of UV radiation. Once atmospheric oxygen levels were high enough the ozone layer formed, meaning that it was possible for living things to venture onto the land.



The seashore would have been enormously important in the colonisation of land. In this zone algae would have been exposed to fresh water running off the land (and would have colonised the freshwater habitat before making the move to terrestrial existence). They would also be exposed to an alternating wet and desiccating environment. Adaptations to survive drying out would have had strong survival value, and it is important to note that seaweeds are poikilohydric and able to withstand periods of desiccation.

The earliest evidence for the appearance of land plants, in the form of fossilised spores, comes from the Ordovician period (510 - 439 million years ago), a time when the global climate was mild and extensive shallow seas surrounded the low-lying continental masses. (These spores were probably produced by submerged plants that raised their **sporangia** above the water - wind dispersal would offer a means of colonising other bodies of water.) However, **DNA-derived dates** suggest an even earlier colonisation of the land, around 700 million years ago.

BRYOPHYTES

The earliest photosynthetic organisms on land would have resembled modern algae, cyanobacteria, and lichens, followed by bryophytes (liverworts & mosses, which evolved from the **charophyte** group of green algae). Bryophytes are described as seedless, nonvascular plants. Their lack of **vascular** tissue for transport of water and nutrients limits their size (most are between 2 and 20 cm high). Bryophytes don't have typical stems, leaves, or roots, but are anchored to the ground by rhizoids. They can grow in a wide range of environments and are **poikilohydric**: when the environment dries so does the plant, remaining dormant while dry but recovering rapidly when wetted. These features make them important pioneer species.
The vascular plants

About 425 million years ago a new type of plant appeared: these were the vascular plants, with their **homoiohydric** lifestyle. The earliest known vascular plants come from the Silurian period. *Cooksonia* is often regarded as the earliest known fossil of a vascular land plant, and dates from just 425 million years ago in the late Early Silurian. It was a small plant, only a few centimetres high. Its leafless stems had sporangia (spore-producing structures) at their tips.

Rhynia is slightly younger but similar in appearance to *Cooksonia*. *Baragwanathia* is much larger & more complex, with what appear to be spirally-arranged leaves. *Baragwanathia* has been described as a **lycophyte** (a vascular plant). For such a complex plant to be present in the Silurian then land plants must have emerged much earlier, perhaps in the Ordovician.

These first land plants evolved from the green algae, with which they share a number of traits. All store energy reserves, as starch, inside plastids. Their cell wall is built of cellulose microfibrils and the photosynthetic pigments are chlorophylls a and b, plus b-carotene.
Solutions to life on land

THE POIKILOHYDRIC LIFESTYLE

Poikilohydry means that the organism relies directly on the environment for its water. As a result, the organism's water content tends to reach equilibrium with that of the environment. Poikilohydric organisms have no mechanisms to prevent desiccation: they desiccate, and remain dormant, when their environment dries out, but can rehydrate when water becomes available again. They usually absorb water directly through their body surface.
Poikilohydric organisms include some green algae, cyanobacteria (blue-green algae), lichens, and the bryophytes.

THE HOMOIOHYDRIC LIFESTYLE

Homoiohydric plants can keep their water content constant, and don't equilibrate with the environment.
This is achieved by:

- Controlling water loss (waterproofing, cuticle)
- Controllable valves in cuticle for photosynthesis (stomata)
- Replacing lost water, internal conducting tissue (xylem): vascular plants
- 3D structure: minimises surface area, provides support
- Ventilated tissue for enhanced gas exchange (internal intercellular spaces)

All modern land plants - with the exception of the bryophytes - have these features.

There was also *competition for light*, leading to pressure to increase productivity, which could be achieved by increasing the area available for photosynthesis (evolving leaves) and/or keeping stomata open for longer. This meant that mechanisms for obtaining and transporting water also needed improvement. Thus, evolution was a slow, continuous, linked improvement in water relations and productivity increase.

DIVERSIFICATION OF LAND PLANTS

Once these features had evolved, there was a substantial diversification of land plants during the Devonian period (408 - 362 million years ago). These included lycophytes (the clubmosses are the best-known modern members of this group:), horsetails (e.g. *Equisetum*), and progymnosperms, intermediate between seedless vascular plants and the seed plants. While the early forms were small & lacked woody tissue, the first tree-like plants (including progymnosperms and tree-sized lycophytes) had appeared by the mid-Devonian. The first real trees (e.g. *Archaeopteris*) had developed by the late Devonian, and the seed-bearing **gymnosperms** had evolved from the progymnosperms by the end of this geological period. The appearance of trees had a significant effect on the environment, because their advanced root systems influenced soil production and led to increased weathering.

While the earliest-known seeds date back 365 million years ago, they must have begun to evolve much earlier. Up till now, precursors of seeds were not known from the fossil record. However, a new fossil discovery, of a seed precursor with a structure seemingly involved in pollination, dates this development to at least 385 million years ago.

SIGNIFICANCE OF THE SEED

While spores are easy to disperse, they have few reserves to establish themselves. This means that a spore reach a wet area, germinate rapidly, and begin photosynthesising straight away to gain energy for the next phase of the lifecycle. Thus spore-producing plants are limited to wet environments for at least part of their lifecycle.

