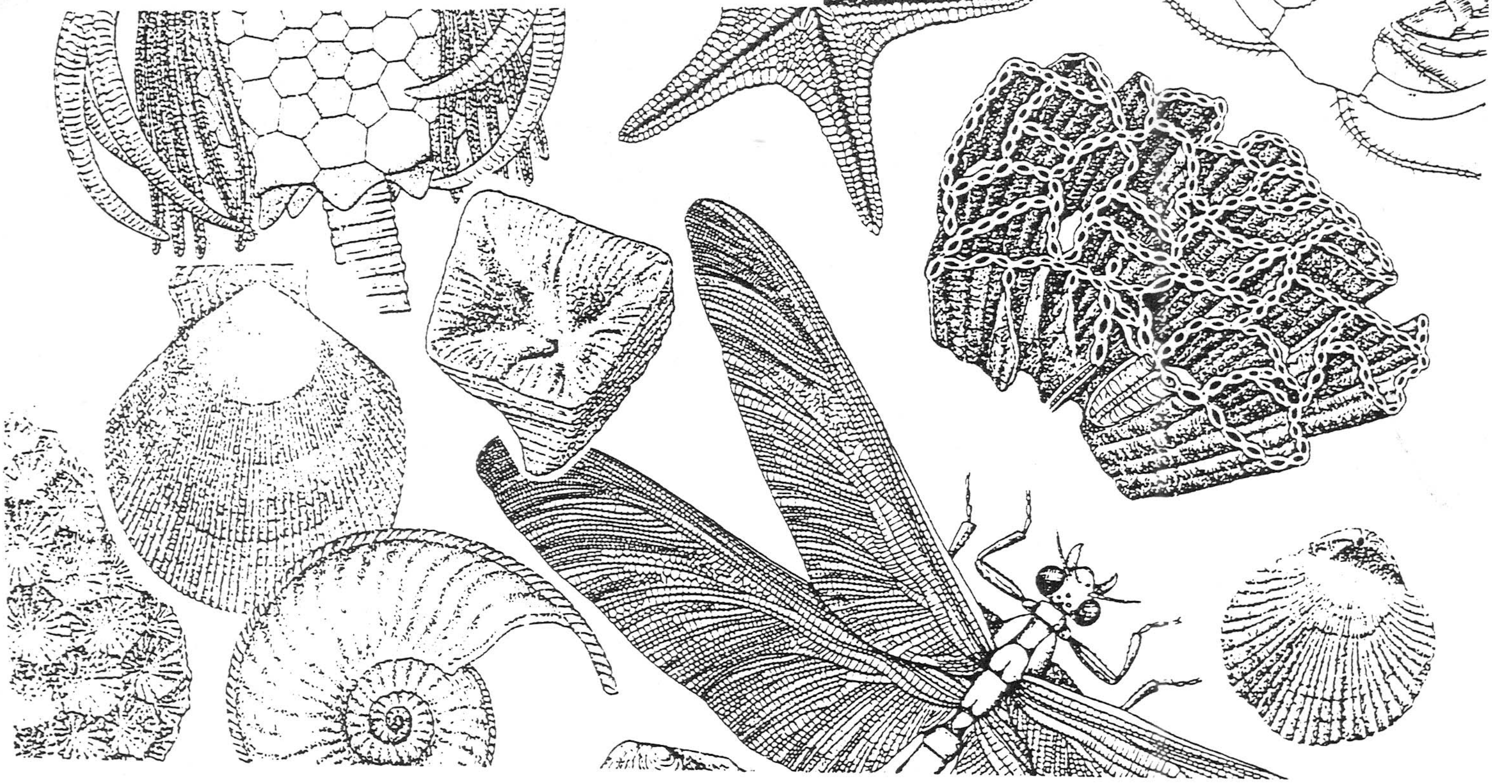
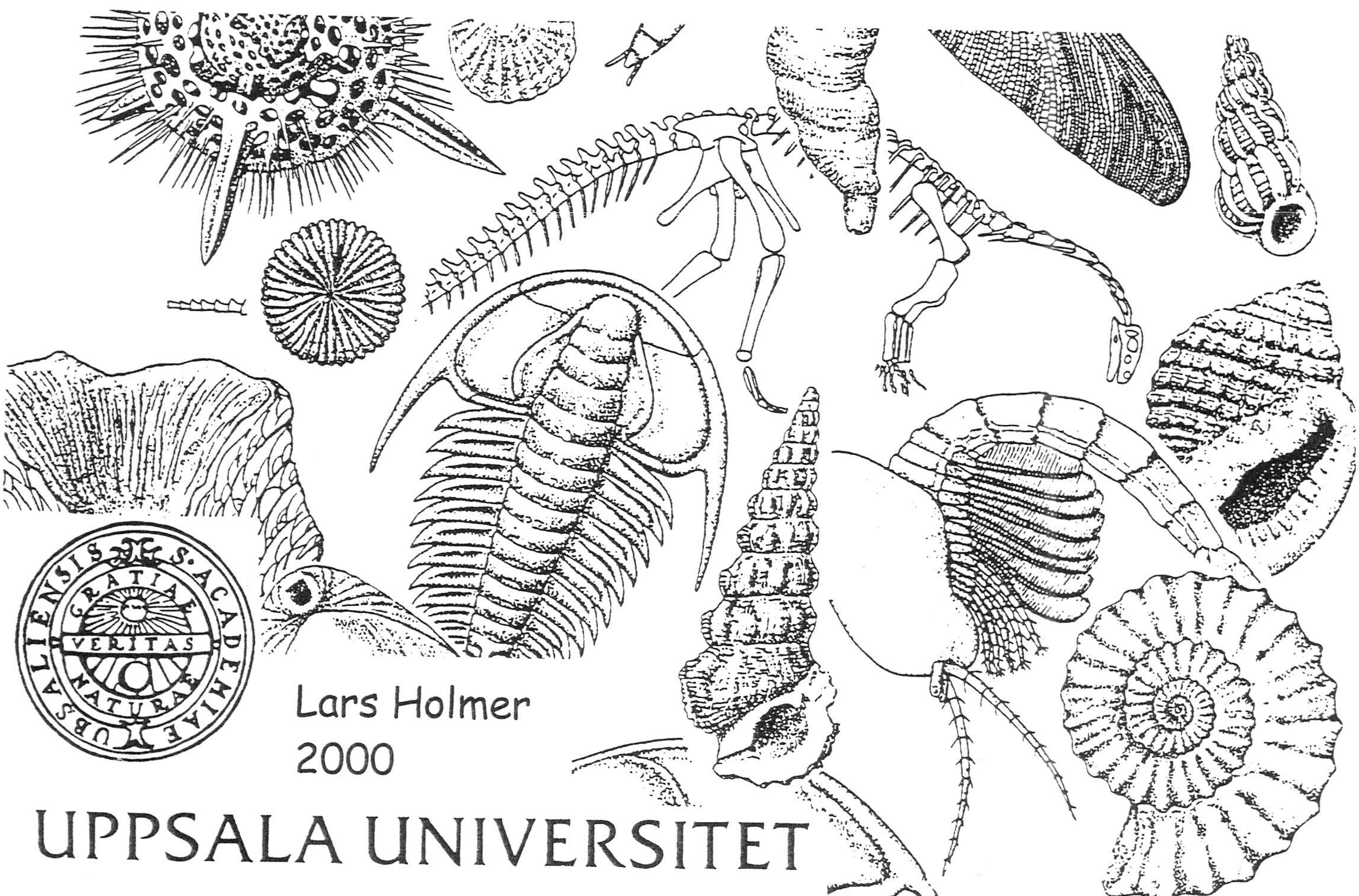
Historical Geology & Palaeontology
Institute of Earth Sciences



Life and Earth History



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2000

UPPSALA UNIVERSITET

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INTRODUCTION

What is palaeontology and historical geology?

Palaeontology is the study of the history of life on Earth, stretching over a period of almost 4 billion years. It is closely tied to **historical geology**, dealing with the study of Earth's ‘archive of time’, as represented by the sedimentary record. The sedimentary deposits contain fossils, the remains of once living organisms. The study of these fossils and the sedimentary rocks is the only way by which we can learn about past environments on Earth and the ways in which life has evolved and diversified. In fact, fossils may be regarded as the only real proof that evolution has occurred. Fossils have also helped in reconstructions of the positions of continents and oceans in the geological past, thus, helping us understand the present world and the environmental problems facing mankind today. It is important to remember that palaeontology is both a biological and geological science.

Uniformitarianism - Catastrophism

Uniformitarianism was first outlined by James Hutton in the 1830´s, and further developed by Charles Lyell (*Principles of Geology* 1830). Lyell held the opinion that the observable geological processes operating in the present should be the basis for everything that we try to infer from the past development of the Earth. In contrast, catastrophism argued that Earth’s sedimentary record includes evidence for more catastrophic events with a much shorter time span. It is now recognized that the rates of geological processes have varied over time and that there are many examples of catastrophic events (e.g. large meteoric impacts) that have not occurred in modern times. Thus, the on-going geological processes of today do not explain every aspect of Earth’s history but they are still very important models for learning about the past.

Geologic time

Earth scientists including palaeontologists and historical geologists are interested in geologic time since it is necessary in order to answer questions like:

- When was the Earth formed?
- When did life on Earth originate?
- When did life invade the land?
- How fast does sediment accumulate?
- What is the rate of biological, chemical, and climatic change?

There are the following two basic methods for measuring geologic time:

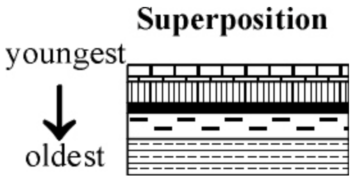
Absolute dating aims at giving an exact numerical value of geologic time. Today this is possible mainly through radiometric age dating, but earlier attempts include the following:

1654 - Archbishop James Ussher; proposed (based on the Bible) that the Earth was created in 4004 BC.
1749 – Count De Buffon; estimated (based on rates of sedimentation) that the Earth is about 75,000 years old.
1897 - William Thomson, Lord Kelvin; estimated (based on the assumed cooling of the Earth from an original molten state) that the Earth formed around 24 - 40 Ma ago.

Since 1918 (and the development of the mass spectrometer) many radioactive elements are used for obtaining geologic dates, based on the fact that elements decay at almost constant rates to stable daughter products, e.g. Potassium-Argon.

It is sometimes possible to get estimates of absolute geologic time by other types of physical measurements, for example the measurement of coral growth lines. Recent corals form thick and fine growth bands corresponding to yearly and daily growth increments respectively. Observations on well preserved fossil corals from the Devonian indicate that there are about 400 such daily growth lines between the thicker thick yearly growth increments. The important conclusion from this is that there were approximately 400 days/year during the Devonian, and thus the Earth's rotation must have slowed probably due to tidal friction.

Relative dating aims at determining the sequence in which the geological events occurred, and is not at all dependent on absolute ages. This type of dating is based primarily on the following three fundamental principles, collectively termed **"Steno's Laws"**, after the Danish scientist Nicholas Steno, who worked in Italy in the 1600's:



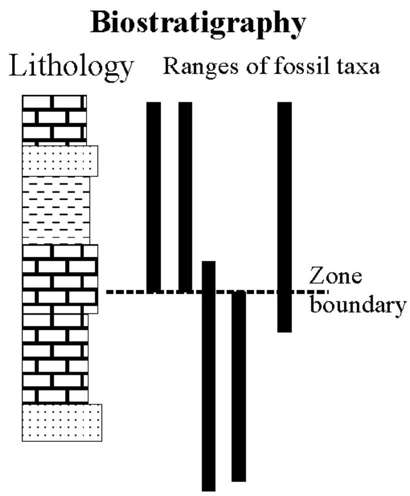
(1) **Law of superposition** (the oldest sediments are at the bottom and youngest on top)
(2) **Law of original horizontality** (sediments were originally laid down as flat layers).
(3) **Law of original lateral continuity** (sediments were originally deposited as continuous layers over extensive areas). Subsequently scientists have added the following four important principles:
(4) **Law of intrusive relationships** (any intrusive bed must be younger than the bed it cuts across).
(5) **Law of crosscutting relationships** (any fault must be younger than the bed it cuts across).
(6) **Law of fossil succession** (successions of fossils through a sedimentary sequence occur in the same vertical order all over the world thus enabling **biostratigraphic correlation** between the sequences (see also below).

Stratigraphy

Stratigraphy is mainly concerned with the application of Steno's Laws (see above) and the study of the relationships of rocks in time and space. An important aspect of stratigraphy includes **correlation**, i.e. determining the equivalency of geographically separated stratigraphic successions.

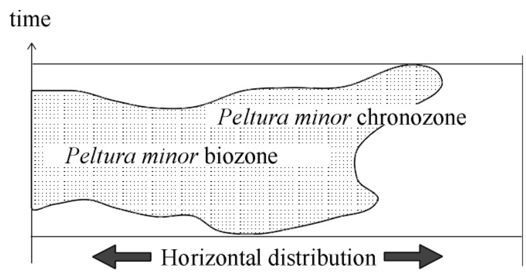
Biostratigraphy is based on the "Law of fossil succession" (see above) and aims at the study and use of fossil organisms for ordering and correlating rocks. The basic unit of biostratigraphy is the **biozone** (e.g. the Cambrian *Peltura minor* Biozone in the figure below) with is usually defined by the first appearance of an index fossil (e.g. the trilobite *Peltura minor*). A good index fossil should have the following characters (e.g. many foraminifera):

- Rapid evolution
- Short geological range
- Rapid and extensive geographic distribution
- Occur in great numbers
- Have great potential for preservation



Biostratigraphy is also closely tied to **chronostratigraphy,** i.e. time stratigraphy. The basic unit of chronostratigraphy is the **chronozone**, which corresponds to the maximum vertical distribution of an index fossil (e.g. the Cambrian *Peltura minor* Biozone in the figure below).

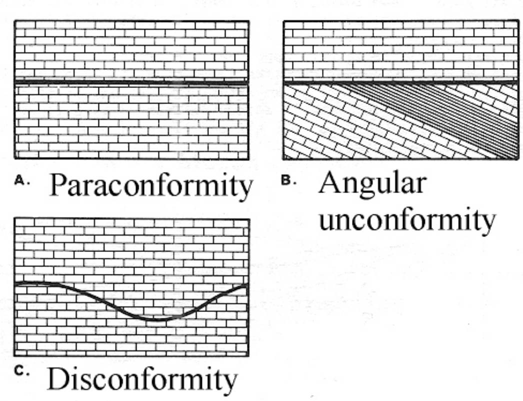
Lithostratigraphy divides rocks into discrete units based on their physical and chemical characters, i.e. the lithology. The basic unit of lithostratigraphy is the formation, which is defined as a mappable unit type of rock, e.g. a limestone that gets its formation name from a type locality (e.g. Boda Limestone, Dalarna). The formation is defined independent of geologic time and can even cross period boundaries.



Relation between a biozone and a chronozone

Boundaries between successive formations can be **conformable** if there is no major break in sedimentation. The boundaries may also commonly be represented by so-called **unconformities**, which are buried surfaces of erosion or non-deposition, representing gaps in the preserved geological record. The following types exist:

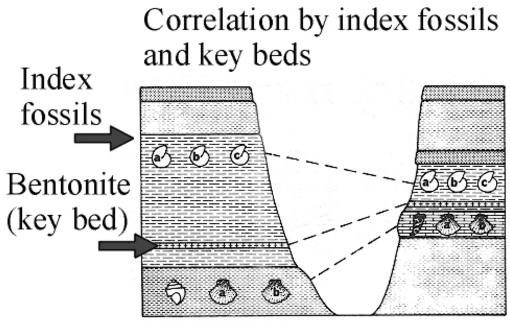
- **Angular unconformities** - implies tectonic deformation and erosion of underlying strata.
- **Nonconformity** - sedimentary strata overlying igneous or metamorphic rocks (excluding intrusions)
- **Disconformity** - irregular surface of erosion between two parallel units.
- **Paraconformity** - planar surface between two parallel units, representing a period of non-deposition, but no erosion.



Unconformities in successions sometimes may be recognised by the following criteria:

- Conglomerates, where the clasts are commonly fragments eroded from the underlying rock.
- Layers of phosphatized pebbles, glauconite (greensand), or manganese-rich beds.
- Abrupt changes in fossil assemblages, e.g. from marine to continental.

Boundaries between lithological units can also be developed as so-called **key beds (=marker beds)** that usually represent some kind of more or less dramatic geological event, e.g. a volcanic eruption with a resulting widely spread bentonite bed. Such types of key beds are obviously very important for correlation since they mark a very short time interval.



Geologic time scale

The geologic time scale has developed without any reference to absolute geologic time. It is based mainly on the "Law of fossil succession" (see above) that was developed by the British engineer William Smith, who also produced the first geologic map in 1815. Thus it was possible to use the successions of fossils in a practical manner for comparing local succession over the world. During the rest of the 19th century, the geologic time scale developed mainly through work on the fossil successions in Europe. The boundaries between the geologic **periods** were defined on the basis of major changes in the fossil successions (extinctions and diversifications; see further below), and mostly derive their names from the geographic areas where they were first defined (e.g. Cambrian from the Latin/Celtic name for Wales, where the period was first defined). The periods in turn are grouped within the three **eras**, **Palaeozoic**, **Mesozoic**, and **Cenozoic** which were named in reference to major changes in fossil content (see further below "Changes in diversity through the Phanerozoic"). The largest divisions of geologic time are the three **eons**, **Archean** (including **Hadean**), **Proterozoic**, and **Phanerozoic**. The Archean and the Proterozoic are often grouped together within the **Precambrian**. All the units above represent so-called "geological time units", which are strictly referring to time. Frequently geologists also need to refer to the rocks as such deposited during these time units and then so-called "**chrono-stratigraphical units**" are used. For example the rocks deposited during the Ordovician Period (time) are referred to as the Ordovician **System** (chrono-stratigraphical).

Sedimentary rocks & environments

Sediment refers to any loose unconsolidated material, such as sand, clay etc. The sediment becomes a **sedimentary rock** through **lithification**. The latter process includes typically **compaction**, **cementation**, and **recrystallisation**.

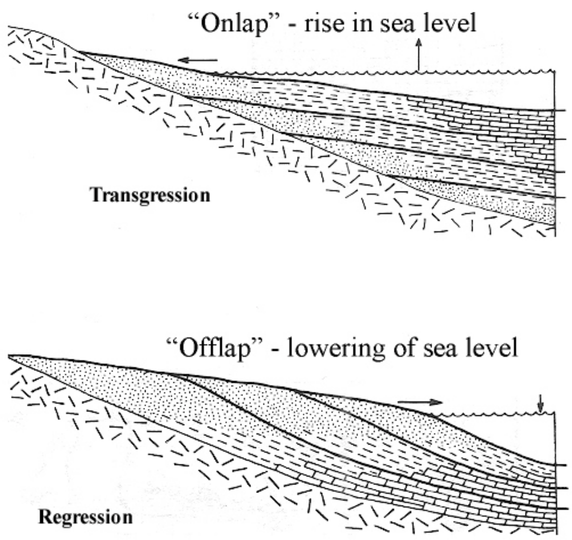
Sedimentary rocks cover approximately 75% of the Earth's surface (Sweden being an exception) and are extremely important both scientifically and economically (oil, coal, gas, building material etc.).

There is no single way of classifying sedimentary rocks, and there are many different schemes of classification. One approach is to differentiate between the place of origin of the sediment, and whether it has been transported or not. **Allochthonous sedimentary rocks** are those that have been formed from transported sediments, and include **sandstones**, **siltstones**, **shales**, and conglomerates. **Autochthonous sedimentary rocks** have been formed in place, and include most types of **limestones**, **evaporites**, and **coal**. Other classificatory schemes distinguish between terrigenous, chemical/biochemical, and organic sedimentary rocks.

Sediments can accumulate in the following types of environments (**sedimentary facies or lithofacies**):

- **Terrestrial environments.** Sediments are derived from mountainous regions and other areas of active erosion, where the weathering processes produces rock fragments that are transported and accumulated through gravity processes, or by water or wind. These fragments are deposited first in a variety of terrestrial environments, including deserts, fluvial, glacial and swamps.

- **Marine environments** are where the majority of the erosional products accumulate after transport off the continents by rivers or by the wind. Thus, marine sedimentary rocks are by far the most extensive of all types of sedimentary rocks. Both siliciclastic sediments and carbonates are common. The marine environments include continental shelves & slopes, carbonate platforms, reefs, and deep oceanic sediments. During **transgressions** (i.e. a landward migration of the shoreline due to a rise in sea level) and **regressions** (i.e. a seaward migration of the shoreline due to lowering of sea level) the marine sedimentary facies are characterised by so-called **onlap** and **offlap**.



- **Transitional environments** are influenced both by continental and marine processes. They are situated on the border zone where there is a fluctuation between these two environments. This group includes among others: deltas, tidal flats, beaches, barrier islands and lagoons.

Sedimentary rocks can also be described by their fossil biota representing a specific environmental condition, and this is termed the **biofacies** (e.g. "graptolite biofacies").

The text below gives an historical account of the history of earth and life through time, and the main types of sedimentary rocks and environments will be discussed at the particular time when they were most typically developed, particularly in Scandinavia.

What is a fossil?

The Latin word *fossilis* originally referred to anything that was dug up, but now it is used in a more restricted way. Fossils are remains or traces of any recognizable organic structure preserved from pre-historic times. Typically they may be impressions of, or preserved structures from leaves, mollusc shells, or parts of vertebrates; an imprint of a dinosaur foot is also a fossil.

The **taphonomic process** includes all events (transportation, burial etc.) that may happen to organisms after death. It usually ends with the complete destruction of the organic remains, but occasionally the process of decay is partially stopped and he organism is preserved as a fossil. It is very uncommon that any organism is preserved completely unaltered in its fossil state.

Many organisms have hard parts of various kinds that have a relatively high potential for being preserved as fossils. However, soft parts almost invariably disintegrate rapidly after death. In the animals without a backbone, the invertebrates, the hard parts are usually confined to an external skeleton, whilst the vertebrates usually have an internal skeleton of bone, in addition to teeth, and sometimes external plates.

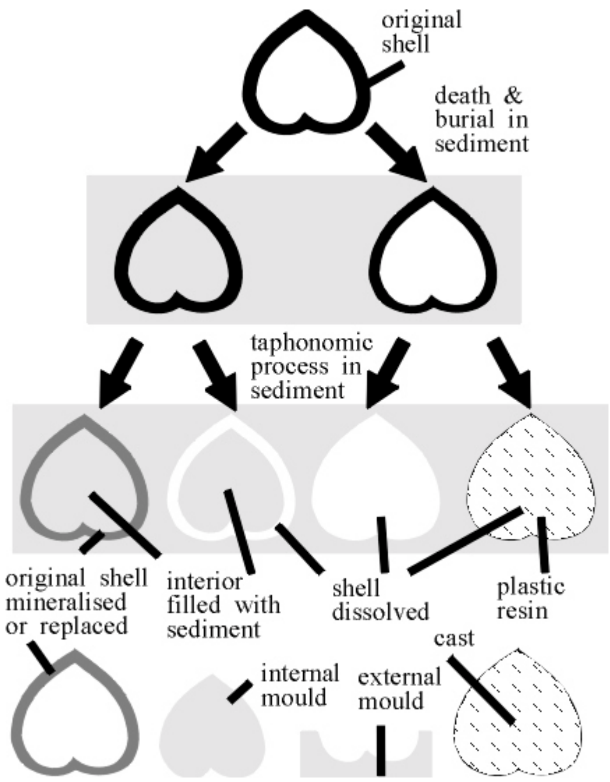
It is important to remember that in most marine environments today, many invertebrates, like most ‘worms’, jelly fish etc., lack hard parts and, thus, have a very low preservation potential, unless very special conditions apply during the fossilisation process. The extremely rare cases where soft-bodied animals have been preserved as fossils (e.g. Burgess Shale, discussed below) give unique ‘windows’ into the past.