In comparison, a seed contains a young plant and a nutrient store for that plant. This means that seed plants (gymnosperms and angiosperms) can colonise areas with transient or sub-surface water as the young plant can establish itself extremely rapidly once it has germinated. The evolution of the seed underpins the success of the gymnosperms and angiosperms.

In the Carboniferous (362 - 290 million years ago) conditions were warm, with little seasonal change in tropical latitudes, and the land was warm & swampy. These conditions suited the widespread forests horsetails & tree ferns that, like most other Carboniferous plants, reproduced by spores. Spores require moist conditions for germination and rapid growth. However, many of these spore-bearers died out as the environment became more arid towards the end of the Palaeozoic. The first conifers began to appear towards the end of the Carboniferous.

The climate became colder and drier during the Permian (290 - 245 million years ago), with widespread glaciation in the southern hemisphere. However, plants still grew in ice-free areas, among them the **seed fern** *Glossopteris*, which is known only from Gondwanan landmasses. In fact, the distribution of *Glossopteris* & other members of the Glossopteridales provided early evidence of continental drift. The seed ferns died out at the end of the Permian, and were replaced by *Dicroidium* and its relatives, which were also found throughout Gondwanaland. Conifers, cycads, & ginkgoes (all gymnosperms) began to replace the earlier forests, and were common across Pangaea during the Triassic (245 - 208 million years ago). New Zealand was present as largely volcanic & easily eroded islands, & was home to ferns, *Dicroidium*, gingkoes, and early araucarian conifers. Early podocarps may also have been present.

THE APPEARANCE OF FLOWERING PLANTS

Gymnosperms, especially the cycads, remained the dominant land plants in the Jurassic (208 - 145 million years ago), but the Cretaceous (145 - 65 million years ago) saw the rise of the flowering plants (**angiosperms**) and their associated insect pollinators (an example of **coevolution**). There are around 235,000 species of angiosperms but they all share a particular set of features: flowers, fruit, and a distinctive life cycle. Because of this, angiosperms are assumed to be a monophyletic group.

The angiosperms owe their success to the evolution of the flower. The flower's pollen and nectar encourage pollinating animals to visit, increasing the odds of fertilisation by ensuring that pollen is transferred efficiently from flower to flower. (The flowers of wind-pollinated angiosperms, e.g. grasses, are very much reduced in terms of size and complexity.) After fertilisation the carpel and other parts of the flower are used to form fruit that aid dispersal of the seeds inside the fruit. In addition, the xylem **vessels** of angiosperms allow very rapid movement of water through the plant. This means that flowering plants can keep their stomata open through much of the day, achieving higher photosynthetic rates than gymnosperms; this "spare" photosynthetic capacity can support the development of fruit.

Two major groups of angiosperms are the dicotyledons (more correctly, "eudicotyledons") and the monocotyledons, which include the grasses. Grasses evolved in the Eocene (56.5 - 35.4 million years ago), and this led in turn to the evolution of browsing mammals during the Oligocene (35.4 - 23.2 million years ago). As the world began to cool during the Miocene (23.2 - 5.2 million years ago) these grasslands spread and the forests contracted; by the Pliocene (5.2 - 1.6 million years ago) there were deserts in many regions. The fragmentation of forest habitats, and spread of grasslands, that accompanied this cooling trend are implicated in the evolution of humans.

THE ICE AGES AND NEW ZEALAND'S ALPINE PLANTS

The Pleistocene Ice Ages were significant in the evolution of New Zealand plants as, together with the new habitats formed by the rise of the Southern Alps, they provided the conditions for the development of our extensive endemic alpine flora.

While New Zealand has been variously forested over a long period of time, at present there are two major types of native forest: rainforest or podocarp/broadleaf forest (a mix of conifers and hardwoods), and beech forest. Other vegetation types are herb fields, grasslands, and shrub-lands, which depending on their situation can be described as coastal, lowland, or montane (alpine).

During the last glaciation, 100,000 - 10,000 years ago, mean annual temperatures dropped by 4.5oC, and the snowline lowered 830 - 850m. There was extensive glaciation along the Southern Alps, extending to sea level on much of the West Coast, and there were small glaciers on the North Island's Tararua ranges and Central Plateau. During the coldest parts of the glacial, so much water was locked up in ice that sea levels were up to 135m lower and NZ was a continuous land mass.

These extreme conditions had particularly marked effects on the evolution and distribution of New Zealand's diverse alpine flora. Prior to the Pleistocene Ice Ages, not only was the climate rather warm but also there was little high country, until the upheavals of the Kaikoura Orogeny in the late Pliocene/early Pleistocene created alpine zones. Hence our high country plants are probably of relatively recent origin (geologically speaking). Alpine plants are those found above the present tree line, but at times during glacial phases they would have extended down to the coast in much of New Zealand.

Many of our alpine plants are **endemic** to New Zealand: 93% of alpine species are endemic; 8 genera are endemic, with a further 15 having only a few of their species outside NZ. These plants have likely evolved in NZ by rapid adaptive radiation from lowland species following the end of a glacial period. Alternating warm and cold periods would have driven plant species up and down the emerging mountains, split up habitat zones, and provided a variety of refugia. All these would significantly increase the evolutionary pressures on this particular set of plants. This hypothesis is supported by the fact that a number of alpine groups show disjunctions in their distribution and are found only on a few isolated sites: the simplest explanation is that they were originally widespread but were wiped out during warmer periods from the lower-lying areas surrounding their present homes, or else were unable to compete with returning lowland plants.