The following different modes of fossilisation may be found:

- **Mineralization** takes place when the cavities or pores within bones and shells are filled with mineral without much change in the original structure of the hard parts. This process will eventually turn a dinosaur bone into a compact, rock-like fossil. The original skeleton may retain its structure to a varying degree, but usually it will be more or less **re-crystallised** (change in crystal structure).
- **Replacement** takes place when the original skeleton or shell is dissolved and at some stage replaced by another mineral. For example, the calcite in a mollusc shell could be replaced by silica, but many other replacement minerals are common (e.g. pyrite, phosphate).
- **Natural moulds** occur when the fossil shell has been dissolved, but not replaced by another mineral. An **external mould** represents the impression of the external (outer) surface of the shell (with a relief opposite to that of the original shell). The mould of the internal (inner) surface of the shell is called an **internal mould**. By pouring a casting material (e.g. latex rubber) into the empty space it is possible to create a positive **cast** of the mould.
- **Carbonisation** is formed by the removal of the ‘light’ constituents in an organic compound, leaving a coal-like film of carbon. This process may lead to the preservation of plant fossils as well as leave impressions of soft parts of animals (as in some of the

Jurassic ichthyosaurs from Germany exhibited in the Palaeontological Museum).

- **Trace fossils** are the remains of any activity undertaken during the life of an organism. This includes footprints of dinosaurs and any other traces of a moving organism, the circular holes left by a boring algae, traces of burrowing worms, dinosaur **gastroliths** (digestive stones) and **coprolites** (fossil excrements), entire dinosaur nests (excluding the eggs!) and many others. Unlike most other remains the trace fossils may tell us something about the way that organisms lived in the past.
- **Special preservation.** In some rare cases, organisms are preserved more or less unchanged, this includes preservation in **amber** (fossil resin containing fossils; in the Baltic mostly from an Oligocene pine tree), **deep freezing** (Siberian fauna from the tundra, including mammoths), preservation in **peat bogs** (the 2000 years old 'bog people' from Denmark), and in **tar pits** (open 'oil wells' like those at La Brea, Los Angeles). **Mummification** may occur when animals die in a very dry climate and dry out completely instead of rotting.



Composition of hard parts

The shells and skeletons of organisms are mainly built up of the following types of chemical compounds (biominerals):

(1) **Calcium carbonate** ($CaCO_3$) is the most common constituent of most invertebrate hard parts, occurring in molluscs, corals, and arthropods. Calcium carbonate occurs in two main forms - **aragonite** and **calcite**, of which the former is more easily soluble and is rarely, preserved in its original state. Aragonite is commonly replaced by calcite during diagenesis.

(2) **Calcium phosphate** ($Ca_5(PO_4)_3OH$) is mainly found in the skeleton of vertebrates. It is more rarely found within invertebrates, but builds up the shell of certain brachiopods (Lingulates). Fossil hard parts consisting of calcium phosphate can be isolated from limestones, by means of etching with weak acids (e.g. acetic).

(3) **Silica** (SiO_2) is usually found only in a restricted number of organisms, such as sponges (as spicules), radiolarians, and some algae. The organically secreted silica it is not a very stable compound and may dissolve after the death of the organism.

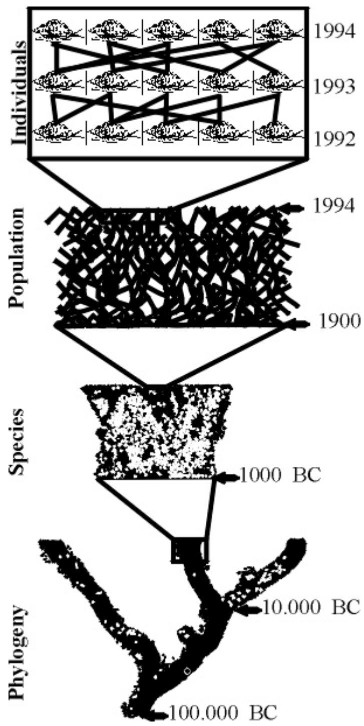
(4) **Organic compounds** of various types builds up the exo-skeleton of, e.g., insects (protein + chitin) and graptolites (protein). When preserved in the fossil state, the organic skeletons can be isolated from the rock, by means of etching with weak or strong acids (e.g. hydrofluoric - HF).

EVOLUTION & PALAEONTOLOGY

What is evolution?

Evolution is the process by which life has changed through geological time. Obviously, the immense time-scale over which most evolutionary changes take place does not permit direct observation. However, direct experimentation and observations can test the basic underlying principles. It is clear that no other scientific theory can equally well explain the immense diversity of life present today on our living planet Earth - 'GAIA'. The present scientific debate is not concerned with *if* evolution has taken place, but rather *how* and *in what way*.

In working with earth's almost 4 billion years of evolution, we are trying to interpret the results of an experiment that has already been carried out. With this view, palaeontology gives the only possible source of data from a sufficiently large time scale in order to understand and interpret the greater patterns in the evolutionary process.



Darwinism & microevolution

Our present view of evolution is still based largely on the work of **Charles Darwin** (1823-1882), and his book (1859) *'On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life'*. There had been many previous attempts at proposing evolutionary mechanisms, but his was the first that rested on a solid foundation. In summary, Darwin pointed out that living organisms produce more offspring than can survive and in the struggle to survive, those best adapted to the environment will be selected - the slogan '*survival of the fittest*' has been commonly used to describe these processes. Darwin himself called his theory '*descent with modification*'. He proposed that the variations favourable to organisms would accumulate during generation after generation until the changes are sufficient to represent a new species.

Darwin did not know how these favourable variations were inherited. Ironically the basic mechanisms of genetics were published (1865) by **Gregor Mendel** (1822-1884), but the importance of his work for understanding evolution was not realised until the modern science of genetics was developed, much later during 1920-1940s.

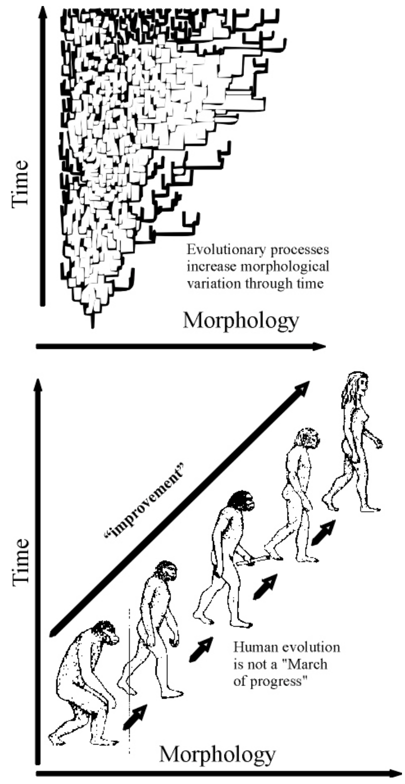
In terms of genetics, species are groups of interbreeding individuals forming populations that have become genetically isolated (e.g. through geographic barriers interrupting the gene flow) from neighbouring groups through time, representing branches of a **phylogenetic tree** (like the imaginary gastropods in the figure). The morphological variation arises from random changes (e.g. mutations) in the genetic material (genes and chromosomes) and selection favours certain variations that are accumulated and passed on within evolving lineages. This type of evolution at the specific level is usually called **microevolution**.

Darwinism & biostratigraphy

The fact that successions of fossils appear in the same vertical order across the world was first noted and discussed by William Smith in the late 1700´s, and as noted above this basic principle of relative dating is termed the “Law of fossil succession”. Darwinism now explain why this succession of fossil species can be found – it is simply the result of Darwinian evolution, which is recorded in the sedimentary record as the appearance and disappearance of species through time, that is biostratigraphy (see further above).

Evolutionary progress?

The evolutionary process is very commonly thought to cause ‘improvement’ in a linear and directional fashion, the most obvious example being our own ‘march of progress’ during the last few millions of years. However, as pointed out by palaeontologist **Stephen Jay Gould**, the evolution of life is much better regarded as ‘*a copiously branching bush, continually pruned by the grim reaper of extinction, not a ladder of predictable progress*’. Although the general level of ‘complexity’ (e.g. number of internal organs etc.) of organisms has certainly increased during life’s long history, it is wrong to think of earlier life forms as being generally ‘inferior’.



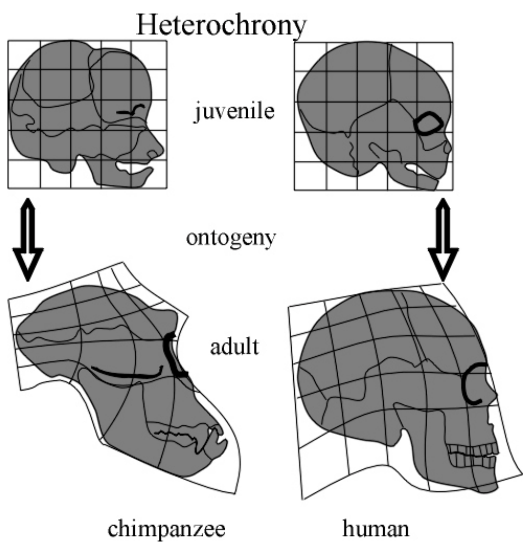
Evolutionary rates

It has been commonly assumed that virtually all evolution proceeds gradually through the accumulation of small favourable changes that spread through large populations at relatively slow rates. This type of microevolution is usually termed **phyletic gradualism**. Since the human life span is too short to directly observe such long-term processes, most research had to rely on searching for gradualistic patterns in the fossil record. However, Darwin and his contemporaries failed to find examples of gradually changing lineages. Their absence was explained by the fact that the fossil record was too incomplete (containing numerous periods of non-deposition). In order for these patterns to become apparent, it was necessary to find areas with more or less continuous deposition.

Since Darwin's time, several examples of phyletic gradualism have been described, but in many or most instances species seem to remain unchanged for long periods of time. This stable background is 'punctuated' by short intervals where new species emerge rapidly without any intermediates. The latter type of evolution has been termed **punctuated equilibrium**. It is probable that evolution proceeds with widely different rates and patterns of change in different groups and that both types of evolution exist.

Macroevolution

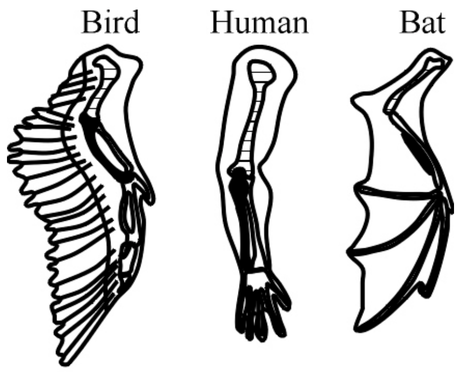
Evolutionary changes above the species level, such as the origin of new body plans and higher taxa are usually termed **macroevolution**. The origin of vertebrates from an invertebrate ancestor, as well as the transition from reptiles to mammals, are examples of macroevolution. According to many scientists, these macroevolutionary changes are simply the effect of normal Darwinian microevolutionary processes working over very long time-spans. However, some scientists claim that macroevolution is caused by special processes that are different from those causing microevolution. Some relatively rapid macroevolutionary changes may be related to changes in the ontogeny (that is, development from fertilised eggs to adults of an individual), so-called **heterochrony**. One type of heterochrony involves the retention of juvenile traits in adults. For example, the evolution of humans from an ape-like ancestor seem to include a neotenic factor in that that adult humans preserve more juvenile characters as compared with, e.g. chimps; thus, we may be regarded as juvenile apes.



Phylogeny & classification

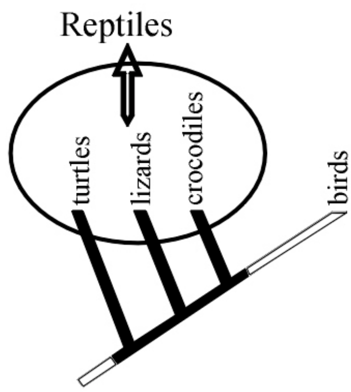
Phylogenetic reconstruction aims at establishing relationships between organisms, fossil and Recent. This work is closely related to systematic classification in which organisms are arranged in-groups in a system from which information can be easily retrieved. In the 1758 edition of *Systemae naturae*, **Carl von Linné** (1707-1778) established the binomial classificatory system (for animals!) of present usage; his system was developed without the evolutionary background, but it is still used for naming groups of animals in a phylogenetic context. Organisms are arranged in a hierarchy where the **species** forms the basic unit, always used together with the next higher unit, the genus as a binomen (*Homo sapiens*). These are grouped into the successively higher units: **families** (Hominidae), **orders** (Primates), **classes** (Mammalia), **phyla** (Chordata), and **kingdoms** (Animalia).

Most systems of classification, including the Linnean, have been based on overall similarity. With the development of evolutionary theory, the basis for the similarity between organisms could suddenly be explained. Most scientists agree that these groups within the system of classification should somehow reflect their phylogeny and genetic relationships as closely as possible, but there is no obvious single correct way to achieve this. An important methodology for phylogenetic analysis is called **cladistics**. The method involves analysing the distribution of characters among the organisms under study in order to separate **analogous** characters (due to convergent evolution) from **homologous** similarities reflecting common ancestry.



The bones in the forelimbs of birds, humans and bats are homologous. However, the wings of birds and bats are analogous and examples of convergent evolution.

Recently developed methods now also permit phylogenetic analyses to be carried out at the molecular level, both by directly determining similarities in **nucleotide bases** (A-adenosine, C-cytosine, G-guanine, and T-thymine) in **DNA** and **RNA**, as well as looking at the **gene products** (proteins etc.).



in cladistic terminology reptiles are paraphyletic because they do not include their descendants, the birds

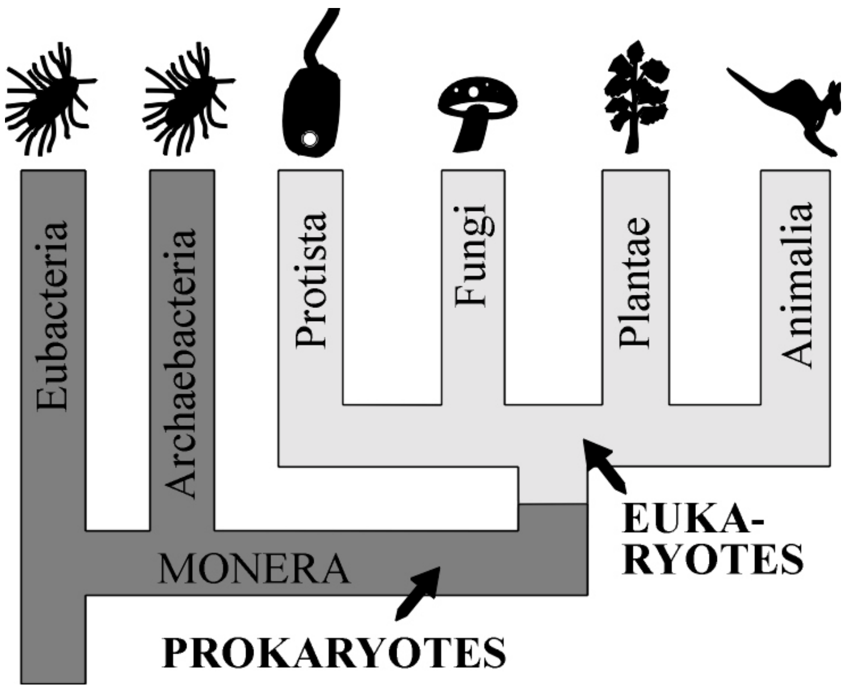
The resulting relationships between the taxa are shown in a so-called **cladogram**. In cladistic terminology, **monophyletic groups** are those that were derived from a last common ancestor including all the descendants; members of a **paraphyletic group** share a last common ancestor but some of the descendants are excluded. A **polyphyletic group** does not possess an immediate common ancestor.

Few scientists accept the use of polyphyletic groups, but many would like to retain old and well-established paraphyletic groups of organisms like reptiles, fish etc.

Life's main divisions

The kingdoms are the highest (most inclusive) division of life. Linné could divide everything between the plant and animal kingdoms, basically equivalent to the **autotroph** and **heterotroph** divisions (that are photosynthetic and non-photosynthetic). However, the plant-like fungi are not photosynthetic, whilst some animal-like single cell organisms (like *Euglena*) are. Since the 1960s most scientists recognise a system with five kingdoms. This system comprises the following kingdoms: (1) the **prokaryotic** (cell lacking a nucleus) kingdom **Monera**, containing all bacteria, and four **eukaryotic** (cell with nucleus) kingdoms of (2) **Animalia** - animals that do not produce their own food, (3) **Plantae** - autotrophic plants, including mosses, conifers, flowering plants etc., (4) **Fungi** - heterotrophic fungi, and finally (5) **Protista** - all unicellular or multicellular eukaryotes that are not animals, plants, or fungi, including algae, forams, radiolarians etc.

Recent molecular studies have further revealed that there are two main types of bacteria - the **archaebacteria** and the **eubacteria**. The former are of great importance in many extreme environments, such as in hypersaline (very salty) conditions, and in the hot waters near the deep-sea vents along the mid-Atlantic ridge, where they form the basis for the aberrant communities of molluscs, arthropods and other forms of animals. The eubacteria includes all other more common types of bacteria (like *E. coli* etc., living in our intestine). It would appear that the archaebacteria are more closely related to the eukaryotes than the eubacteria.



SYSTEMATIC SYNOPSIS OF LIVING & FOSSIL ORGANISMS

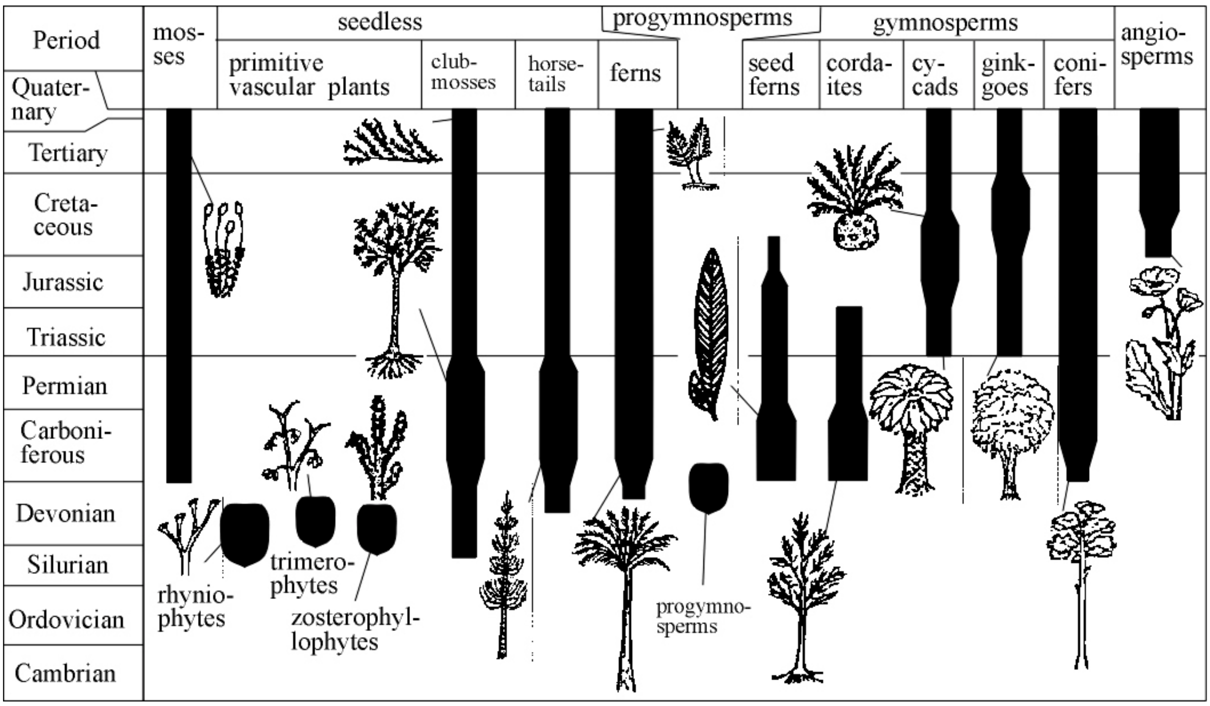
The text below gives an historical account of the history of life through time. Thus, the major groups of fossils will be discussed at the particular time when they appeared (or became dominant), rather than treated in a systematic way, group by group.

KINGDOM MONERA
- Eubacteria
- Archaebacteria
- Cyanobacteria

KINGDOM FUNGI

KINGDOM PROTISTA
- Algae
  - Coccolithophores
- Sarcodina
  - Foraminifera
- ? Acritarchs
- ? Chitinozoans

KINGDOM PLANTAE
- Mosses
- Vascular plants
  - Seedless
    - Rhyniophytes
    - Trimerophytes
    - Zosterophyllophytes
    - Club mosses
    - Horsetails
    - Ferns
- Progymnosperms
- Gymnosperms (plants with naked seeds)
- Seed ferns
  - Cordaites
    - Cycads
    - Ginkgos
    - Conifers
- Angiosperms (flowering plants)

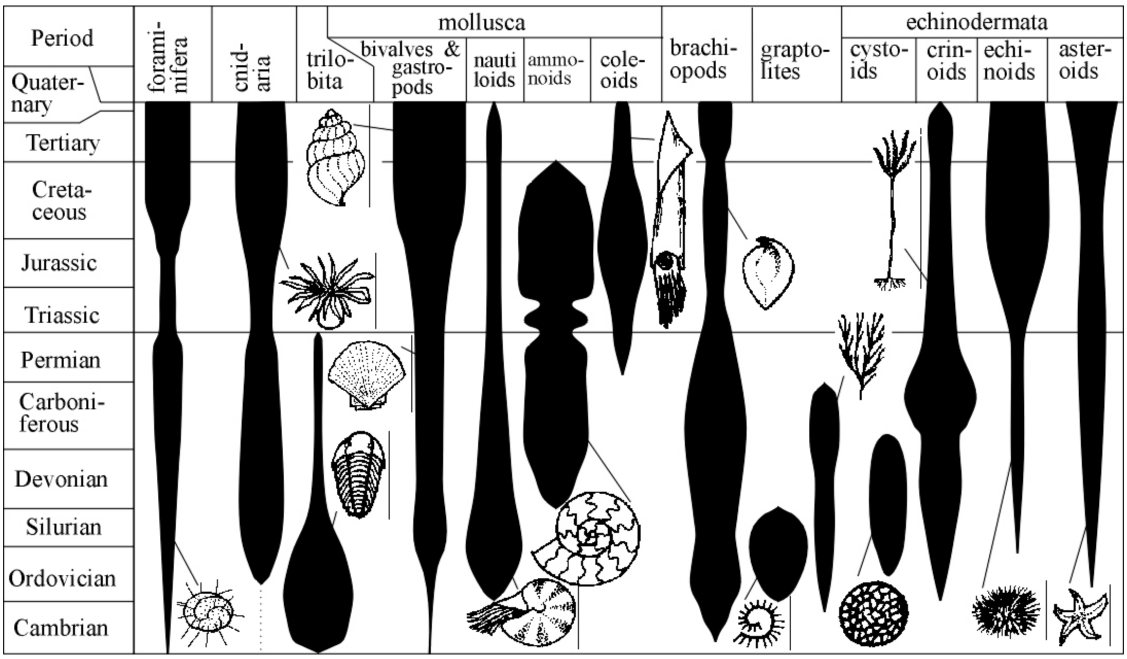


KINGDOM ANIMALIA
- Phylum Cnidaria
  - Anthozoa (corals)
    - Rugosa
    - Tabulata
    - Scleractinia
- Phylum Arthropoda
  - Trilobita
  - Crustacea (crabs etc.)
    - Ostracoda
  - Chelicerata (spiders etc.)
    - Eurypterids
  - Hexapoda (insects)
- Phylum Brachiopoda
  - Craniiformea
  - Linguliformea
  - Rhynchonelliformea
- Phylum Mollusca
  - Gastropoda (snails etc.)
  - Bivalvia (bivalves)
  - Cephalopoda (octopuses etc.)
    - Nautiloidea
    - Ammonoidea
    - Coleoidea
- Phylum Echinodermata
  - Cystoidea
  - Asteroidea (sea stars)
  - Echinoidea (sea urchins)
  - Crinoidea (sea lilies)
- Phylum Hemichordata
  - Graptolithina
    - Dendroidea
    - Graptoloidea

Phylum Chordata
- ?Conodonts
- Tunicata (sea squirts)
- Cephalochordata (lancelet)
- Vertebrata
  - Agnatha (jawless lampreys etc.)
  - Acanthodii (spiny sharks)
  - Placodermi (armoured sharks)
  - Chondrichthyes (sharks)
- Osteichthyes (bony fish)
- Actinopterygii (ray-finned)
- Sarcopterygii (lobe-finned)
  - Dipnoi (lungfish)
  - Coelacanthini
  - Rhipidistii

Amphibia (frogs etc.)
- Labyrinthodonts

Reptilia
- Anapsids (turtles etc.)
- Synapsids (mammal-like)
- Diapsids (crocodiles etc.)
- Archosaurs
- Thecodonts
- Dinosaurs
  - Saurischia
  - Ornithischia
- Pterosaurs (flying reptiles)
- “Euryapsids” (marine diapsids)
  - Ichthyosaurs
  - Pleisiosaurs
- Aves (birds)
- Mammalia
  - Monotremes
  - Marsupials
  - Placentals

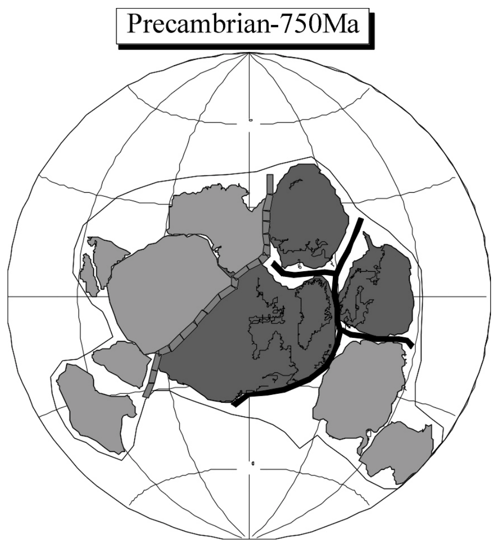


THE DAWN OF LIFE ON EARTH - PRECAMBRIAN

General

The Precambrian comprises approximately 90% of geologic time from 4.6 Ga to about 540 Ma (start of Cambrian), and is divided into the Archaean (including Hadean) and the Proterozoic. It is not well known because most of the Precambrian rocks are poorly exposed or have been eroded or metamorphosed. Most exposures are from the interior of cratons and termed **Precambrian Shields** (e.g. Canadian Shield).

The oldest rocks on Earth are from the Canadian Shield and approximately 3.9 Ga. It is likely that the earliest atmosphere lacked oxygen because many rocks that are readily oxidised today are found unoxidised in the Precambrian.



It is probable that the Earth's continents were assembled into a supercontinent (**Rodinia** or **Pangea I**) towards the end of the Precambrian (late Proterozoic, 850-650 Ma). There is also strong evidence for a very long glaciation (or several glaciations) at around the late Proterozoic (maybe the longest and biggest ever) – this glaciation event is termed the **Varanger Ice Age** (from the Varanger Peninsula in Norway). During the latest Proterozoic and early Cambrian the supercontinent started to split up.

Scandinavia

Sedimentary rocks of late Proterozoic age are found mostly in Norway, Härjedalen and in Jämtland. No fossils have been found, but sedimentary structures such as cross bedding and ripples have been found indicating shallow water environments. In south central Sweden, the late Proterozoic sequence comprises the Visingsö Formation, consisting mostly of **arkoses** and shales. The Visingsö Formation has yielded numerous **acritarchs**.

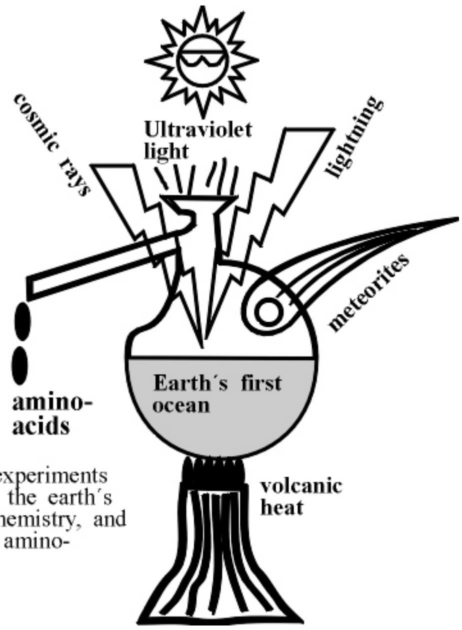
Origin of life

There are many different hypotheses concerning the origin-of-life. Creation myths aside, it was believed since ancient times that living organisms could arise suddenly and almost anywhere by so-called '**spontaneous generation**' from dead matter. Around the 1860s, **Louis Pasteur** experimentally demonstrated that spontaneous generation did not occur. Most scientists today agree that life probably originated on earth only once and that non-living matter became organised gradually into more complex compounds, until finally it had the ability of **self-replication** and **metabolism**. However, there are many conflicting models as to how this might have occurred.

During the 1920s, the so-called **Oparin-Haldane hypothesis** (formulated by the Soviet scientist A. I. Oparin and the British J. B. S. Haldane) was developed. In short, they proposed the following: (1) the earliest earth had a reducing atmosphere, free of oxygen, but dominated by methane (CH_4), ammonia (NH_3), hydrogen (H_2), and water. (2) The first organic compounds were formed by chemical reactions fuelled by volcanic heat and lightning, as well as solar radiation, or partly brought in from meteoric showers. (3) The organic compounds accumulated until '*the primitive oceans reached the consistency of hot dilute soup*' - sometimes referred to as the **primordial soup** or **prebiotic broth**. (4) In the final stage, the organic compounds became more and more complicated and finally life originated by some unknown process.

The Oparin-Haldane hypothesis was 'tested' experimentally by **Stanley Miller** in the 1950s; he simulated the proposed chemical composition of the early atmosphere in a flask and passed electric sparks through the mixture. The reaction produced amino acids - the building blocks of proteins and all living organisms - but we still cannot explain the chemical evolution from non-living compounds to living organisms. In particular, the origin of the genetic information and the heriditary system is a major problem.

Some scientists have tried to avoid the problem by placing the actual origin of life (or the necessary very complex non-living compounds) on a different planet somewhere in the Universe - this hypothesis is called **panspermia**.

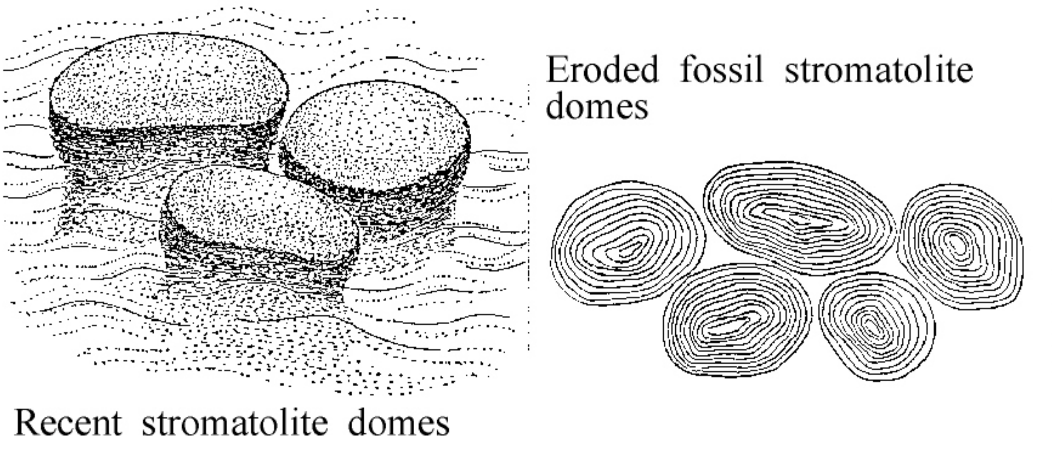


Miller´s experiments simulated the earth´s earliest chemistry, and produced amino-acids

Early life

During the time of Darwin it was believed that there were no fossils older than the Cambrian, and only since the mid 1950s (and the development of high-resolution microscopes) has the fossil record been extended well into the Precambrian. Some of the oldest rocks, around 3.8 billion years old, have been found on Greenland and elsewhere. Although they lack true fossils, their carbon chemistry appears to indicate that photosynthetic organisms had originated.

The oldest undoubted traces of living organisms are found from rocks, about 3.5 billion years old, from **Warrawoona, Australia**. These sediments contain well-preserved **stromatolites**, which are fossilised mats formed by the activity of **cyanobacteria** (‘blue-green algae’). Apart from the dome-shaped, decimetre high, laminated macroscopic structures, the rocks at Warrawoona contain preserved traces of the prokaryotic cells that can be observed in thin sections. Today, stromatolites are formed by photosynthetic cyanobacteria, only in extreme environments (e.g. at Shark Bay, Australia).



The **Gunflint Chert** (2 billion years old) in Minnesota is another famous locality with stromatolites and preserved bacterial filaments. In Sweden, Precambrian stromatolites are known, e.g., from Sala and from around Omberg.

Stromatolites became very abundant at around the end of the **Archaean**, about 2.5 billion years ago, greatly increasing the production of oxygen. The increased levels of oxygen may have lead indirectly to the formation of the so-called **banded iron formation** (approximately 2 billion years) old that form the main source of iron ore (mainly haematite) today. The release of oxygen oxidised the inorganic and organic compounds in the sea and caused precipitation of iron. Fluctuations in the oxygen production may have lead to the regular alternation of iron and chert in the banded iron formation.

The amount of free oxygen in the atmosphere could only have increased when all the iron and other compounds had been oxidised, and this seems to have taken place at around 1.8 billion years ago. Solar radiation (UV) will act on oxygen in the atmosphere to form **ozone**, protecting the earth from these harmful rays - the formation of the ozone layer was necessary before more complex organisms could evolve.

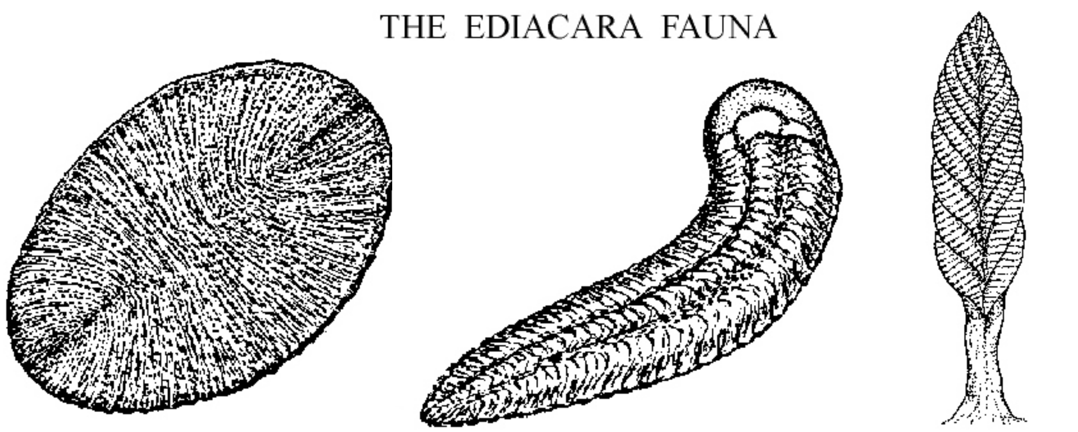
The eukaryotes must have originated from a prokaryote ancestor. According to American biologist **Lynn Margulis** it is likely that the first eukaryotes evolved by so-called **endosymbiosis** - the process by which two different organisms become so mutually dependent on each other that one of them lives inside the other. Thus it is possible that the **mitochondria** and other parts of the eukaryotic cell may once have been independent organisms. The first more or less undoubted traces of eukaryotic organisms are **acritarchs** - spherical protistan microfossils that may represent cyst envelopes of some kind of phytoplankton. Acritarchs are first found in rocks around 1.6 billion years old; however, there are other, more problematic spherical eukaryote-like fossils from around 2 billion years ago. The level of free oxygen probably must have reached a level of around 1-% of the present value in order to support the first eukaryotes. Practical distinction between fossil eukaryotes and prokaryotes is based mainly on their cell size, around 40-60 μm in eukaryotes, whereas most prokaryotes range between 1-30 μm.

The Ediacara fauna & the origin of multicellular animals

The first traces of true multicellular animals (**metazoans**) come from the so-called **Ediacara fauna**, in rocks deposited during the youngest part of the Precambrian - the **Vendian** (about 650 - 540 million years ago). The fauna consists entirely of soft-bodied animals completely lacking hard parts; it was discovered first in sandstones from the Ediacara Hills, South Australia, but it has now been found to have a worldwide distribution in rocks of this age.

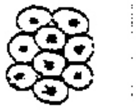
For a long time all the fossils were interpreted as representatives of living phyla, mostly belonging to jellyfishes and sea-pens (Phylum Cnidaria), but including possible arthropod-like (Phylum Arthropoda) and echinoderm-like (Phylum Echinodermata) forms, as well as several worm-like phyla. In a provocative alternative interpretation, the German palaeontologist **Adolf Seilacher** has argued that most if not all of these fossils may represent an entirely extinct group of essentially two-dimensional, gas-filled 'animals', lacking internal organs, and living by the uptake of nutrition directly through the body wall.

Regardless of how we interpret the Ediacaran fossils, true animals must have originated during the late Precambrian where there is a sudden increase in the number of trace fossils found, showing that 'normal animals' existed. We do not know how the first multicellular animals arose, but a popular theory involves the colonies of single-celled eukaryotes gradually becoming more and more symbiotic and thus turning into true metazoans.



Dickinsonia ("worm-like") *Spriggina* ("arthropod--like") *Rangea* ("sea-pen-like")

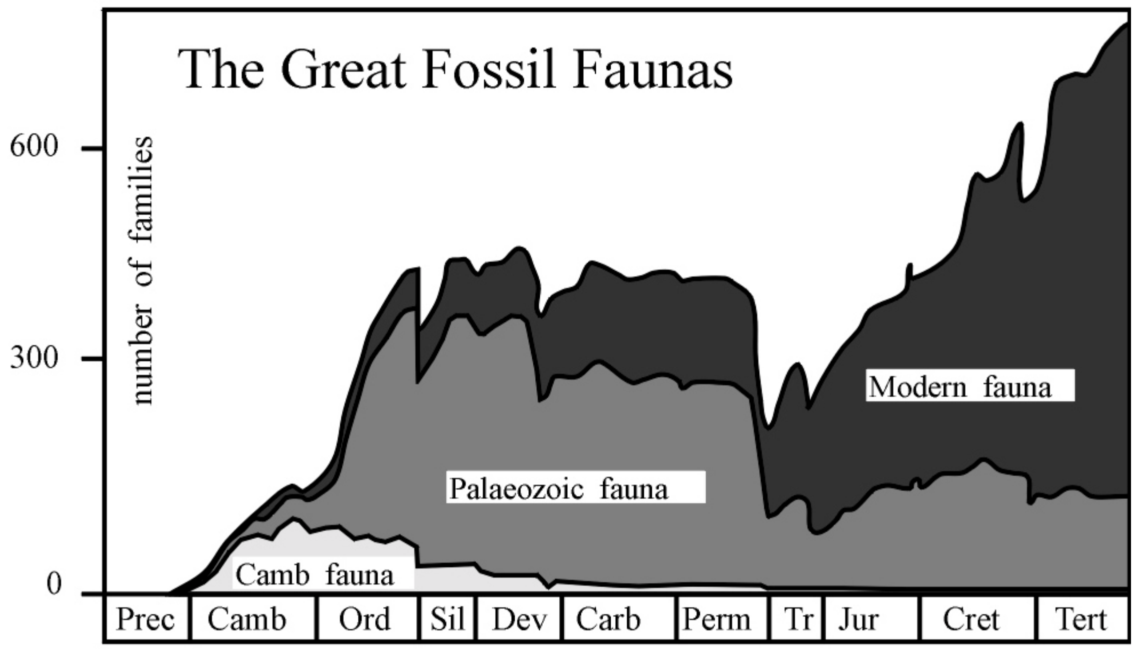
THE EARLIEST EVOLUTION OF LIFE

important events	Myr	relative	%oxygen
Normal levels of oxygen	400	 fish, first land plants	100
Metazoans with hard parts - "Cambrian Explosion"	540	 Cambrian fauna	10
First metazoans	650	 Ediacara fauna	7
First eukaryote	1400	 larger cells	>1
Oxygen resistant cyanobacteria	2000	 cyanobacterial filaments	1
Fotoautotrophic cyano-bacteria starts to produce oxygen	2800		<1
Chemo-autotrophic bacteria?	3500	 stromatolites	0
ORIGIN OF LIFE ON EARTH!!	3800 ?		

THE TIME OF INVERTEBRATES - PALAEOZOIC

Changes in Diversity through the Phanerozoic

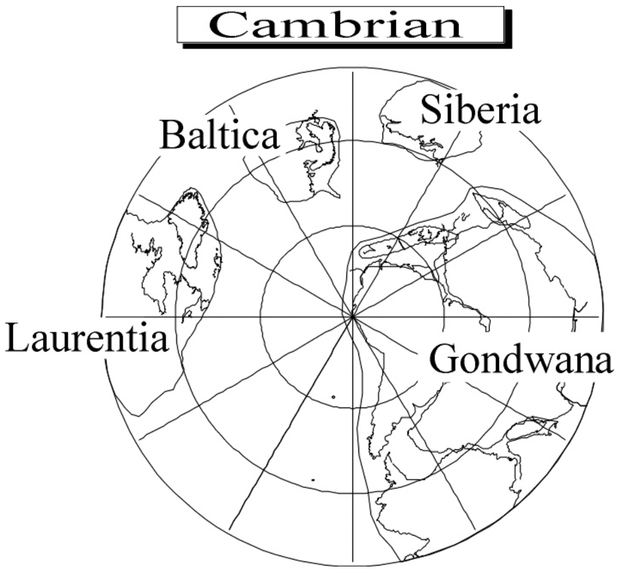
The **Palaeozoic Era** **(540-245 million years ago)** marks the beginning of the **Phanerozoic Eon** (with 'visible life'). Estimation of the global diversity of families of marine animals from the beginning of the Cambrian to the present made by American geologist **J.J. Sepkoski** indicates that there are mainly three great fossil faunas (or evolutionary faunas): (1) the Cambrian, (2) the Palaeozoic, and (3) the Modern fauna, each dominated by a distinctive set of organisms. The work by Sepkoski also shows that although there is a general increase in the diversity of the faunas through time, it is not uniform, but punctuated by several periods of rapid reduction representing extinctions. The two most important ones are at: (1) the end of the Permian, and (2) the end of the Cretaceous ('K-T extinction'). These coincide with the boundaries between the three Phanerozoic eras.



Cambrian fauna	Palaeozoic fauna	Modern fauna
Trilobites	Rhynchonelliformean brachiopods	Gastropods
Worms	Crinoids	Bivalves
Linguliformean brachiopods	Ostracods	Bony fishes
	Cephalopods	Crabs & Lobsters
	Corals	Echinoids

CAMBRIAN

General



The **Cambrian Period** **(540-505 million years ago)** was first defined based on sequences in Wales. During this period, the first supercontinent Pangea I started to break up, **Laurentia** (North America) and **Baltica** (Northern Europe) drifted towards north, separated by the **Iapetus Sea**. This ocean widened during the rest of the period, due to rifting and ocean floor spreading. Most continents were situated on the southern hemisphere (but not at the south pole). The great landmass **Gondwanaland** (Gondwana) comprised most of Africa, South America, Antarctica and India. Siberia and Laurentia straddled close to the equator during most of the period, whereas Baltica was approximately situated at the latitude between 50 - 60° S.

The Cambrian was a period of great transgressions and growing **epicontinental seas**. This is well seen in Cambrian sequences in North America were the warm equatorial water conditions resulted in extensive carbonates.

No higher life forms existed on land during the Cambrian (see further below). Most modern phyla were however present in the seas. The fact that no vegetation was present on land obviously greatly influenced the rates of erosion and the transport of sediments.

Scandinavia

In Baltica, the Cambrian transgression began in the south were sandstones overlying thin conglomerates are found on Bornholm and in Scania. Early Cambrian sandstones are also found in Västergötland and Östergötland, Öland and Närke. The sandstones are usually not very rich in body fossils (some brachiopods and trilobites), but trace fossils are common.

The boundary between Early and Middle Cambrian coincided with a short regression, and in the following Middle Cambrian transgression, a new kind of sediment - the **alum shale** – started to form over large areas of Baltica. The Alum Shale Formation formed through deposition of clays with a high organic content (it is the most important source of oil in Sweden). The bottom conditions were starved with oxygen (=**dysaerobic**) or completely free of oxygen (=**anaerobe**). Within the alum shales, carbonates generally occur as lens-shaped concretions called **orsten** (=**stink stones**). These are highly enriched in trilobites (mostly the genera *Agnostus* and *Peltura*). The deposition of alum shales continued through the Late Cambrian ending with a worldwide regression.

Cambrian sedimentary rocks & environments

In many areas, such as the Baltic Plate, the Cambrian sequences are dominated by allochthonous sediments (=terrigenous or clastic). Such types of sediments originate from weathering (mechanical, chemical, and biological) and are transported and deposited as e.g. fluvial sands, beach sands & gravels, and marine clays & silts. For example, the weathering of a granite or a gneissic rock produces clay (which become claystones and shales), dissolved material (e.g. salt), and resistant quartz grains (which become sandstones). The resulting allochthonous sedimentary rocks have a clastic (fragmented) texture, and consist of: clasts (e.g. gravel), matrix (mud between the clasts), and cement (e.g. silica or calcite). They can be classified according to their grain size, grain shape & composition, most importantly the following:

- **Conglomerates** are very coarse-grained sediments, with clasts more than 2 mm in diameter. The clasts are rounded and worn by water action. The matrix between the clasts may consist of sand and silt, cemented by calcite or silica. A conglomerate with a great number of different types of clasts is termed **polymict**, whereas a **monomict** conglomerate consists of only one type. The depositional environments for conglomerates are normally fluvial and littoral environments. In a sedimentary transgressive succession, a conglomerate is often the first sedimentary rock to be deposited.
- **Breccias** are essentially like conglomerates in texture, but the clasts are sharply angular reflecting the "catastrophic" events that created the rock. Two common types of breccias are slump breccias derived from slumping of rock material and collapse breccias, which were formed by a sudden break in a lithified layer.
- **Tillites** are a grey to dark brown coarse sediments with a great variation in grain size, and without internal stratification. The clasts are highly angular, but lack sharp corners (as in breccias). Tillites are glacial sediments and consequently good indicators of palaeoclimate.

Sandstones can be divided into: **immature sandstones**, which are poorly sorted with angular grains, generally indicating short transport in a dry climate (e.g. **graywacke** & **arkose**), and **mature sandstones**, which are well sorted with rounded grains, generally indicating long transport in a humid climate.

Important types of sandstones are the following:

- **Quartz arenite -** mature sandstone completely dominated by quartz (95% of the mineral content), with small amounts of other minerals, including potassium feldspar and iron oxides. The grains are usually well sorted and well rounded. The cement is usually secondary in origin (silica or calcite). Quartz arenite usually occur as well sorted lenses of marine sands from the beach down to the deeper part of the shelf. They commonly grade into silt/shale at about the middle part of the shelf. The Early Cambrian sandstones in Sweden are of this general type. Quartz arenites may also occur in deserts, with grains often stained by red hematite.

- **Arkose -** sandstone with a content of more than 25% of feldspar. The other main component is quartz (50% or more). The grains are angular and cemented by calcite or clay minerals, or to minor extent by secondary quartz. The presence of feldspar and some iron oxides give the arkose a typical light red coloration. Arkoses are mostly deposited in fluvial and lacustrine environments and show ripple marks and cross bedding. The source area is generally a highland of granitic origin where extensive weathering is taking place. In the Caledonides of Scandinavia, arkoses are found in the Early Cambrian and Late Proterozoic beds. They are commonly also termed **sparagmites**.
- **Wackes –** these are immature sandstones consisting of significant quantities of dark, very fine-grained material. This dark matrix generally consists of clay, chlorite, mica and silt. The matrix constitutes about 1/3 of the rock content; the remaining coarser grains are quartz, feldspar and rock fragments. The wackes are dark brown to black in coloration; they have a "dirty" appearance. The poor sorting, the high angularity of grains and the mixed composition indicate an unstable source area and rapid deposition. A common feature of wackes is the **graded bedding** (=sets of repeated beds, which have the coarsest grains at the base and successively finer grains towards the top of the sediment particles), resulting from the deposition in mass movements, usually in the form of underwater suspension streams called turbidities. Wackes and associated rocks may contain fossils or debris of deep-water origin. In the geological record, wackes indicate unstable conditions in a subsiding basin.

Mudstones & "shales" are fine-grained siliciclastic sediments with a grain size less than 0.062 mm. Depending on the average grain size, the rocks in this category is either termed siltstones or claystones. Mudstones may have a dark appearance, where the colour depends on the amount of organic material. Some mudstones may have a substantial amount of iron compounds giving the rock a brown to red colour.

"Shales" are composed of sediment particles finer than 0,004 mm, and contain mainly flaky clay minerals which means that they are easily compacted as the grains are aligned parallel to the bedding plains. Usually this type of fine sediment is deposited in environments characterized by low water energy (usually deep). Shales (like the Scandinavian Alum Shale) can have high contents of organic material, and are thus frequently a good source rock for oil.

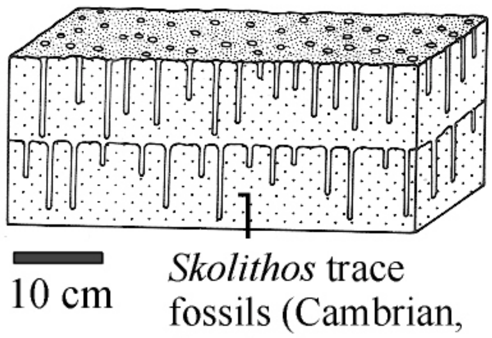
Clastic sedimentary rocks commonly contain many examples of **primary sedimentary structures** resulting from processes such as waves, currents etc. These processes result in:

- **Cross-bedding**, which is an arrangement of beds or sets of lamina, in which one set is inclined relative to others. This is common in desert sand dunes and in deltaic sediments. The direction of the inclination of the sloping beds give a direct indication of the direction of the current
- **Asymmetrical ripple marks** are formed by air or water currents with a marked asymmetry of the crests (in the direction of the current). Ripple marks form at right angles to the current direction. In the aquatic environment ripples are mostly of shallow water origin, although they can be found at greater depths on the shelves, where currents are prevailing.

- **Symmetrical ripple marks** are formed by the oscillatory motion of a wave, and indicate shallow water, within wave base.
- **Mud cracks** indicate subaerial exposure and drying. These conditions are commonly found in dried ponds or on tidal flats. Mud cracks are a result of the shrinkage of mud as water evaporates.

Secondary sedimentary structures are those that develop in the sediments after deposition. These involve such things as compaction structures and structures due to mineralogical changes and the activity of organisms:

- **Load casts**, which are common sole structures occurring in sediments where a layer of higher density has been deposited on top of a layer with lower density. For example, sand over uncompacted clay can cause instability at the boundary as water escapes from the clay resulting in sand flowing down in small pockets in the clay.
- **Stylolites**, which result from pressure dissolution due to compaction. This structure is generally seen in lithified sandstones or limestones as a zigzag pattern.
- **Biogenic structures**, which are formed by organisms and range from chaotic bioturbation to distinctive trace fossils (see also above) that can be connected to a particular animal. With many trace fossils, it is not clear what sort of organism was responsible for a certain trace. The Early Cambrian sandstones of Sweden locally abound in trace fossils. The most common are *Skolithos* and *Diplocraterion*, which both are dwelling structures from endobentic organisms.



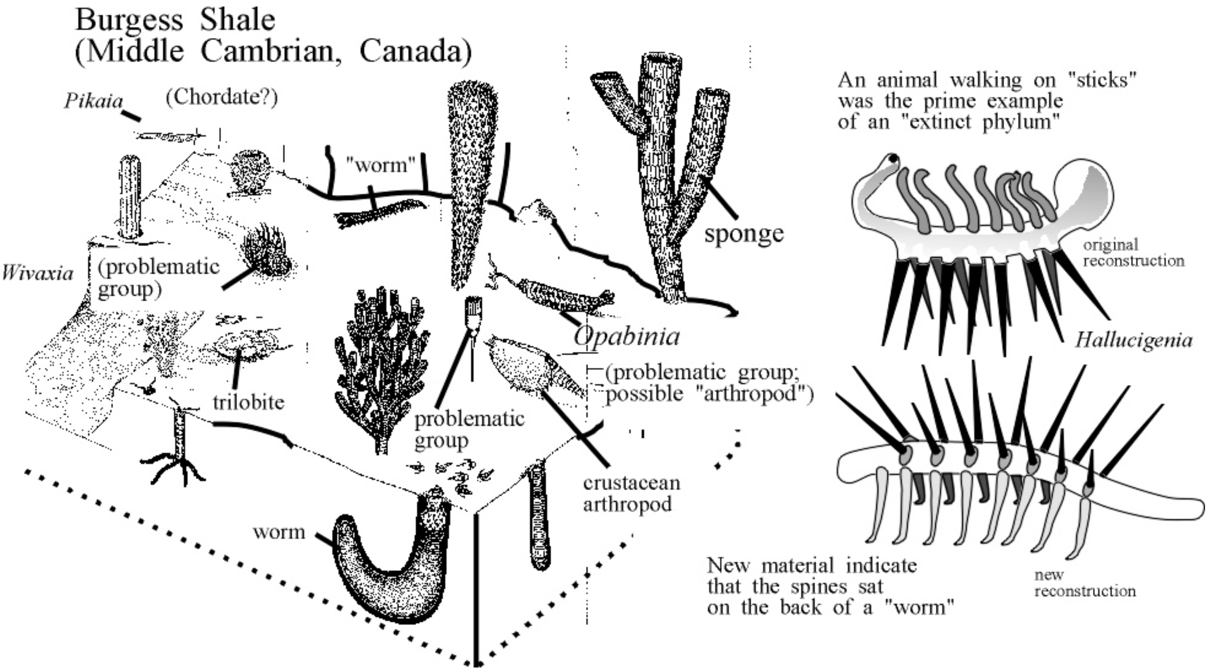
Skolithos trace fossils (Cambrian, Sweden)

The Cambrian explosion

The beginning of the Cambrian Period is marked by a sudden and enormous rise in diversity of both body-fossils and trace fossils: the so-called '**Cambrian Explosion'**. Almost all of the animal groups alive today appear in the fossil record at this time, with little evidence of their origins. It is likely therefore that the representatives of the groups arose either in the latest Precambrian, or very quickly indeed at the base of the Cambrian: in either case we know little of this period of evolution. Part of this 'explosion' came about because of the evolution of hard parts in many different groups (shells, spicules, tubes etc.) that are easily fossilised.

We know a great deal about life in the Cambrian because of the discovery of several exceptionally preserved faunas around the world, including the famous middle Cambrian **Burgess Shale** fauna from British Columbia, the **Chengjiang** fauna from China and the **Sirius Passet** fauna from North Greenland (both early Cambrian). These have revealed a wide diversity of soft-bodied animals that would not normally have left a fossil record, and have allowed the reconstruction of some aspects of Cambrian ecology.

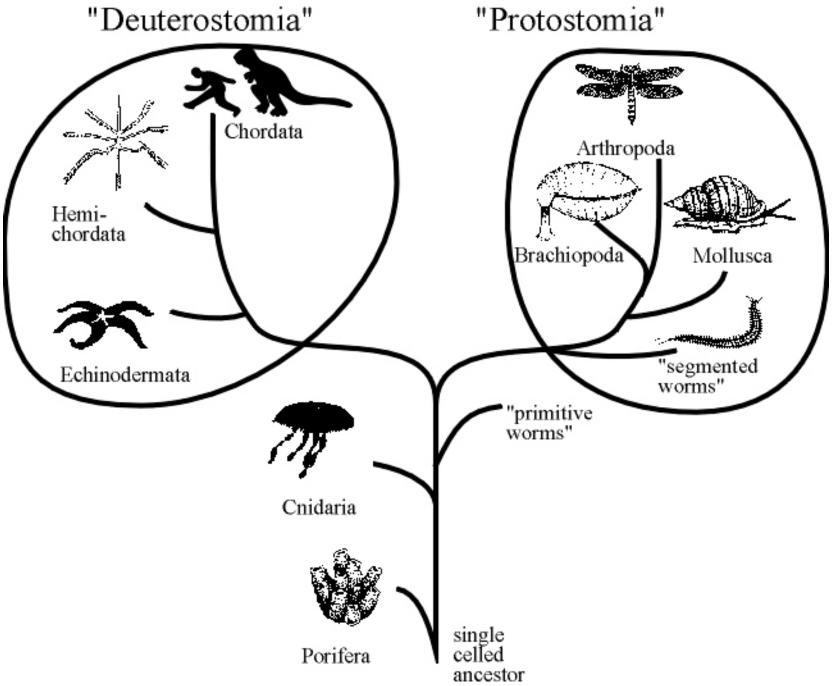
A number of the fossils, in particular from the Burgess Shale, are so different from animals living today that they cannot obviously be placed within an existing phylum; thus, it has been proposed that they may represent extinct phyla - a point most recently argued by Stephen Jay Gould. Examples would include the spiny *Wiwaxia* and the two predators *Anomalocaris* and *Opabinia*. However, the best example of '**an extinct phylum**', the odd-ball ***Hallucigenia*** has now turned out to be a possible close relative of a Recent group of animals called the velvet worms, and most other examples of 'extinct phyla' have alternate interpretations as members of living phyla.



The exceptionally preserved Cambrian faunas have allowed an almost unsurpassed picture of Cambrian life to be reconstructed. It is clear that even at this early stage of metazoan evolution, many important ecological strategies were being employed, including filter feeding, scavenging, predation and parasitism. Some types of calcifying algae and an extinct group of sponge-like organisms, the **Archaeocyatha**, formed large mounds rather like reefs. Nevertheless, the overall ecological structure of Cambrian communities was probably simpler than it is today.

Protostomia - Deuterostomia

The detailed relationship between the animal phyla is open to many disputes among scientists, and although new molecular data have been very useful, we are still quite far from understanding the way that most of the 15-30 phyla of animals living today have originated. A major problem is also that they all seem to appear at about the same time in the Cambrian explosion. It is clear that the filter feeding, sponges (**Phylum Porifera**) and the Cnidarians are more 'primitive' as compared with all other animals; they are also less complicated in that they have fewer internal organs etc. when compared with other animals. The more complicated phyla (Arthropoda, Echinodermata, Chordata, Mollusca etc.) seem to have mainly two types of ontogenies. For example, the cleavage of the fertilised egg is radial in all chordates and echinoderms, whilst in molluscs and arthropods it is spiral. Thus, it has been proposed to divide the 'higher' animal into two major groups ('superphyla'), the **Deuterostomia** (radial cleavage) and **Protostomia** (spiral cleavage) based on these differences. This major division also has some support from new molecular data.



Typical Cambrian organisms

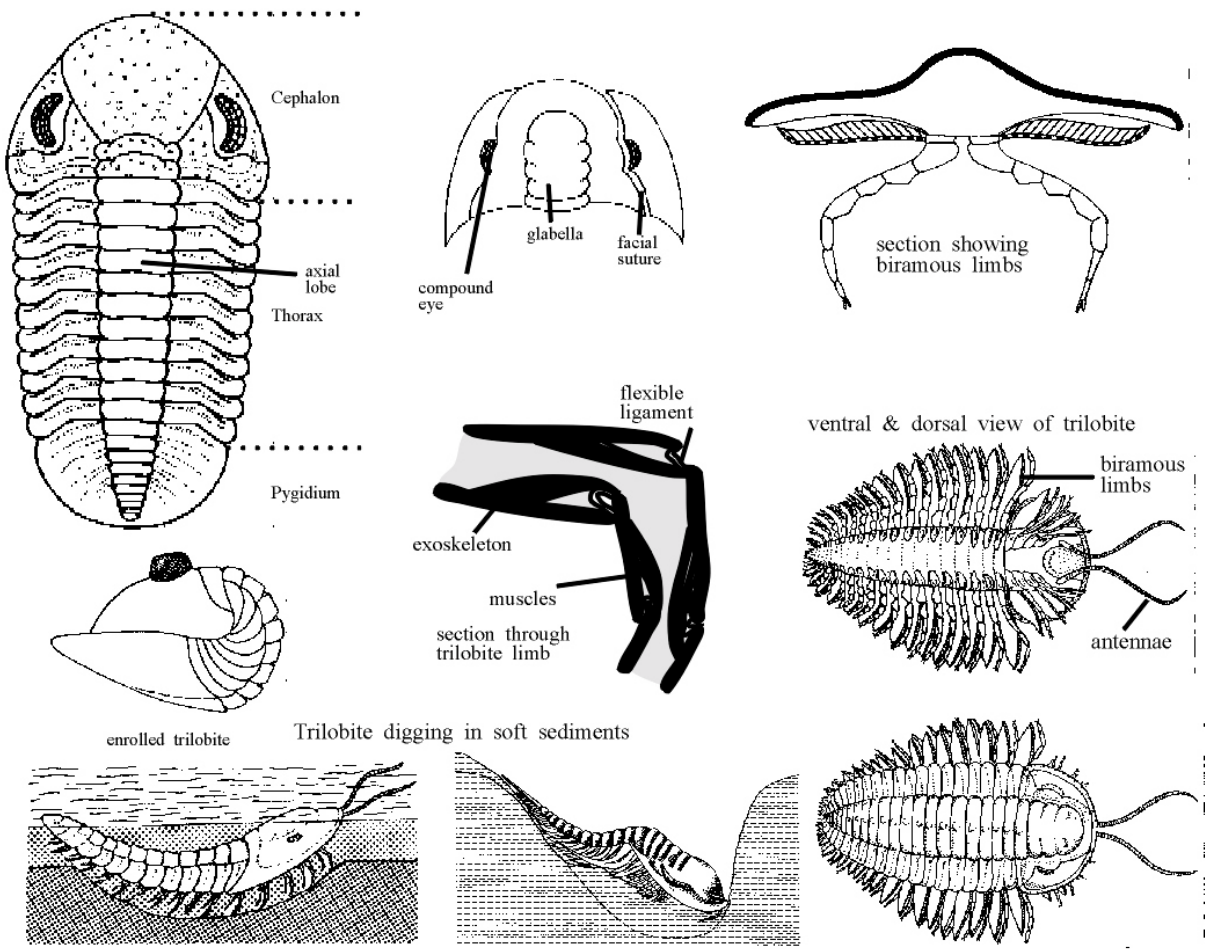
The normal Cambrian rocks are usually dominated by two major groups, the trilobites (arthropods) and the brachiopods. However, other groups represented include the echinoderms and the molluscs (bivalves, gastropods, and by the end of the Cambrian, the cephalopods). Although, ***Pikaia*** from the Burgess Shale might be a chordate, there are virtually no vertebrates known, nor is there any evidence for land plants (or land animals!). However, a wide variety of marine algae are known, including some, which could calcify.

Arthropods

The Phylum **Arthropoda** (Cambrian-Recent), including among others the crustaceans (Class Crustacea, crabs etc.), chelicerates (Class Chelicerata, spiders etc.), and insects (Class Hexapoda), makes up about 80% of all animals living today, and it is clear that they were also dominant in the Cambrian. Arthropods are characterised by a hard exoskeleton and jointed limbs, and are segmented. Although the Burgess Shale-type faunas have revealed a wide range of Cambrian arthropods and their close relatives, the most important examples normally preserved are the trilobites.

The **trilobites (Class Trilobita; Cambrian-Permian)** are the most familiar arthropod fossils. They appear in the fossil record just after the beginning of the Cambrian and rapidly diversify, although they suffered a severe extinction at the end of the period. They recovered during the following period, the Ordovician, but decline in importance after this, and finally become extinct at the end of the Permian. They are characterised by an exoskeleton divided into three regions: a head-shield, **cephalon**, typically including a pair of **compound eyes**; a trunk region, **thorax**, consisting of a number (2-40) of articulating segments and a fused tail-plate, **pygidium**. The often-complicated articulations between the various parts of the exoskeleton allowed many trilobites to enrol, presumably as a defence mechanism. This exoskeleton, as with all arthropods, was periodically **moulted** to allow the animal to grow. The largest trilobites were Cambrian and grew up to 70 cm long, although most trilobites were much smaller than this. Once moulted, water currents easily broke up the old exoskeleton. About 90% of trilobite fossils are found in this disarticulated state. The soft-parts of a few species of trilobite are known: they consist of a pair of antennae, and behind these, a series of **biramous limbs** (including three associated with the cephalon), which were probably used for walking, digging and breathing. Trilobites produced some distinctive trace fossils, although the exact behaviour, which produced them, is controversial. It is clear that trilobites exhibited a wide range of behavioural patterns, including burrowing, swimming, floating and predation.

ARTHROPODA: Trilobita



Brachiopods

The **Phylum Brachiopoda (Cambrian-Recent)** is a group of shelled organisms. Apart from their free-living larval stages, they almost all live attached to the sea bottom. They were very important in the Palaeozoic, but declined afterwards. Although about 30 000 fossil species are known, there are only about 260 species alive today.

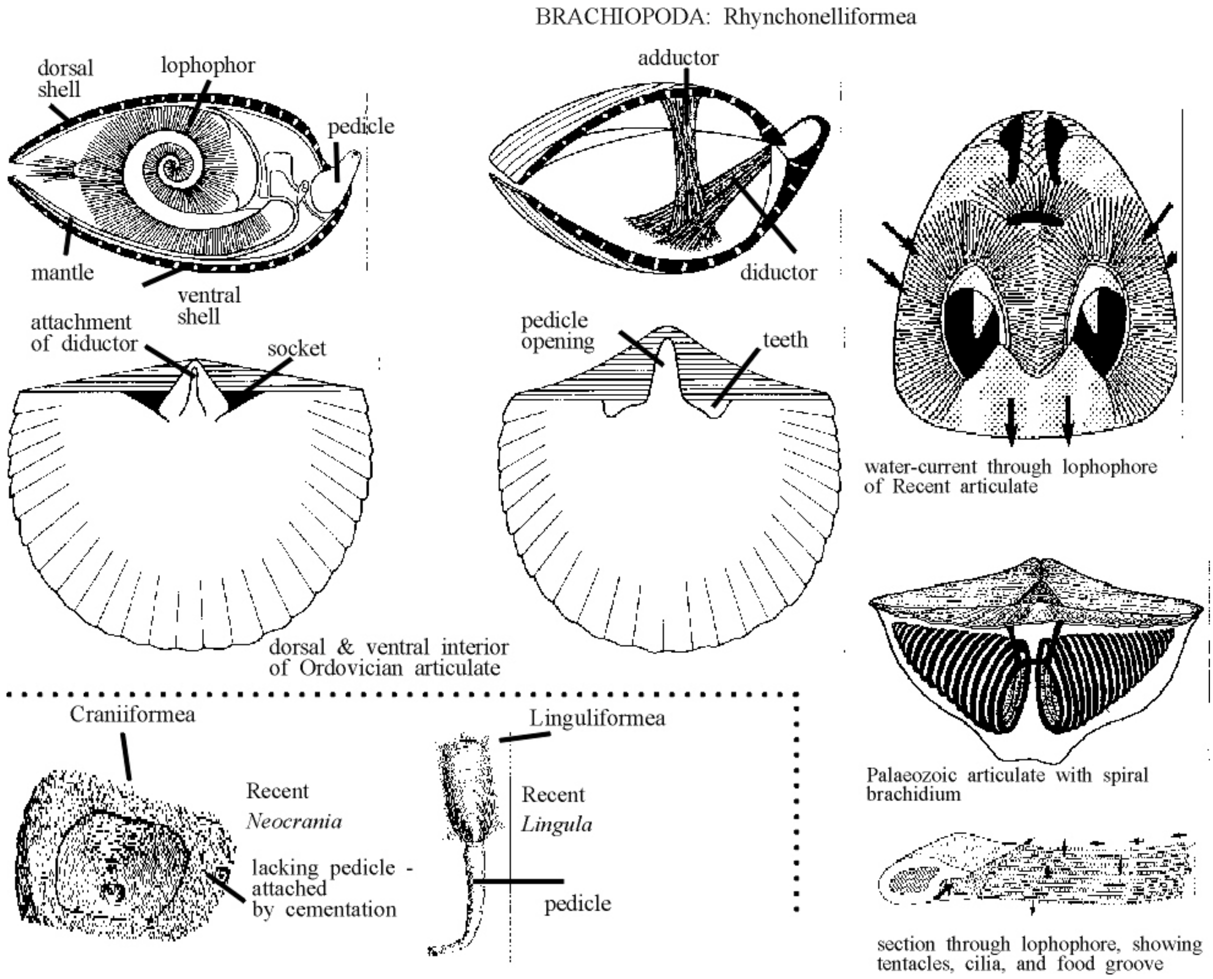
The soft-parts are enclosed in two unequal shells, a **brachial** or **dorsal** shell, and a **pedicle** or **ventral** shell (in life position, however, the ventral shell is usually uppermost!). The shells are secreted by two thin folds of the body called **mantle folds**. Each shell is bilaterally symmetrical, and is made of either calcium carbonate or calcium phosphate. The shells are opened and closed with the help of **adductor** and **diductor** muscles respectively. A soft stalk called the **pedicle** sticks through a hole at the rear of the ventral shell, which attaches the brachiopod to the sea floor with the help of a glue-like secretion. Therefore brachiopods cannot change their position once the larva has settled and become attached. A muscle in the pedicle allows only slight rotation of the body. Other forms, like the craniiformean *Neocrania*, actually cement the ventral valve to the substrate.

Brachiopods live off fragments of organisms and microscopic organisms, which they filter out of the seawater. The filtering device is called the **lophophore**, which is situated in the dorsal valve. This usually consists of a pair of spiral projections, which grow out from the body, and is often supported by a calcitic structure called the **brachidium**. The lophophore is equipped with rows of numerous small tentacles which are movable and which project toward the shell margin. The tentacles are covered with **cilia**, the movement of which creates a water-current through the lophophore. The water is sucked through the network of tentacles where food particles are filtered out, and transported by the cilia to a food-groove, which runs along the lophophore. Food particles are transported along the food-groove to the mouth, which is situated at the base of the lophophore. The lophophore also serves as a respiratory organ.

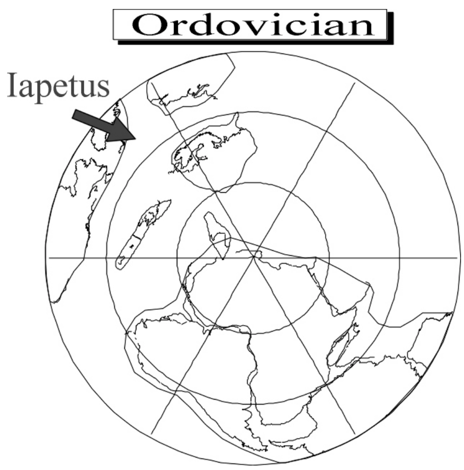
The brachiopods have traditionally been divided into two classes, the **Inarticulata** and the **Articulata**. This division has recently been replaced with three subphyla. In the **Linguliformea (Cambrian-Recent)** the shell consists of calcium phosphate. The best-known and most common Recent linguliformean is ***Lingula***, representing one of the oldest and most morphologically conservative groups of brachiopods - a classic example of a ‘living fossil’. *Lingula* has an elongate shell with a long pedicle, and lives infaunally in shallow waters. The **Craniiformea (Cambrian-Recent)**, like the Recent *Neocrania*, has a shell of calcite and form a monophyletic group of their own. The shells of both groups lack a hinge with teeth and sockets, and instead are held together by a complicated system of muscles.

The linguliformeans were the dominant brachiopods during the Cambrian. However, the diversification of rhynchonelliformean brachiopods and, later, the bivalve molluscs were contributory factors in forcing the linguliformeans into relatively unfavourable environments such as very shallow and very deep water. Today they are numerically insignificant.

The **Rhynchonelliformea (Cambrian-Recent)** always possess calcium carbonate shells, chiefly calcitic. The shells articulate along a hinge, with **teeth** and **sockets** along the ventral and dorsal shells, respectively. In many forms the lophophore is supported by the internal **brachidium**, which can be either spiralled or looped. No anus is present. Most Cambrian rhynchonelliformean brachiopods were relatively small, and only locally abundantly represented.



ORDOVICIAN



General

Like the Cambrian, the **Ordovican Period** **(505-440 million years ago)** was first defined based on sequences in Wales. Laurentia and Siberia remained at about the equator for most of the early Palaeozoic, whilst Baltica moved towards the north. This movement result in the gradual closing of the Iapetus and a subduction zone developing in the western part of the sea, involving the orogeny called the Taconic in Laurentia.

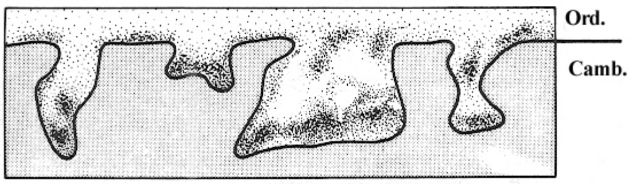
On the other side of the sea, the same movement also caused the onset of the Caledonian orogeny towards the end of the Ordovician. The vulcanism in the Iapetus generated windblown ash that were deposited in the epeiric seas of Baltica, where they are found as distinct layers of bentonites in the limestones (Middle and Late Ordovician). In Laurentia, the Ordovician transgressions are the most extensive during the entire Palaeozoic. Most of the continent's interior was covered by a shallow and warm epicontinental sea, where carbonates were being deposited.

On the southern part of the globe, the great landmass of Gondwanaland was slowly moving towards the polar region. During Late Ordovician, major glaciations occurred in what is today the Sahara desert. Glacial striations and tillites have been found in Western Sahara.

Scandinavia

The position of the Baltic plate during the Ordovician was at the latitude approximately 25-30° S. In Scandinavia, the Ordovician begins with a transgression from the south, and soon a shallow epicontinental sea covers most of southern, western and middle Sweden, with extensions towards the west and east into Norway and the east Baltic (Baltic states, Russia) respectively. In the earliest Early Ordovician the Cambrian type of sedimentation continued for a short time with alum shale deposition over a large part of the plate.

During most of the Ordovician, central Sweden and the east Baltic are characterized by a very slow deposition of carbonates, very abundant in nautiloid cephalopods. Short to long term unconformities are very common and in the limestones they are usually developed as so-called **discontinuity surfaces**, which are commonly stained with various types of iron minerals.



Discontinuity surface
(Orthoceras limestone, Sweden)

The Baltoscandian limestones are usually termed the "**Orthoceras Limestone**" (after a common cephalopod genus). At the same time, clayey deposits with abundant graptolites - the "**Graptolite Shales**", dominated the western parts of Baltica (Scania and the Oslo District). Unlike the alum shales, the graptolite shales are commonly grey and have a low organic content.

The Baltic Epicontinental Sea obtained its largest extension during the Middle and Late Ordovician. In central Sweden (Dalarna), reef-like calcareous mud mounds are formed. Exactly how these mounds originated is not known, but since they grew without organic control, they are not true organic reefs (see further below).

Towards the end of the Ordovician, the carbonate deposits include evidence of warmer climates, and the first so-called **Bahamitic sediments** are found, including calcareous ooids (see further below). The end of the period is also associated with a major worldwide regression, which is most likely controlled by the glaciation in North Africa.

Ordovician sedimentary rocks & environments

In Baltica and elsewhere, the shallow epicontinental sea included extensive deposition of carbonates. Carbonates can be either autochthonous or allochthonous. If they are composed of calcium carbonate ($CaCO_3$) they are termed **limestones**. If composed of dolomite ($CaMg(CO_3)_2$), they are termed **dolomites (dolostones)**. Carbonates can form through chemical precipitation (e.g. aragonite ooids), but most importantly they form as the result of biological processes (e.g. organic reef). Occasionally, it may be difficult or impossible to distinguish between these two processes.

The majority of all carbonates are marine subtropical or tropical sediments produced on **carbonate platforms** in shallow seas. A modern example of such a carbonate platform is the Bahamas, which is separated from the Florida peninsula by a deep submarine channel (Straits of Florida). As a result, the clastic sediments from North America never influence these islands, resulting in a deposition of so-called **Bahamitic carbonates**, including lime muds, sand size carbonate grains and oolites. Carbonate platforms also exist along the inner part of the Gulf of Mexico and to some extent in the Persian Gulf where the carbonate sedimentation is mixed with evaporite deposits (see also below). As will be seen in the following, carbonate platforms were much more extensive during parts of the Palaeozoic and Mesozoic, when vast epicontinental seas covered areas of the continents.

There are several possible ways of classifying carbonates. Most schemes involve analysis of the type of matrix and the carbonate grains. For example, the following important types of carbonates exist:

- **Micrite** or **calcilutite –** is a very fine-grained limestone composed almost entirely of fine lime mud. The micritic texture is the result of consolidation of carbonate mud particles, which are mostly composed of microscopic fragments of carbonate shells (or possibly chemically precipitated).
- **Biosparite –** is a fossiliferous limestone with sparry matrix (crystalline calcitic cement) if the content of fossils is very high it can sometimes be termed a **coquina**.
- **Oolitic limestone** - contains ooids (spherical laminated grains), which can be of different composition. In Bahamitic carbonates, the ooids form by chemical precipitation of aragonite around grains in agitated environments. In the Middle Ordovician of Baltica ooids are composed of iron compounds (hematite, chamosite etc.), but probably formed in a similar way by precipitation of layers of iron around a central grain in agitated environments. Many important iron ores are oolitic in origin (e.g. Jurassic in France).

The colour of carbonates (and other sedimentary rocks) is strongly controlled by the content of iron oxide content. Iron forms two sorts of oxides, ferrous and ferric oxide. Ferric minerals like hematite tend to colour the rock red, whereas the ferrous compounds result in a green colour. Hydrous ferric oxide (limonite) is generally yellow to dull brown.

The Ordovician Radiation

The beginning of the Ordovican Period is marked by another major radiation and great increase in diversity. Although not as significant as the ‘Cambrian explosion’, many important groups diversify at this time. These include planktonic graptolites and many types of molluscs, echinoderms and arthropods that are described below.

The rise of the massive skeleton builders, the corals, allowed the large-scale development of reefs, which developed a complex ecology, all of their own. The trilobites and brachiopods also underwent a strong diversification. Some people think that the invasion of the land by both plants and animals occurred during this period, although the evidence is extremely limited. Another important development is the rise of the vertebrates. The ability of Ordovician communities to partition food resources efficiently between their members is notably greater than in the Cambrian. The first true organic reefs appear.

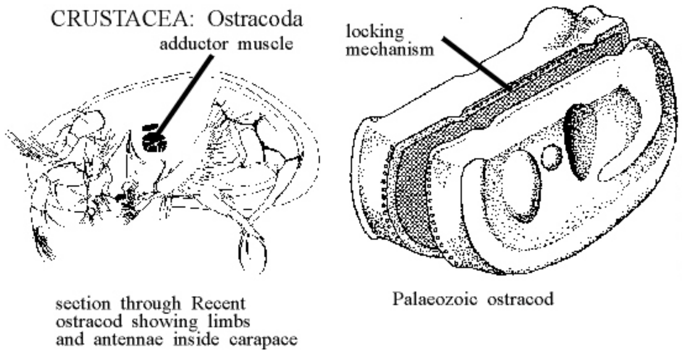
The severe glaciation at the end of the period seems to have caused widespread extinctions, especially in groups with planktonic larvae and adult stages such as the graptolites; the trilobites were particularly badly affected, and never regained their earlier dominance of the sea-floor communities.

Typical Ordovician Organisms

Ostracods

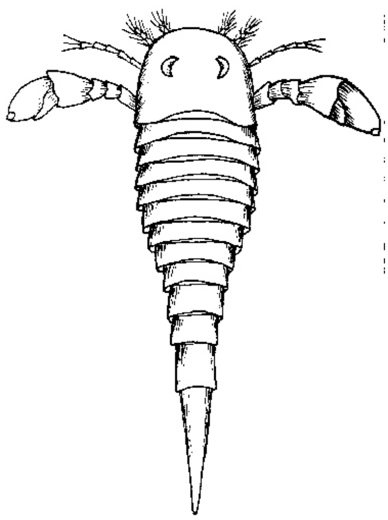
The **Order Ostracoda (Cambrian-Recent)** belongs to the Class Crustacea; they are small (usually 1 cm long arthropods, whose body is enclosed, in a two-shelled carapace. Rather like the bivalve molluscs, the shells have a locking mechanism along the hinge and an elastic ligament attached to each shell that is used to open the shells; they are closed with an adductor muscle as in the brachiopods and bivalve molluscs.

CRUSTACEA: Ostracoda



Ostracods are widely distributed, and today live in the sea and in fresh water. They are often useful for determining the relative age of the rocks in which they occur because they evolved quickly. Thus, rocks units of different ages preserve characteristic ostracod assemblages.

CHELICERATA: Eurypterid

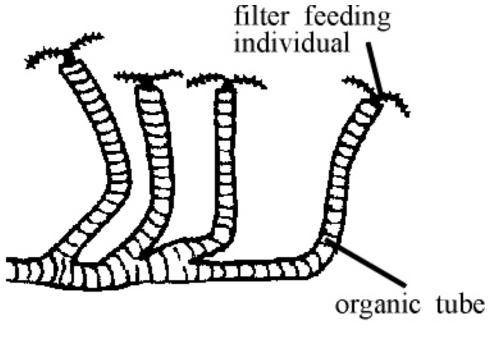


Eurypterids

The **eurypterids**, or so-called **‘sea scorpions’ (Ordovician-Permian)** are large members of the arthropod **Class Chelicerata**, and known both from marine, brackish and fresh water environments. Most species were relatively small, 10-20 cm long, but some could reach up to 3 m, representing the largest known arthropods of all times! They undoubtedly were some of the most ferocious predators of the early Palaeozoic.

Hemichordates

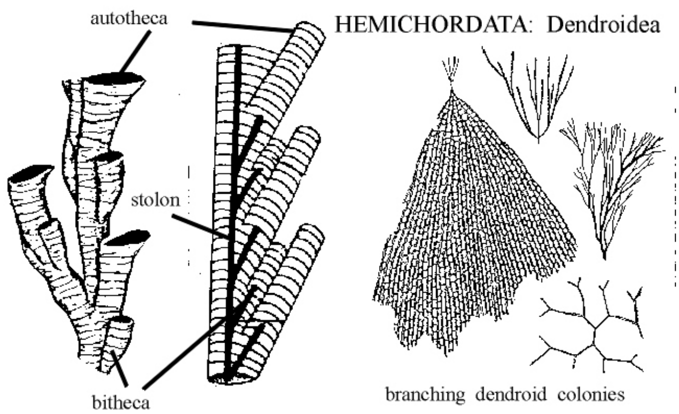
The **Phylum Hemichordata (Cambrian-Recent)** are represented today by only a hand full of genera. Most of them are small, colonial animals that live in tubes and feed by filtering, in a somewhat similar way to the brachiopods. One genus known from the middle Cambrian is almost identical to the living forms; it is a very good example of a 'living fossil'. The most important types of hemichordates, however, were the now extinct graptolites, which were very common in the Ordovician and Silurian.



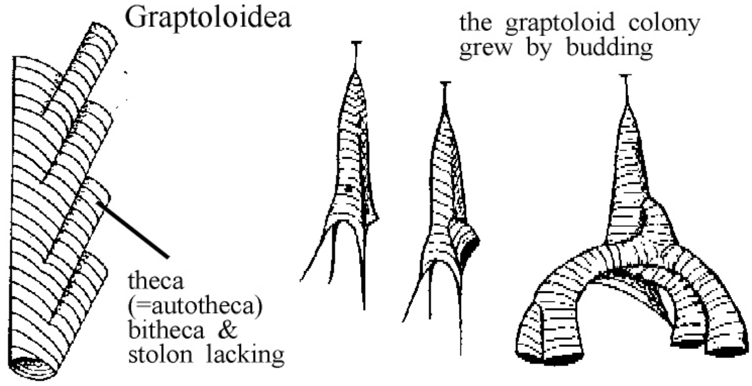
Recent hemichordate

The **graptolites (Class Graptolithina; Cambrian-Carboniferous)**, like the living hemichordates, were tube dwelling colonial animals that lived by filter feeding. Little is known about their soft-parts apart from by comparison with the living hemichordates. They constructed their tubes out of the protein **collagen**, which they secreted in half-rings, and then covered with other material. Although they first appear in the fossil record during the middle Cambrian, they only strongly diversified at the start of the Ordovician. There are a variety of benthic (bottom-living) forms, but by far the most common of these are the dendroids.

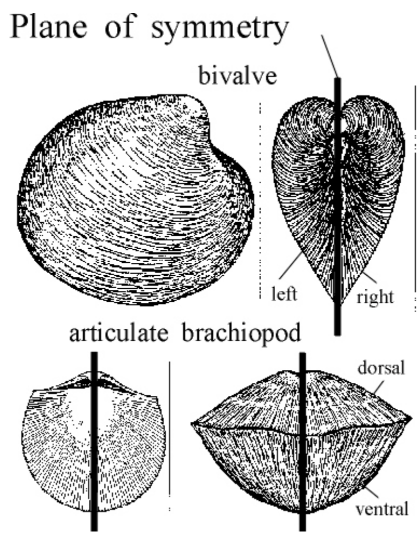
The **dendroids (Order Dendroidea; Cambrian-Carboniferous**) were the most morphologically conservative of the graptolites, and changed little from the Cambrian to the Carboniferous. Their colonies formed net-like structures, which were rooted in the substrate on which they grew. Like all graptolites, their colonies were composed of a number of tubes called **stipes**, out of which grew open-ended tubes called **thecae** in which the individual animals or **zooids** probably lived. The dendroids possessed two types of thecae: large, **autothecae** and, accompanying them, smaller **bithecae**. It is not clear what the distinction between the zooids that occupied these was. In addition, the stipes was cross-connected with many **dissepiments**, which strengthened the colony, and allowed it to maintain an upright, fan shaped position. The individual zooids appear to have been all connected together with a black **stolon** that is sometimes preserved running along the stipes and up into the thecae: a similar structure is known in the living hemichordates. The stolon thus divided in groups of three: one branch went into the bitheca, one into the autotheca, and one continued up along the stipe (this is named Wiman's Rule after the famous first Professor of Palaeontology & Historical Geology in Uppsala).



At the beginning of the Ordovician, some unusual types of dendroid graptolite appear, which are widely distributed and lack a holdfast or rooting structure. It is clear that these forms were free-floating, planktonic dendroids. From these early forms evolved an enormous variety of planktonic forms called the **graptoloids (Order Graptoloidea; Ordovician-Devonian)**. They are most commonly found in compressed form in shales, but are also known from limestones. It is possible to dissolve specimens out of the limestone and examine their three-dimensional structure, which is often very beautiful. The methods of secretion of the tubes may also be studied with the scanning electron microscope, and it is now clear for example that the zooids could leave their thecae and wander over the surface of the colony. Major trends in graptoloid evolution are simplifications of the ancestral dendroid structure. The proximal end (where the rooting structure used to be) is considerably simplified, and both the dissepiments and the bithecae are lost. Instead the colonies developed a number of flotation structures. It is not clear whether or not, as has been suggested, the colonies could actively move themselves, or whether they could only drift. The colonies could grow to a great size: some examples 1 metre across is known, with hundreds of thecae. Graptolite diversity was badly affected by the glaciation at the end of the Ordovician, but recovered strongly during the early and middle Silurian. Thereafter, graptolites declined, and finally became extinct during the early Devonian. Their distinctive forms and rapid evolution have made them the most useful fossils for biostratigraphy during the Ordovician and Silurian.



Molluscs



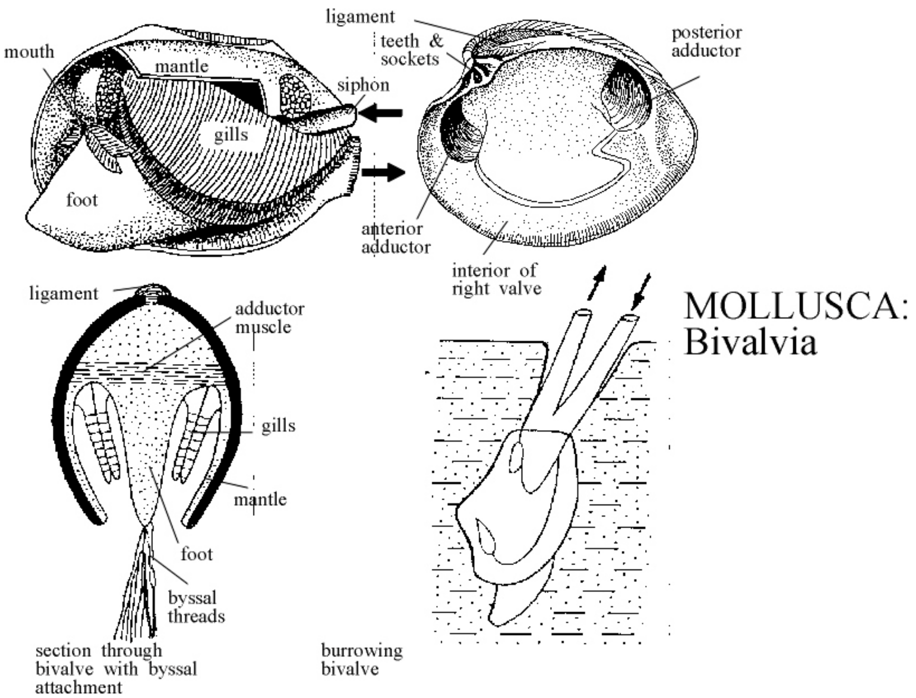
The **molluscs (Phylum Mollusca; Cambrian-Recent)** are a very diverse and important invertebrate group, second only to the arthropods. Most of them are marine, although some gastropod groups have successfully invaded land. The body is surrounded by a fold of skin called the **mantle**. Within this lies a **mantle cavity** with gills and openings of the hindgut, excretionary organs and gonads. The head is clearly delimited (apart from the bivalves), and in the mouth there is a band-like **radula** with rows of small teeth. The underside of the body forms a flat or wedge-shaped **foot**, which is a muscular organ for locomotion. The inner organs are often contained within a so-called 'body-sack' which lies dorsal to the foot, and which is protected by a calcareous shell. There are several distinct forms of molluscs, but three classes have an important fossil record: the Gastropoda, Bivalvia and Cephalopoda.

The **bivalve molluscs (Class Bivalvia; Cambrian-Recent)** are characterised by the possession of a pair of calcareous shells or valves, which lie along the left, and right sides of the body (contrast the brachiopod shells which are dorsal and ventral). An elastic **ligament** runs along the **hinge** between the shells, which hold the shells open. The hinge itself is usually articulated with a set of **teeth** and **sockets**, the morphologies of which are important in bivalve classification. These reduce the degree of sideways motion between the shells, which is important for activities such as burrowing. The shell is closed by a pair of **adductor muscles**; the points of attachment of the muscles to the shells leave characteristic muscle scars. In some groups, such as oysters, the anterior adductor muscle is lost.

Bivalves lack a head, and sensory functions are taken over by the mantle edge, which sometimes has a row of small eyes. There is a deep mantle cavity, which contains a pair of **comb-gills**. In most bivalves the gills are greatly enlarged to form doubled gill-blades on both sides of the body. The gills are extremely effective filtering devices. Motions of the cilia that cover the gills create strong water currents through them, and small food particles such as organism fragments and microorganisms are filtered out and taken by the cilia currents to the mouth.

Despite the lack of a head, the bivalves are a very successful group, and employ a wide range of ecological strategies: their mode of life is often strongly reflected in their morphology. Their ecology can be divided into three main categories: burrowing, attachment/reclining and free-swimming. The burrowers tend to have ornamented shells, which allow the organism to dig effectively through soft sediment. The mantle is extended into a long tube called a **siphon**, which sticks out of the top of the sediment, and which supplies nutrition and oxygen to the buried bivalve. Some bivalves can retract the siphon into a cavity called the **pallial sinus**. Attached and reclining forms either rest on or attach themselves to the substrate. Some attached species produce short, strong threads called **byssal threads** from a gland next to the foot, which secure the animal to a hard substrate. Other bivalves can secrete calcareous cement, which works as glue. Reclining bivalves on the other hand, rest free in soft sediment on one of their shells, which are often greatly enlarged relative to the upper one. Finally, the free-swimming groups have developed the ability to swim by clapping the shells together. A few other lifestyles are also known, such as boring into hard substrates, sometimes by excreting acid that dissolves away the rock.

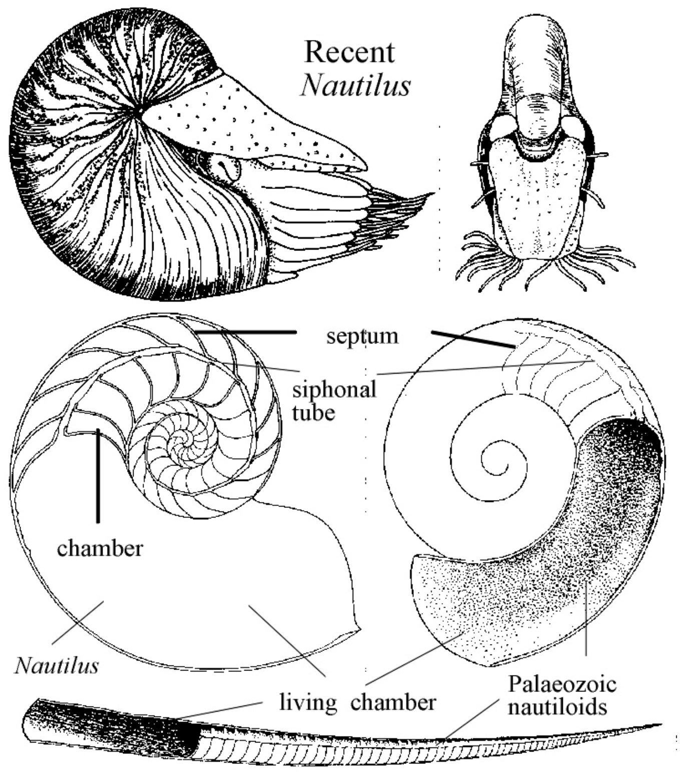
Bivalves became common in the Ordovician, although at this time the brachiopods were still dominant. Bivalves only really underwent their major radiation during the Mesozoic. Bivalves have several functional advantages over brachiopods: a) The ligament holds the shells open, which removes the need for separate diductor muscle that constantly have to expend energy; b) The gills are more effective filtering devices than the lophophore; c) The bivalve foot is adapted to burrowing; d) the mantle can be grown out into a siphon; e) the byssal threads can be easily repaired or regrown, and f) whereas brachiopods have always to maintain a conservative shape in order to support the lophophore, bivalves have had much greater morphological freedom, allowing the exploitation of a wide range of ecologies.



The **Class** **Cephalopoda** **(Cambrian-Recent)** contains the largest and most highly developed marine invertebrates. The modern giant squid for example, can reach tens of metres in length. They are all active predators, and have complex brains and sensory organs. Many are active swimmers, but others were more or less passive floaters. The foot has been transformed into a moveable funnel, through which the animal can squirt strong water jets from the mantle cavity. This allows the animals to swim by means of **jet propulsion**. Most fossil forms had an outer shell, which was internally compartmentalised by calcareous **septae** into several chambers or **camerae**. The main part of the body was contained in the last chamber called the **living-chamber**. Although many organisms build similar chambers, those of the cephalopods are characterised by a continuous tube, the **siphuncle** that passes through each septum. The cephalopods with this type of shell could adjust their buoyancy in the same was as a U-boat: they could pump water out of the camerae through the permeable siphonal tubes, and slowly replace it with gases. Removing liquid reduces the mass of water displaced, increases upthrust and causes the animal to rise. Conversely, pumping water into empty chambers will cause the animal to sink. With unequal pressure either side of the shell wall (water-pressure on one side and the diffused-in gas pressure on the other) the shell is clearly subjected to great strain, or to counteract this, the edges of the septae are folded in order to provide extra support. Even so, experiments on the living form ***Nautilus*** show that the shell implodes at depths greater than about 800m. The shell of most living cephalopods is reduced. In these forms, strong development of the mantle musculature allows effective and powerful swimming by jet propulsion.

A few **nautiloids (Subclass Nautiloidea; Cambrian-Recent)** appear in the late Cambrian, but the group underwent a spectacular radiation at the beginning of the Ordovician. The nautiloids have an outer shell, which can be straight, curved or spiralled. The position of the siphuncle varies from the center of the septae to being more peripheral; likewise the diameter varies considerably. The nautiloids characteristically have simple, convex to the posterior septae. The peripheral edge of the septae, which is in contact with the inside of the outer shell, is often visible in fossils where the outer shell has broken and fallen off. These edges are called **suture lines** and in the nautiloids are straight or gently curved. The Cambrian nautiloids were small and rare, mostly with gently curving shells. The many Ordovician forms can be placed in several more or less specialised groups. Among others, these include: a) A straight-shelled group (in Sweden, often found in steps and paving stones of Ordovician limestone). These are loosely referred to as **orthocones**, and the largest ones reached 9 m or more in length. Most orthocones, however, had much shorter shells than this, between 0.5 - 3 m in length. They were probably poor swimmers as they totally lacked any stabilising devices such as fins; b) groups with curved or spiralled shells. They are reminiscent of the modern form *Nautilus*, and in all probability could swim quite well; 3) groups with short, egg-shaped shells with a reduced shell opening. These were probably poor swimmers.

CEPHALOPODA: Nautiloidea

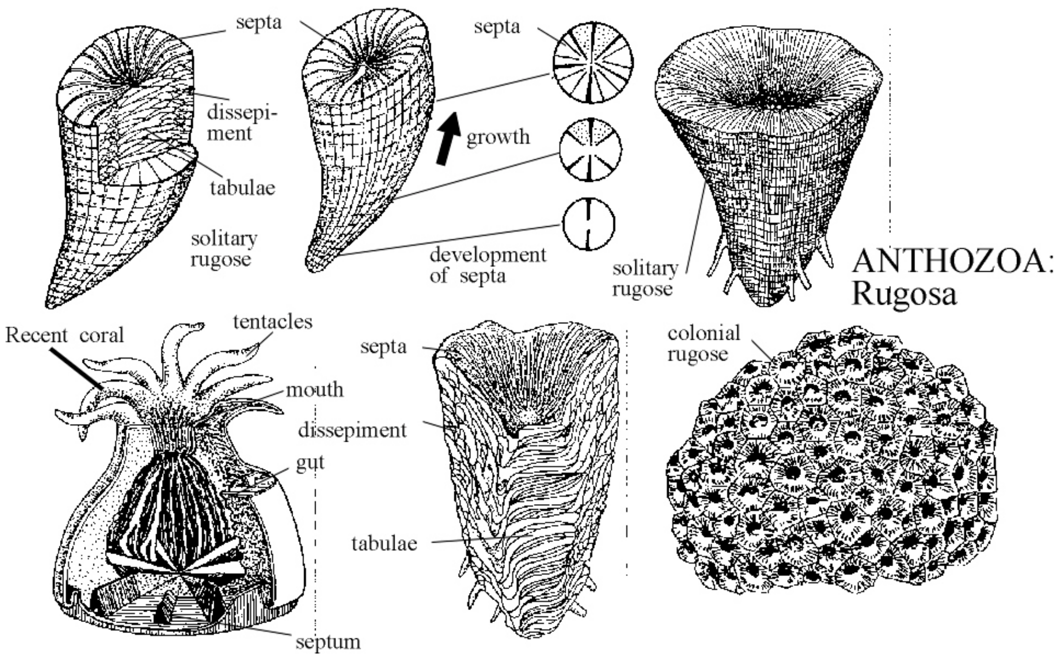


Cnidarians

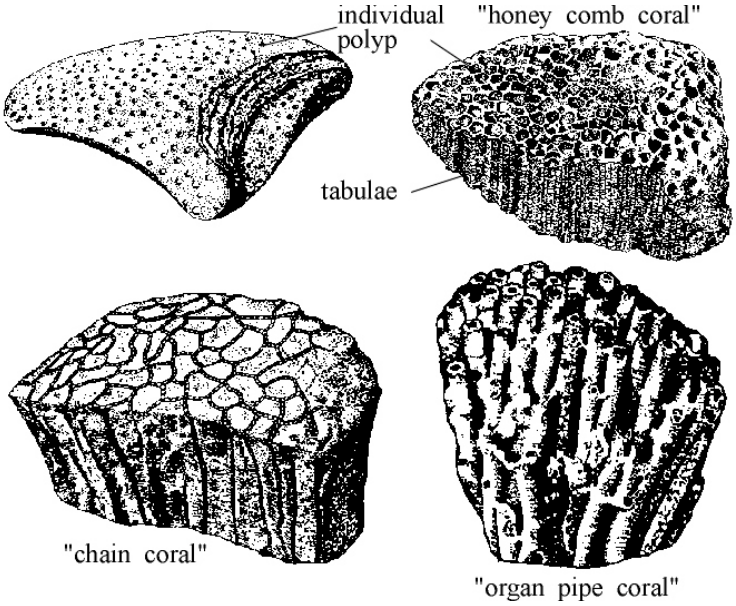
The **cnidarians (Phylum Cnidaria; ? Late Precambrian-Recent)** are rather simply built, radially symmetrical animals. The mouth is surrounded by **tentacles**, which are supplied with stinging cells - so-called **cnidoblasts** that give them their name. The gut is bag-shaped, without an anus. There are several groups, including some probable Precambrian stalked (sea pens) and floating forms (from the Ediacara fauna; see above), making them among the oldest of multi-cellular animals. However, in the Ordovician corals with calcareous skeletons arose, and from this time onwards the group has a good fossil record.

The **corals (Class Anthozoa; Ordovician-Recent)** are marine animals that appear in the Ordovician fossil record, but do not become abundant until the latter part of the system. They can either be **solitary** or **colonial**. Colonies grow by budding off of new individuals. Most groups develop a calcareous skeleton, which has the form of a cup, horn or tube in which the individuals live. Despite the corals having a fairly low level of organisation, their colonies can show a highly complicated construction. Each cup consists of an outer wall, within which are radial, vertical, calcareous partitions, or **septae**, and horizontal calcareous platforms, the **tabulae. Dissepiments** (curved calcareous lamellae) occur between the septa. All these elements (septae, tabulae and dissepiments) support the soft parts and increase the mechanical resistance of the coral skeleton, and have therefore been important for coral evolution. The Palaeozoic corals are placed in two subclasses, both of which are extinct: Rugosa and Tabulata.

The **rugose ('tetracorals') corals (Subclass Rugosa; Ordovician-Permian)** can occur either singly or as colonies. The earliest growth stage consists of just the skeleton wall and six primary septae. New septae arise only in four of the spaces between the primary septae. It is thought that the Rugosa gave rise to the living **Subclass Scleractinia ('hexacorals')**, which first appear in the Mesozoic. The latter also form six primary septae, but afterwards build secondary septae in all six spaces. There were relatively few rugosans in the Ordovician, but their numbers and diversity increased in the Silurian and Devonian.



The **tabulate corals (Sub-Class Tabulata; Ordovician-Permian)** are exclusively colony-builders. They differ from the rugosa in that genuine septae are entirely lacking. The tabulae and dissepiments are, on the other hand, well developed. In Sweden, large tabulate colonies are often found in the Silurian reefs of Gotland. The relationship between tabulates and other groups of corals are unclear, and a few people think that they should not be grouped with the other corals at all.



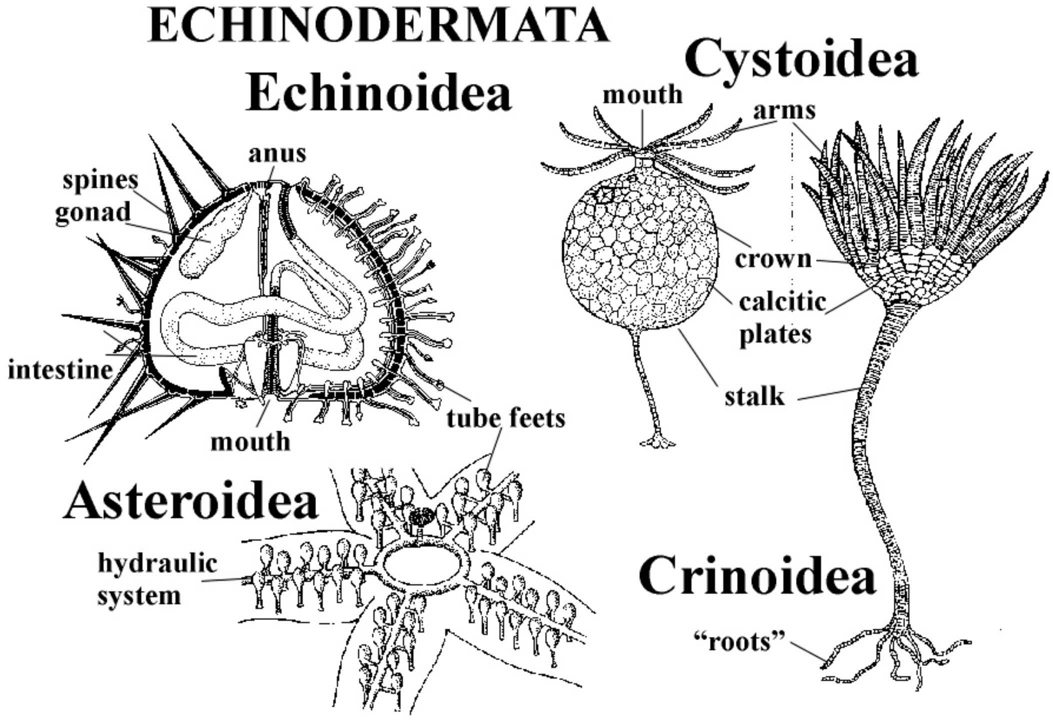
ANTHOZOA: Tabulata

Echinoderms

The **Phylum Echinodermata (Cambrian-Recent)** consists of marine, usually bottom-living animals. They can live either fastened to the surface or lying freely. In their development, modern echinoderms have a more or less obvious five-fold radial symmetry: this is sometimes obscured in the adult animal. Echinoderms have many distinctive features. Their skeleton is made up of plates of calcite, each one composed of a single calcite crystal. The plates have a characteristic porous construction called the **stereom**. Over the surface of the skeleton is a thin, soft skin: the echinoderm skeleton is thus technically an **endoskeleton** like ours rather than an exoskeleton like that of most other invertebrates. Another important feature of echinoderms is their water-canal system, which is composed of a ring-canal and five radial canals that branch off it. **Tube feet** extend out from the radial canals and can be extended and retracted by changes in the water pressure: the whole system is therefore a highly developed **hydraulic** system. The tube feet serve in many groups as walking organs.

The four important groups of living echinoderms all arose in the Ordovician: Crinoidea (sea lilies): Asteroidea (sea stars); Ophiuroidea (brittle stars) and Echinoidea (sea urchins). However, especially in the Cambrian there were several groups of now-extinct forms, some of which do not appear to have possessed five-fold symmetry. One Ordovician group, now extinct, was the Cystoidea, members of which are commonly found in the Ordovician of Sweden.

The **cystoid (Class Cystoidea; Ordovician-Permian)** skeleton consists of numerous calcitic plates, somewhat irregularly organised. They are punctuated with characteristic pores. The skeleton can be round or more or less bag-shaped. After death the interior of the skeleton is often filled with large crystals of calcite. The mouth is situated on the top surface of the skeleton and was surrounded by a varying number of branched or unbranched short food-grooves. At the ends of the grooves were short unbranched arms, which are, however, only rarely preserved. The water-canal system ran along the food-grooves. Some cystoids were directly attached to the substrate; others were stalked.

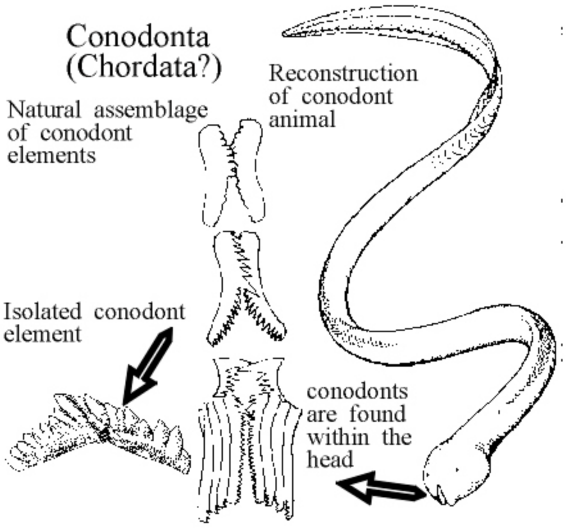


Chitinozoans

Chitinozoans (Ordovician-Carboniferous) are acid-resistant microfossils of problematic affinity, which are found in marine rocks. They are flask or vase-shaped and can be covered with spines. The wall of a chitinozoan is made entirely of an organic substance, which is not, however, as the name might suggest, chitin itself. They are mostly between 0.1 and 0.5 mm in height. It is possible that all forms were originally stuck together in chains, with the opening of one being in contact with the base of the next. Most chains however have become separated during burial. Certain shapes have a short geological range and are therefore good biostratigraphic indicators. Since they occur in considerably greater numbers than larger fossils, and are also acid-resistant, they can be used with advantage for relative dating of rocks, especially in bore cuttings.

Conodonts

Conodonts **(Cambrian-Triassic)** are microscopic, tooth-like fossils, which are composed of calcium phosphate. They are found in all types of marine sediments, and show several distinct forms. Individual elements may look like simple teeth, like rows of assembled teeth, or as toothed plates, covered with tubercles or ridges. They are usually between 1-3 mm long, although an Ordovician form from South Africa is known that is several centimetres long! It has been clear for some time that the various types of conodont occur in natural groups, each called an apparatus: up to seven conodont elements may be present in each apparatus.

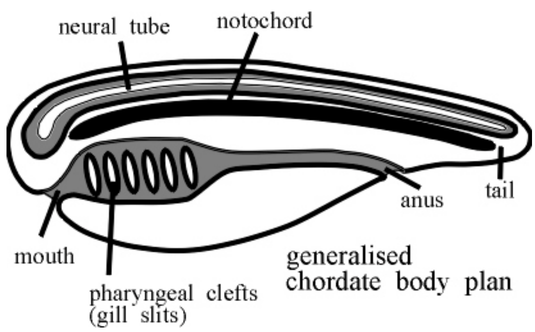


Like the chitinozoans, the conodonts are much used in biostratigraphy, because of the ease by which they are extracted from rocks, their rapid evolution and abundance. They also have the unusual property of changing colour according to the temperature to which they have been subjected, through brown and black to white. They are therefore very useful to the oil industry for assessing if oil or gas is likely to be present in rocks.

The affinities of conodonts have been traditionally highly problematic: almost every phylum has been suggested. However, during the 1980s, several specimens of the much searched-for **conodont animal** were discovered in Scotland. Since then our understanding of conodonts has advanced a great deal, and it is now almost universally accepted that the conodonts were a primitive group of vertebrates, related to the agnathans. They have a long evolutionary history, and are exceptional in that they appear to pass through the severe extinction at the end of the Permian with little or no effect. However, they became extinct in the following period, the Triassic.

Chordates

The **Phylum** **Chordata** **(?Cambrian-Recent)** includes three living subphyla, tunicates, cephalochordates, and vertebrates, and possibly also the extinct conodonts. The body plan exhibited by the living chordates is highly variable due to the different life habits. However, all chordates have the following characters: (1) a **notochord**, which is a flexible rod running along the dorsal (upper) side of the animals, providing support for the body, (2) a **dorsal neural (nerve) chord** placed just above the notochord, (3) a set of **pharyngeal clefts (gill slits)**, and (4) a post-anal tail.



The **tunicates** may have been ancestral to the other chordates; the adult tunicate (sea squirt) is a sessile, bag-shaped, filter feeder unlike other chordates. However, the free-swimming larvae looks like very much like the fish-like **cephalochordates** **(lancelet).** According to one model, the cephalochordates may have arisen from a tunicate larva that became adult while retaining the juvenile fish-like characters ('neoteny').

Fossil tunicates are very poorly known, but we know a possible fossil fish-like animal (*Pikaia*) from the Burgess Shale that may belong to the cephalochordates. The evolutionary step from the cephalochordates to an early vertebrate is not very long.

In members of the **Subphylum Vertebrata (Cambrian-Recent)** the notochord is turned into a **vertebral column** during ontogeny and the head section of the dorsal nerve chord is protected by a braincase (cranium). The earliest traces of true vertebrates are phosphatic scales from the Late Cambrian, but well-preserved fish fossils are only known since the middle Ordovician. All the earliest fishes belong to the **jawless agnathans (Class Agnatha; Cambrian-Recent)** and were protected from predators by heavy external armour consisting of phosphatic scales and plates. The agnathans include two still living members, the soft-bodied lampreys and the hagfishes.

SILURIAN

General

Like the two previous periods, the **Silurian Period** **(440-410 million years ago)** was also first defined in Wales. After the regression at the end of the Ordovician, sea level rose again and covered vast areas of the Silurian continents. The Iapetus Sea became still narrower and in the Late Silurian, it was completely closed. The global climate was mild, and there is no evidence for glaciations during the period, in spite of the fact that Gondwanaland remained at the South Pole. The North American continent was entirely covered by a shallow sea with land areas only in the northern Canadian Shield and in the highlands of the Taconic Mountains in the east. Vast carbonate deposits formed in this warm and shallow sea with the exception of clastic influence from the Taconic Mountains. Barrier reefs (see further below) formed in the area of the Great Lakes.

Scandinavia

The Silurian deposits in Scandinavia are not as complete as those from the Cambrian and Ordovician. Extensive Silurian sequences are found in Scania and on the island of Gotland. But there are good sections also in the Baltic States and in the Oslo graben to the west. The

Silurian rocks in Scania represent a continuation of an Ordovician lithofacies, and comprise grey graptolitic shales. During the later parts of the period a general regression took place and a shallowing upward sequence formed in Scania, starting with carbonates shifting upwards to sandstones. The same general trend is apparent also in Oslo and is related to the growth of the so-called "**Old Red Continent**" (from the general red colour of the sediments). This developed first in the British Isles as a result of the Caledonian orogeny. The last terrestrial so-called **"Old Red Sandstone"**, which characterises this continent is developed in the Mjösa region (Ringerike Sandstone) and maybe also in Dalarna (Orsa Sandstone). Silurian carbonates are best known in the Silurian of Gotland, where organic reefs (see further below) developed in the warm and shallow water of an epicontinental sea. In the lagoons behind the reef structures, a mixed sedimentation of clay and carbonates dominated. The Silurian on Gotland also shows a shallowing upward sequence being capped by the Burgsvik Sandstone in Late Silurian. Towards the end of the Silurian, the sea disappeared from Scandinavia, and the Baltic plate was elevated due to the Caledonian orogeny in the west.

Silurian sedimentary rocks & environments

The Silurian was a time of extensive reef building: the examples from Gotland (see above) are particularly well known, but there are many other beautiful examples in Europe and North America. In the present, organic reefs form as the result of the activity of carbonate secreting organisms (now mostly corals). Reefs only form was the following environmental criteria are fulfilled: large rivers should be distant (since they transport fresh water and mud into the ocean), the sea must be light and warm and the water should be well oxygenated.

Recent reefs usually have a wave resistant reef front facing the open ocean, followed by a shallow reef flat, and on the backside a lagoon, protected from the ocean waves. Examples of reef types are:

- **Fringing reef**, with a shallow and narrow lagoon not far from land (e.g. Eilat reefs in the Red Sea)
- **Barrier reefs**, which are very large and elongated up to tens to thousands of kilometres in length along a continent or a large island. A very wide lagoon separates the reef from the land (e.g. Great Barrier reef in Australia).
- **Atolls** are circular or semicircular reef structures around a lagoon. They frequently occur as isolated a group of islands in the ocean associated with sinking volcanic islands (e.g. many of the islands in the South Pacific Ocean).

The calcite and aragonite hard parts of organisms, today mostly corals, form the core of the reef. The Recent corals (see further above) have endosymbiotic photosynthetic organisms, which are the main reason why the corals can manage to secrete vast amounts of calcium carbonate necessary to build a reef.

Reef production is clearly associated with periods of global warming and high sea levels, like in the Silurian and Devonian in the Palaeozoic and the Jurassic and Cretaceous in the Mesozoic.

There are also many examples of Silurian deep-sea environments, such as continental slope deposits. The continental slope has a steep gradient (about 1:40, that is a drop of 1 m for every 40 m horizontally). Sediments on the edge of this slope are characterised by gravity instability, and tectonic movements causes submarine mass movements, usually in the form of underwater suspension streams called **turbidites**. These flow rapidly down the slope and further out on the ocean floor. Well-developed Silurian turbidites are known e.g. from Wales.

The Invasion of Land

The beginning of the Silurian is marked by a strong biotic recovery from the end-Ordovician extinction. In particular, planktonic forms of graptolites radiated spectacularly. For several groups, especially the graptolites, some groups of brachiopods and trilobites, the Silurian was a period of decline. Post-Silurian faunas typically have a much more ‘modern’ look to them, being dominated by molluscs rather than brachiopods, and crustaceans rather than trilobites.

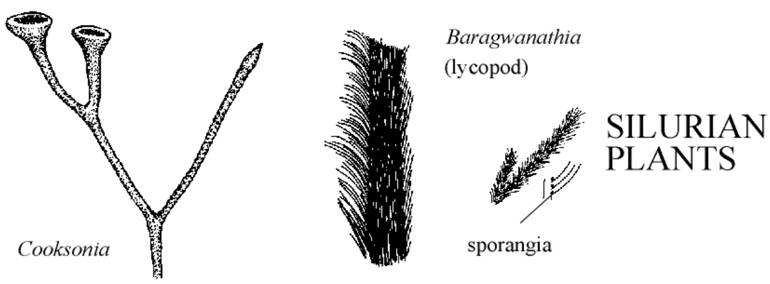
The Silurian marks the end of the early Palaeozoic fauna: the great faunal changes in the ensuing Devonian period caused a revolution both in the sea and on land. The most significant feature of the Silurian is the invasion of land. The earliest land plants are known from the middle Silurian, and the earliest animals (arthropods) from the late Silurian. Although no Silurian land vertebrates are known, they too appear in the fossil record shortly afterwards.

Typical Silurian Organisms

Land plants

Land plants (?Late Ordovician, Silurian-Recent) are characterised by several adaptations designed to counteract the special problems of living on land. These include: (1) the difficulty of water conservation, (2) difficulty of support in a non-buoyant medium such as air, (3) the difficulty of reproduction without water to spread gametes, and (4) the difficulty of transport of nutrients and water from the soil. Land animals are faced with similar problems, and solve them in a variety of ways. Land plants developed a complex polysaccharide called **lignin**, which provided support, and various types of vessels for transporting water and nutrients.

The earliest land plants were quite small, simply branching forms referred to the genus *Cooksonia*. Some of the stems bore small **sporangia** at their tips, which were full of maturing **spores**. Shortly after, other forms appear, such as the Australian *Baragwanathia*, which appears to have been the ancestor of the modern-day **club mosses** or **lycopods**. Most other early plants appear in the Devonian.



Land animals

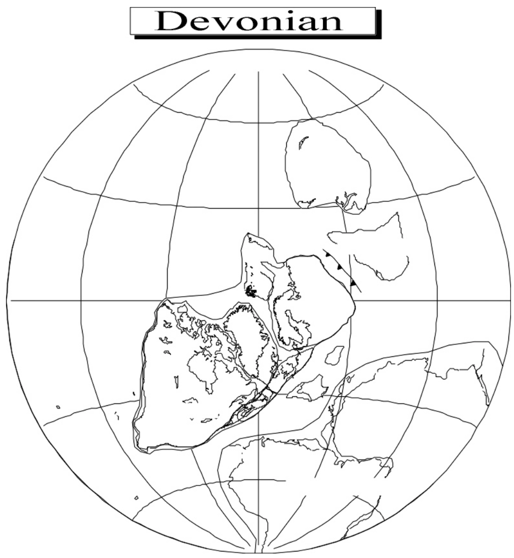
Recently described land animals from the late Silurian of England appear to have been related both to the modern day **spiders (Class Chelicerata)** and the **myriapods ('millipedes')**.

Vertebrates

Fishes were considerably more common in the Silurian than in the Ordovician. The first jawed fish (the acanthodians) are found during this period. In Sweden, both jawed and jawless fish have been found in the Silurian of Gotland.

DEVONIAN

General



The type area of the **Devonian Period (410-360 million years ago)** is in Devonshire, south England. During the Devonian the orogenies around Iapetus ended with the formation of a mountain chain from northern Scandinavia through parts of the British islands and further south on the American continent - the Caledonian-Appalachian mountains. The Old Red Continent was situated about 10° N of the equator. The deposition of the Old Red Sandstone continued in an environment with rivers, lakes and desert conditions. The south coast of this continent went through central Europe, from southern Ireland to Poland and southern Russia.

The **Tethys Sea** represents the oceanic arm between Gondwanaland and the northern continents. The western part of the Old Red Continent was still partly submerged, with land areas in the east and to the north. In the central parts of North America, epicontinental seas still existed with reefs fringing the shores of this basin. Towards the end of the Devonian unusual anoxic events occurred in this sea, resulting in wide spread deposition of black bituminous shales similar to the Swedish alum shale.

Scandinavia

No rocks of undoubted Devonian age have been found in Sweden, and only in western Norway, Devonian deposits are known. These include coarse sand and conglomerates of very large thickness. These may be regarded as weathering products from the Caledonian mountains, deposited in deep lakes. Plant fossils have been found in the fine-grained sediments. In the Baltic States, deposition of Old Red Sandstone continued in lakes, rivers, and near shore environments. These beds are very rich in fossil fishes and also contain fragments of the earliest tetrapods (see further below).

The Age of Fishes

During the period**,** the evolution of life on land continued with the invasion of the **tetrapods** in the late Devonian, and a considerable proliferation of the arthropods and plants. In many respects, the Devonian was a period rather like the Silurian. However, many more 'modern' groups such as the bivalves, gastropods and crustaceans proliferated, possibly at the expense of the brachiopods and trilobites.

Typical Devonian Organisms

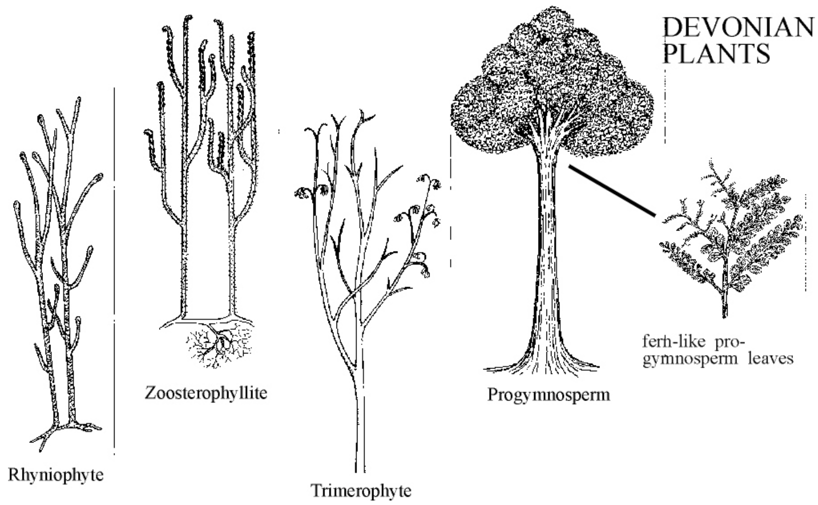
Plants

The early Devonian floras are considerably better known than the Silurian examples. Three main groups of plants were established: **rhyniophytes**, which were slender branching forms like ***Cooksonia***, **trimerophytes**, which had a rather more complicated branching pattern, and were probably the ancestors of most modern groups, and the **zosterophyllophytes**, which encompass ***Baragwanathia***-like forms, and were the ancestors of the modern club-mosses or lycopods. Towards the end of the period, the earliest seed-like structures evolved.

The **seed** is basically an enclosed fertilisation chamber equipped with its own food supply, so that early development of the embryo can also take place within it. It has the advantage that only the male spores of land plants need to be shed (compare pollen of most modern plants), and fertilisation of the female gamete took place within the proto-seed. Fertilisation and early growth therefore all take place within a highly controlled microenvironment, as opposed to the dehydrating and unpredictable environment of the world outside.

The **progymnosperms (Devonian-Carboniferous)** are interesting as they are thought to be intermediate between seed-less plant and seed plants. They are tree-like and the leaves look like those of ferns (they were first classified as ferns), whereas the trunk looks like that of the later conifers. The progymnosperms are the first plants to evolve **wood**, giving them greater strength, and they also evolved true **roots**.

Concurrent with the evolution of the seed habit, plants started to form quite large tree-like forms, and the first forests were formed.



Invertebrates

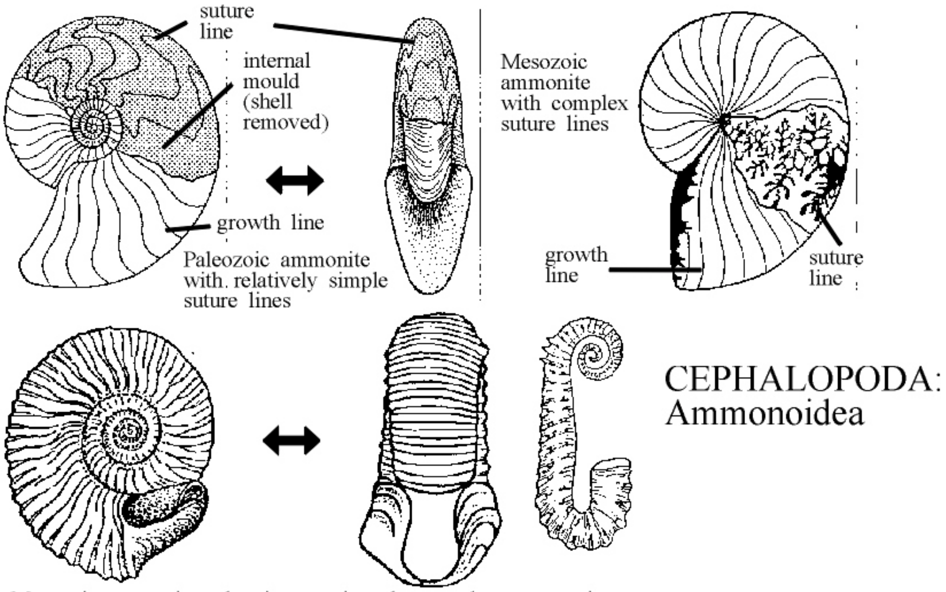
The graptoloids died out early in the Devonian, although the benthic dendroids continued to the Carboniferous. Devonian trilobites are mostly rather similar to Silurian ones. Brachiopods continued to be important, and new groups developed. However, during the middle and late Devonian, severe extinctions affected all marine groups, resulting in reductions in trilobites, brachiopods and cephalopods. On the other hand, the first examples of the enrolled ammonoids (cephalopods) are known from this period, a group destined to undergo spectacular radiation during the Mesozoic.

Several famous localities have given us a good understanding of life on land during the Devonian, including **Rhynie** in Scotland. It is clear that several groups of arthropods had invaded land at this time, including myriapods and arachnids. Additionally, the earliest insect (Class Hexapoda) is known from the Rhynie Chert, *Rhyniella praecursor*. This is a wingless form represented today by the collembolids or springtails. However, the first major radiation of insects did not occur until the Carboniferous, when the first winged forms appear.

Ammonoids

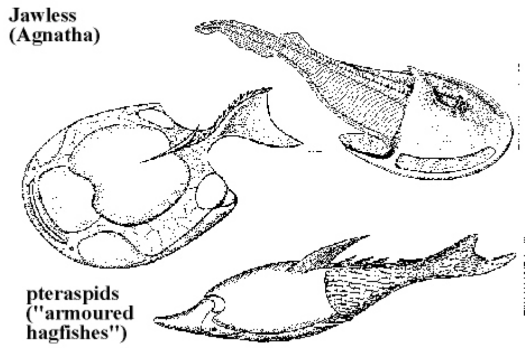
The **ammonoids (Subclass Ammonoidea; Devonian-Cretaceous)** are a group of entirely extinct cephalopods (Phylum Mollusca). They appear to have evolved from straight-shelled cephalopods in the Devonian. From then on, they underwent several important radiations. Tightly enrolled shells characterise most ammonoids, and they are among the most beautiful of fossils. Although their shells are superficially rather similar to those of the nautiloids, including the presence of a siphuncle and septae, it is thought that in fact they are rather more closely related to the group of cephalopods that includes the squid, octopus and cuttlefish. The soft parts of ammonites are poorly known, but they appear to have possessed an ink sac, like the octopus. Their jaws are occasionally preserved and, again, these are rather octopus-like.

Ammonoids exhibit a considerable range of sizes. The smallest mature specimens are about 1 cm in diameter, but some truly monstrous forms in the Jurassic reached diameters of about 2.5 m. The siphuncle was normally along the inner surface of the shell, on the ventral side, unlike the generally central position of the nautiloid siphuncle. This may have been a more efficient position for extracting liquid from the chambers. The external surface of the ammonite shell was often highly sculptured. In addition, a keel often ran along the outside. Some species developed elaborate spines around the aperture of the shell, although most Palaeozoic forms had simple apertures. These curious features may have been sexual differences: ammonites are some of the few fossils where two morphological forms may be distinctly seen in the same species, and it is assumed that these represent the male and female. The lines along which the internal septae meet the outer shell are known as **suture lines**. They are extremely important in ammonoid classification. Those of Palaeozoic forms are generally simple curves. However, Mesozoic ammonoids developed some beautifully complex sutures, with almost unbelievable levels of intricacy. It is generally assumed that the deflection of the sutures was a device to strengthen the shell, although the more complicated examples seem to go beyond such usefulness. The suture changes both through ontogeny (development) and phylogeny (evolution), and is thus useful for comparing the two processes. The rapid evolution of ammonoids makes them some of the most useful of all biostratigraphic indicators, especially in the Mesozoic.



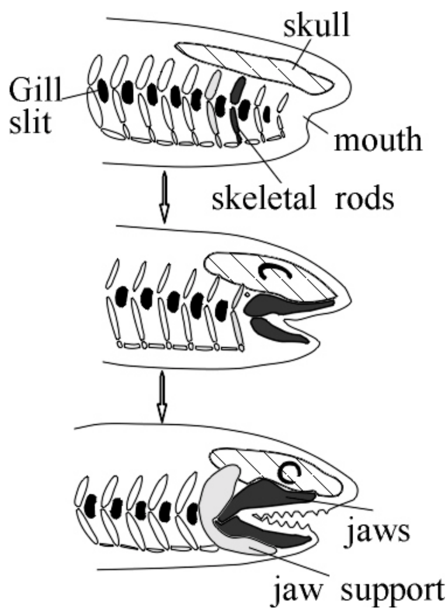
Mesozoic ammonites showing varying shape and ornamentation

Jawless fishes



The Palaeozoic **agnathans** **(Class Agnatha)** are provided with about 10 gill slits that were used in the filter feeding life habit, and it is probable that they could live in both marine and fresh water conditions. The peak in their diversity was reached at about the Silurian/Devonian, and sediments of this age contain a rich fossil fauna with a variety of differently shaped agnathans. It is probable that the extremely heavily armoured, flattened forms were bottom dwellers, whilst the more slender, less armoured species more likely were free-swimming. At the end of the Devonian all the armoured agnathans became extinct, and from the Carboniferous there is only a scant fossil record representing the soft-bodied, still living lampreys.

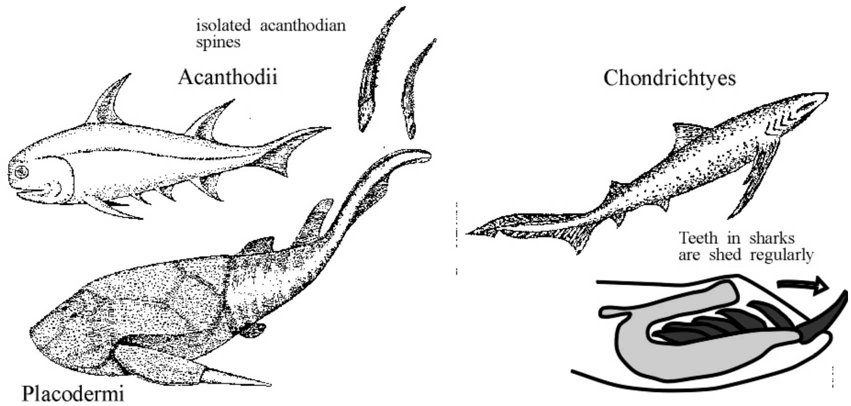
Jawed fishes



The detailed structure of the head of some fossil agnathans indicate that the anatomy is basically similar to that of the jawed fishes, and it is likely that some jawless group gave rise to the first **jawed fishes (gnathostomes)**. Exactly how the first jaws originated is still uncertain, but an elegant 'classic theory' attempts to derive the jawbones from the skeleton supporting the gill slits in the agnathans. The number of gill slits is reduced in the early jawed fishes. The evolution of jaws opened up an enormous potential for diversification into different life habits, as revealed by the richness of gnathostome remains in the Devonian.

The earliest known remains of jawed fishes belong to the **Class Acanthodii (Silurian-Permian)**. These somewhat shark-shaped fishes were quite small, around 10-20 cm long, and appear to be highly specialised; their relationships with other fishes are poorly understood. Acanthodians are mostly known from isolated phosphatic scales and the long distinctive fin spines. The group became extinct during the Permian.

The **placoderms (Class Placodermi)**, sometimes called 'armoured sharks', are known only from the Devonian, when the dominated the fish fauna. The earliest forms are quite small and may have been bottom dwelling. Later forms were huge, up to about 10 m long, and many were active predators in open waters. The internal and external skeleton in some placoderm lineages seems to have a tendency to contain less and less amounts of **bone** (lower amount of phosphate). This may indicate that the are directly related to the earliest **true sharks (Class Chondrichthyes; Devonian-Recent)**, which are typified by having a skeleton consisting of **cartilage**, without true bone. The earliest true sharks are known from the Devonian, and they virtually have not changed their morphology and life habit since that time. The diversity of sharks became particularly great during the Carboniferous. During the Cretaceous, some sharks seem to have reached a length of more than 13 m. Due to the lack of real bone, the remains of complete shark skeletons are rare, but the robust teeth, which are continuously



formed and shed during the life, are usually extremely well preserved and common fossils.

Bony fishes

The bony fishes (Class Osteichthyes; Devonian-Recent) differ from the sharks mainly by having an internal bony skeleton in addition to a lung or swim bladder. In the advanced bony fishes the swim bladder enables the fish to stay afloat even when it is not swimming; in contrast the sharks will sink if they stop swimming. The first bony fishes are known from the Devonian (with some questionable Silurian forms), but are poorly preserved. The two main types of bony fishes are the ray-finned actinopterygians and the lobe-finned sarcopterygians. However, the relationships of the forms placed within the latter group have been much disputed.

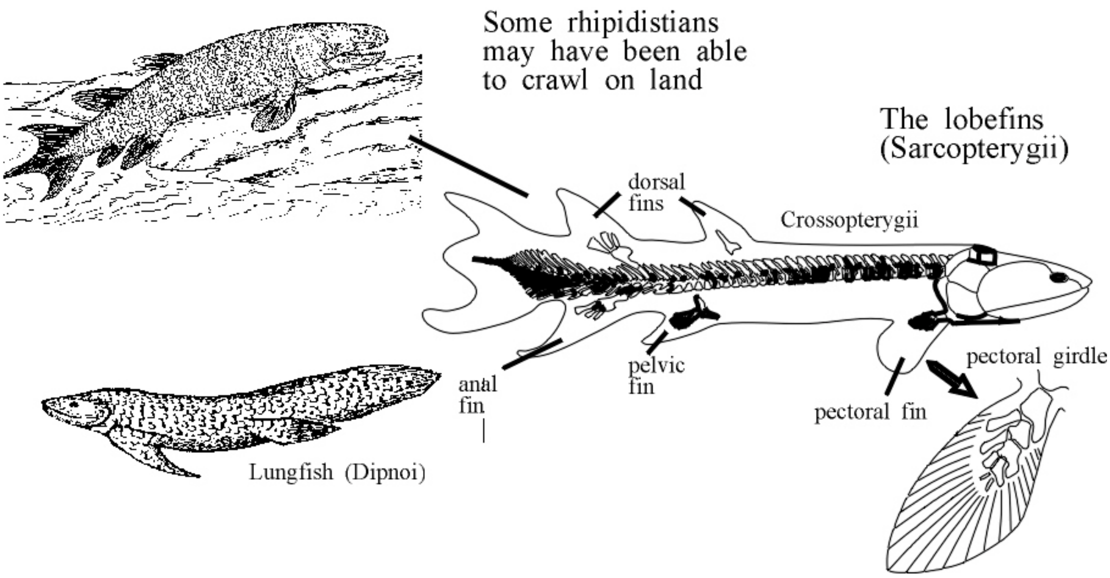
The **actinopterygian (Subclass Actinopterygii; Devonian-Recent)** fins lack muscles and have a ray of spines, supported by a basal row of cartilaginous rods, whilst the sarcopterygians have fleshy muscular fins with a bony axis. The actinopterygians were not very prominent during the Devonian, but have increased their importance since that time, so that in present environments about 95% of all fishes belong to this group. The swim bladders of primitive bony fishes developed as pouches from the oesophagus, which were filled by swallowing air.

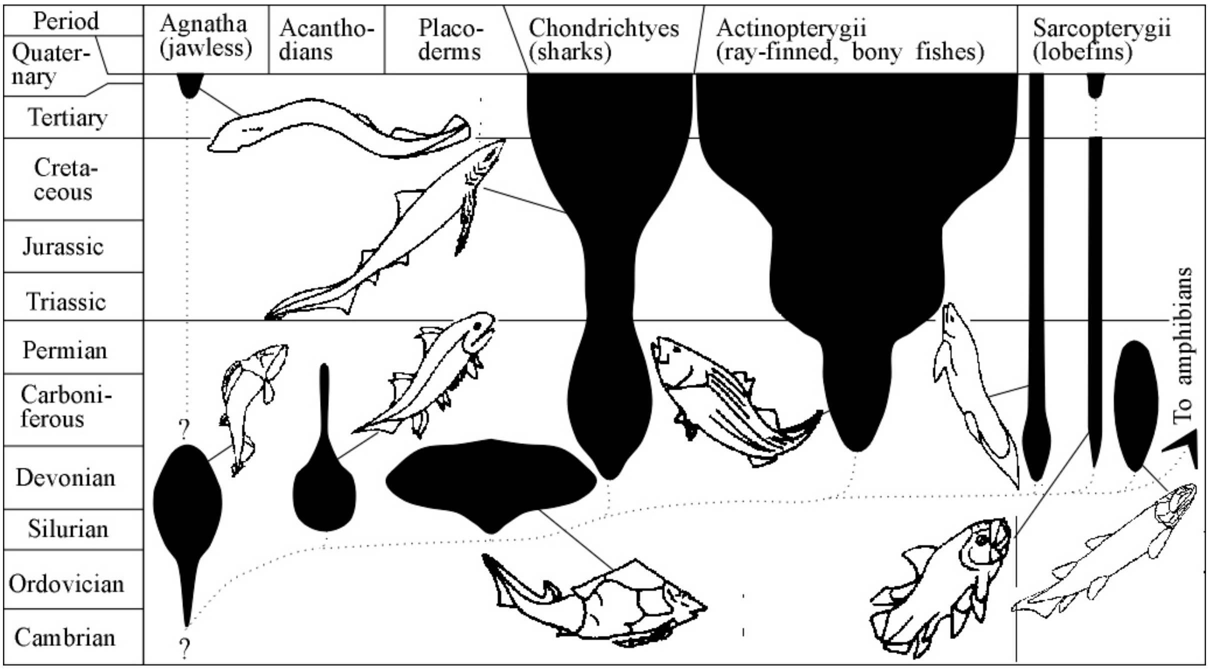
The **sarcopterygian (Subclass Sarcopterygii; Devonian-Recent)** fins are muscular and lobe-shaped with a bony skeleton, and these fish are sometimes called the **lobefins**. The pouches from the oesophagus have developed into lungs. The following three types of lobefins exist:

(1) The **lungfishes (Order Dipnoi; Devonian-Recent)** represent a very conservative lineage, and the 6 fresh water species known today (South America, Africa, Australia) are very similar to the earliest, more diverse Devonian forms. By developing lungs to breathe air, they have been able to survive in environments prone to drying out that are closed to other types of fishes.

(2) The **coelacanths (Order Coelacanthini; Devonian-Recent)** are known since the middle Devonian and were for a long time thought to be extinct, being represented by fossils only up into the Cretaceous. However, in 1938 live specimens of a single surviving form (*Latimeria*) were discovered living in South Africa (they live in the deep waters off the Comoro Islands). A research team in Stockholm had by that time just worked out the detailed internal anatomy of the fossil sarcopterygians and suddenly their results could be completely checked on a live specimen!

(3) The **rhipidistians (Order Rhipidistii; Devonian-Permian)** also mainly occur in the Devonian but survive into the Permian. They are particularly interesting, because it has been proposed that the earliest land living amphibians originated from an ancestor within this group. Thus, the strongly developed and movable paired lobed pelvic and pectoral fins would be homologous with the limbs of all subsequent land living vertebrates (including yours truly!). The rhipidistians also had strong lungs, and may have been able to crawl up on land. However, some scientists claim that the ancestor of the amphibians is to be found among the lungfishes.



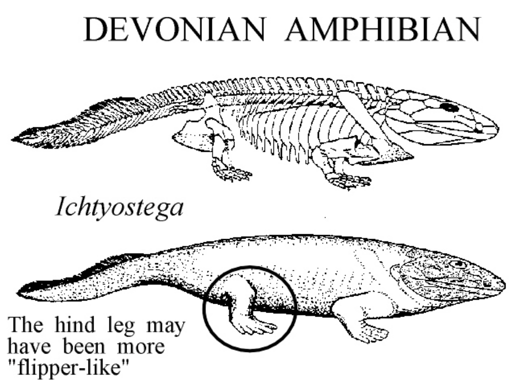


Land-living vertebrates - Tetrapods

The first vertebrates to gain a foothold on land are the **amphibians (Class Amphibia; Devonian-Recent)**. There are possible trace fossils of land-living tetrapods (**Superclass Tetrapoda**) already from the middle Devonian; the earliest known amphibians, *Ichthyostega* and *Acanthostega*, belong to the **labyrinthodonts** (from the 'labyrinth-like' teeth), and are from the Late Devonian of East Greenland. Although these metre long amphibians were capable of moving on land, it is probable that they remained in the water for most of their life; they look like flattened fishes with feet and seemingly were not adapted for an active life on land.

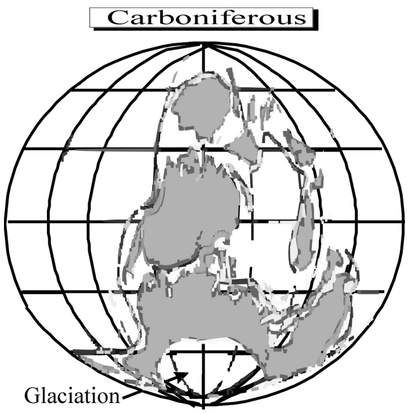
It was previously believed that the limbs of all tetrapods had five digits, but some labyrinthodonts have up to eight digits on the front limb and seven on the hind limb!

The still living amphibians (**frogs, salamanders,** and **leg-less caecilians**) are all dependent on water for reproducing, laying jelly-coated eggs in water (or other wet places). The amphibian skin is soft and moist, prone to drying out if the climate becomes too dry. Thus, they are not truly completely land-living animals. All the Recent amphibians are poorly known from the fossil record.



CARBONIFEROUS

General



The **Carboniferous period (360 - 290 million years ago)**, was defined from sequences in the coal district of north central England. The name is derived from the Latin name of coal. In the United States, this period is divided in two parts, a lower called **Mississippian** and an upper called **Pennsylvanian**. Climates were generally warm and humid, and in England and central Europe carbonate sedimentation and reefs are common in the northern parts of the Tethys Sea. During the period a major glaciation started in South Africa, and glacial environments seem to have been widely spread during some intervals.

Gondwanaland drifted northwards and in about the mid-Carboniferous, collided with Laurasia, resulting in the **Hercynian** (or Variscan) orogeny and the highlands in Bretagne, Ardennes, central Germany and Bohemia. This is the start of the Supercontinent **Pangea II**. During the later part of the period, huge equatorial swamp forests developed in the rivers and deltas of the lowlands that covered large areas of Europe and North America. As the plants died, thick organic-rich deposits accumulated which eventually turned into thick beds of coal (now stretching from North America to Russia.

Scandinavia

In Scandinavia, rocks representing this period have never been found. Apparently, the northern part of Baltica was a continent with mountains, lakes and rivers. The sediments that presumably were deposited on the Scandinavian shield have since been eroded away. In deep bore holes in southern Denmark, Carboniferous sediments have been found, comprising Early Carboniferous limestones and shales (at a depth of 400 m below surface). Towards the east, the Uralian seaway constituted a narrowing basin as the Siberian plate started to collide with the eastern margin of Baltica.

Carboniferous sedimentary rocks and environments

The Carboniferous deltas were extremely extensive and associated with the coal forests (see further below). In terms of sediment volume, deltas are very important depositional environments. A delta is formed when a river is transporting big loads of sand, silt and clay into a basin (e.g. ocean), where the velocity of the stream is rapidly decreasing. The mouth of the river soon becomes blocked and the main channel splits into smaller distributary streams. Most major deltas are situated along the open shore line, and thus under constant marine influence. Deltaic sedimentation is typically intermittent and variable. The shifting distributary streams may rapidly alter the configuration of the delta. Fluctuations in sea level and marine currents are also responsible for changes over longer periods of time. The delta is built out seawards and the stability is maintained only by the huge quantities of sediment transported from the interior of the continent. If this supply decreases, coastal erosional processes begin removing material until equilibrium is reached between removal and river supply.

The majority of the deltaic sediments consist of sand and silt sized particles. Between the distributary channels there are commonly swampy lowlands and numerous ponds. In the outer part of the delta, the silt and clay sediments accumulate to create a gently steeping delta front.

The most typical sedimentary rock of the period is **coal.** This is a type of autochthonous organic carbonaceous rock formed by the accumulation of plant matter in a swampy environment. The process of coalification may produce a series of products with increasing depth of burial (temperature and pressure) from peat (porous mass of brownish plant fragments resembling peat moss) and lignite (brown coal) to bituminous and anthraconite coal. The amount of pure carbon increases in this series. Anthracite is composed of 99% pure carbon, whereas lignite is made up of only 30%l. For coal to form, the plant tissues must be buried quickly in an anoxic environment. This occurred in the Carboniferous swamps. The Carboniferous coal deposits accumulated in so-called **cylothems** (coal cycles), which may reflect either eustatic cycles or local instability of the basin. The cycles consist of terrestrial deposits at the base, clay and coal in the middle and marine layers on top. The type of sedimentary environment represented by the coal cycles is usually called **paralic.**

The Age of Coal Swamps

During the Carboniferous, life on land diversified with origin of the first true land tetrapods – the amniotes and the diversification of insects. These land animals lived in the huge equatorial swamp coal forests that covered large areas of Europe and North America.

Typical Carboniferous Organisms

Plants

The trees of seedless vascular plants and some early seed plants dominate the Carboniferous forests. The seedless plants include the following:

(1) The **club mosses (lycopods; Devonian-Recent)** reached their highest diversity during the Carboniferous, with 25-45 m high trees like *Lepidodendron*, with closely spaced branches that gradually fell of during growth, creating distinctive leaf scars. Other examples include *Sigillaria* (up to 30 m high). Not all lycopods were of tree size; today only five small genera persist.

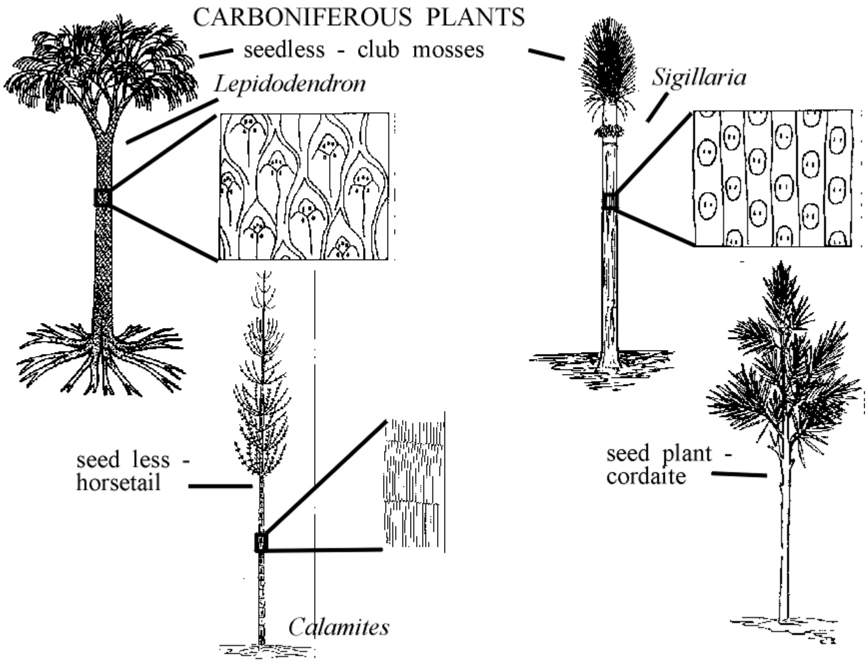
(2) The **horsetails (sphenophytes; Devonian-Recent)** were also tree-sized during the Carboniferous (up to 20 m high), including the common *Calamites*. Today a single genus survives.

(3) The **ferns (pteridophytes; Carboniferous-Recent)** were mainly small sized during the Carboniferous attaining about the same size as today, only a few forms reached tree size.

The first seed plants seem to have evolved already during the Devonian. The Carboniferous seed plants include the following:

(1) Most of the **seed ferns (Devonian-Jurassic)** are externally very similar to the ferns, but probably evolved from the progymnosperms.
(2) The **cordaites (Carboniferous-Permian)** and **conifers (Carboniferous-Recent)** both have **a cone (that is** needle-like or scale-like leaves) and were common during the Carboniferous. The former extinct group formed 30-40 m high trees with extremely long leaves, whereas the latter constitute the still living pines, spruces etc.

At the end of the Carboniferous the swamps dried out and this dramatic environmental disaster caused the extinction of the tree-sized seedless plants in the early Permian.



Land living arthropods

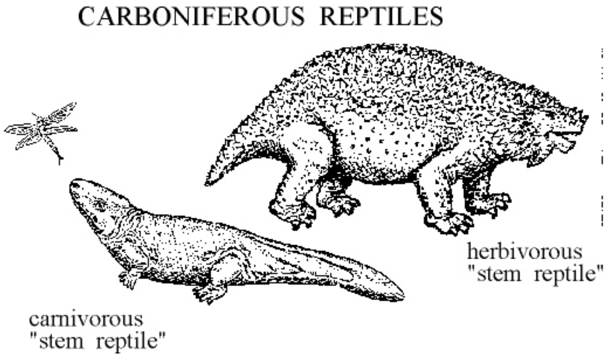
The Carboniferous forests provided new territory for land living organisms, and there is an explosion in the number of arthropods, like spiders and millipedes, but also including huge dragonflies with wingspans of about 70 cm.

Land living vertebrates

The **amphibian labyrinthodonts (Devonian-Cretaceous)** are the dominating vertebrates on land during the Carboniferous, in particular during the later parts of the period, when they abound in the humid and warm environments of the swamps that covered a large part of the earth. Some forms were several metres long and evidently active predators.

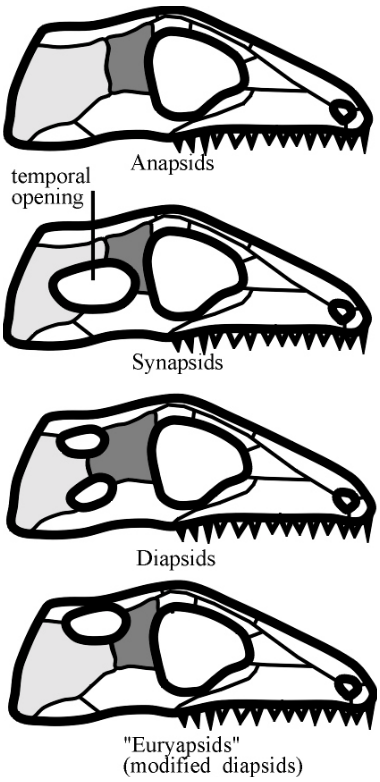
Origin of amniotes

Sometime during the Carboniferous the first **amniotes** must have evolved - the **amnion** is the fluid-filled sac in which the embryo floats in all-true amniotes (including all reptiles, birds, mammals etc.). This evolutionary break through enabled the land living vertebrates to become independent of water for their reproduction unlike the amphibians. Amniote eggs are covered by tough membrane with a leathery or calcareous outer skin, designed to allow gas exchange in order to supply the growing embryo with oxygen - nourishment is provided by the **yolk**.



Radiation of the reptiles

In addition to an amniote egg, **reptiles (Reptilia; Carboniferous-Recent)** are distinguished from the amphibians by having internal fertilisation and a scaly waterproof skin. The first reptile is from the early Carboniferous of Scotland (the popular 'Lizzie' recently purchased by the Royal Scottish Museum in Edinburgh for a huge sum of money). The evolution of the earliest (so-called **'stem reptiles'**) from their amphibian ancestor is still poorly known.



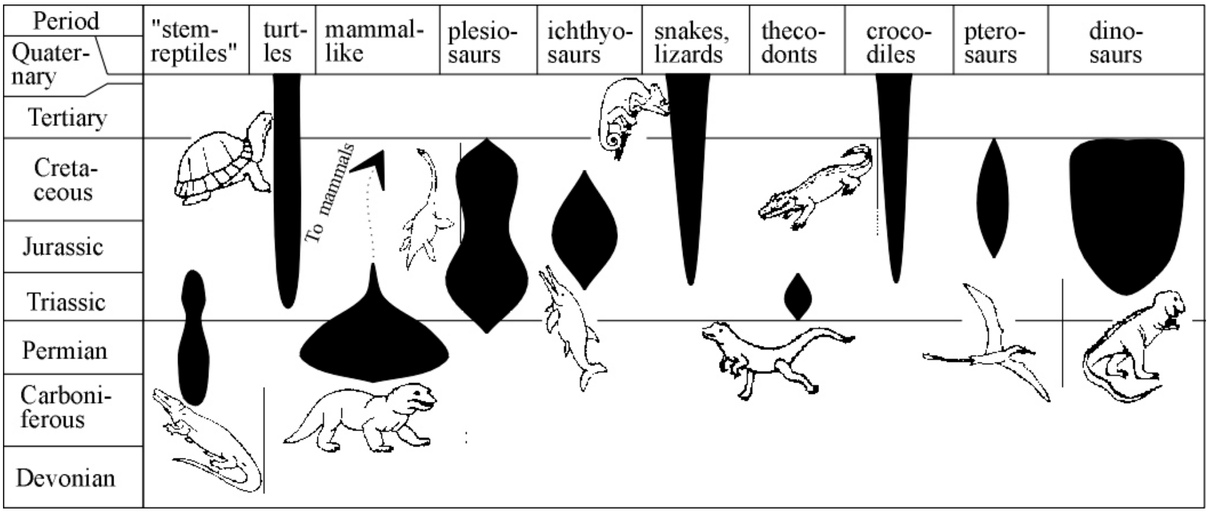
The reptiles evolved rapidly during the late Carboniferous and radiated into the following four main groups that are characterized by the morphology of the skull and the number and distribution of **temporal openings** (related to the jaw muscles) in the cheek region:

(1) The **Anapsids** represent the primitive condition in the 'stem reptiles' and lack a temporal opening - this condition is also present in the **turtles**, known since the late Triassic.

(2) The **synapsids** have a single lateral temporal opening low on the cheeks; the synapsids first appear in the late Carboniferous, and include the **mammal-like reptiles** that were ancestral to mammals.

(3) The **diapsids** have two temporal openings; this group contains all the remaining reptiles (snakes, lizards, and crocodiles) living today as well as the dinosaurs.

(4) The **'euryapsids'** have a single opening high on the cheek, but this type of skull has probably evolved several times and probably represents modified diapsids; the euryapsids include the **plesiosaurs** and **ichthyosaurs**.



PERMIAN

General

The **[Permian Period]** **(290-245 million years ago)** was defined in the area around Perm in the Ural Mountains, Russia. The last period in the Palaeozoic Era is a time of great changes in the geography of the globe. The Supercontinent Pangea II was finally completely assembled as the landmass of Gondwanaland was brought into contact with the other continents, and at the end of Permian. This completed the Hercynian and Uralian orogenies.

The majority of the epicontinental seas disappeared, with catastrophic environmental consequences (see further below). The Early Permian was a dry period with desert-like environments in Europe. Europe and North America were now located at about 20-30° N of the equator, and as the smaller seas dried up huge basins of evaporites developed. The salt deposits from this age are the most extensive from any period of the Phanerozoic. A shallow marine basin was centred in the North Sea and central Germany dried up and was again covered by waters in cycles. This resulted in evaporite sequences of gypsum, anhydrite, dolomite and rock salt (halite). The climate shifted rapidly, with glaciations on the Southern Hemisphere.

Scandinavia

Rocks from the Permian period are scarce in Scandinavia. In Sweden, there are no sediments preserved at all; all rocks of this age are of volcanic origin (e.g. dolerite dykes capping the Palaeozoic sequence in Västergötland). In the Oslo district, sediments accumulated in a basin with fresh water environments (containing plants and molluscs), and were later covered by volcanic rocks.

Permian sedimentary rocks and environments

Desert-like environments were typical for the Permian. Today about 20% of the Earth's surface may regarded as deserts. About 25 % of the desert areas are classified as sandy. During rare events stones and gravel can be transported in flush floods and by debris flows, but the main transport is by the wind (**aeolian**). The windblown sand fraction is very well sorted with an average grain size of 0,2 mm. Grains of this size are transported in a jumping pattern termed **saltation**. Frequent collisions create a pronounced roundness and a surface which is frosted, that is whitened by microscopic marks of impact. Ancient desert deposits like those of the Permian are frequently well preserved, showing structures of wind ripples and cross bedding. Old desert sandstones are often red and brown in colour, due to ferric oxides on the grain surfaces. Most of the gas in the southern North Sea is trapped in the Permian aeolian sandstones.

The arid Permian sedimentary environments also commonly include the economically important **evaporites**. Evaporites are chemically formed rocks deposited in an arid to semiarid areas (where the annual precipitation is lower than evaporation). Fossil evaporites are thus good indicators of palaeoclimate. They almost invariably formed in around 30° from the equator. Restricted marine basins with extensive tidal areas and shallow waters are essential factors for forming evaporites. Important evaporite minerals include **gypsum**, **anhydrite**, **halite**, and **potassium/sodium salts**.

Today evaporites accumulate e.g. around the Persian Gulf and the Bay of California. Larger and more extensive tidal flats with evaporates are termed **sabkhas**. Fossil salt tend to plastically flow upward due to the lower density. This commonly creates structures called diapirs. Under pressure, salt behaves like a viscous fluid and the movement of the salt causes the arching of the overlaying strata, leading to faults and dome structures. Such structures are sometimes excellent traps for petroleum (e.g. Mexican Gulf).

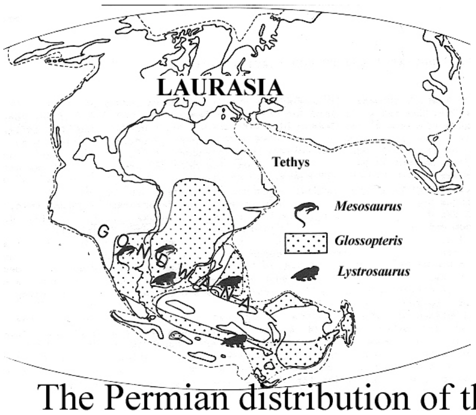
The Earth's Greatest Ecological Disaster

The end of the period coincides with the end of the Palaeozoic Era, is marked by the greatest extinction event in earth's history, in which well over 90% of the species on earth may have been wiped out. Most scientists agree that the catastrophe was due to the combination of many extreme environmental factors including: (1) the formation of Pangea and the associated glaciations causing dramatic sea level fall and loss of most shallow marine habitats, and formation of huge deserts in the continental interiors, (2) large scale volcanic activity affecting the global climate, (3) a drop in the level of atmospheric oxygen. On land most amphibians and reptiles became extinct and in the seas all the rugose and tabulate corals disappeared completely along with the trilobites. Other groups, including crinoids, rhynchonelliformean brachiopods and cephalopods where dramatically reduced. The typical Palaeozoic benthic sessile communities were wiped out and replaced by an essentially modern type of community with mobile molluscs, arthropods, and echinoderms.

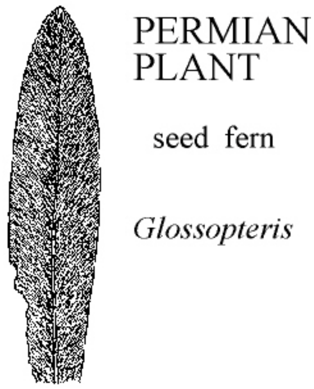
Typical Permian Organisms

Plants

The rich Carboniferous forests persisted for a time into the Permian, but eventually disappeared and the tree-sized lycopods, horsetails, and cordaites became extinct. The flora of the Southern Hemisphere was dominated by the so-called ***Glossopteris*-flora** (which was important for the development of the theory of Plate Tectonics – see figure below), named after an abundant seed fern; it also included conifers and several different types of ferns. Conifers dominated the flora of the Northern Hemisphere.

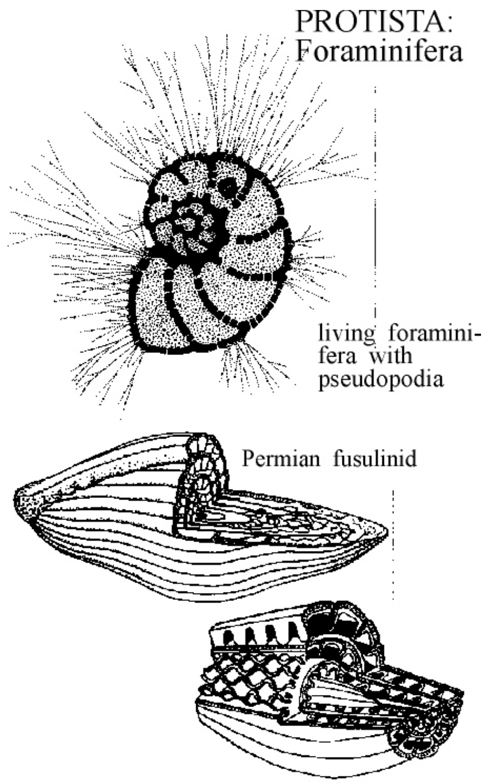


The Permian distribution of the *Glossopteris* flora and associated faunas were important in the discovery of Pangea



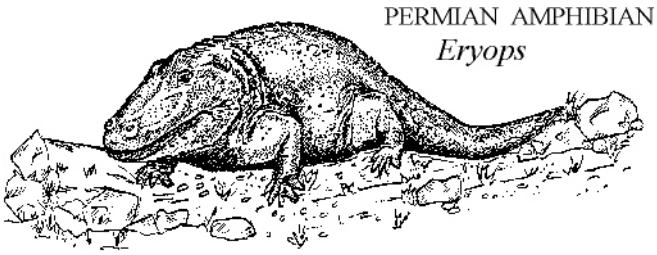
Invertebrates

The trilobites were drastically reduced in number and importance and eventually died out completely at the end of the period. The brachiopods and crinoids were important parts of the benthic fauna through the period; they were dramatically reduced in number during the Permian extinction, but survived into the Mesozoic. Ammonoids became important faunal elements and are vital for biostratigraphy. During the period, most groups of modern insects first appear.



Protistans

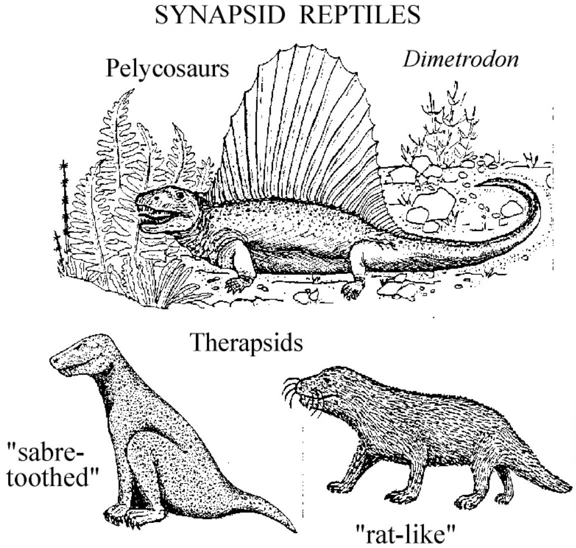
The single-celled **Foraminifera** **(Cambrian-Recent)** became important and diverse for the first time during the Carboniferous-Permian interval, when they are important biostratigraphic and environmental indicators. The Foraminifera were previously considered to be 'protozoan animals', but are now placed in the **Kingdom** **Protista** (sometimes within the **Phylum Sarcodina**). They secrete a test of calcium carbonate or build their skeleton from various sand grains. The test is commonly perforated (giving them their name). The **pseudopodia** are small temporary extensions from the **cytoplasm** used for building the test, locomotion, and feeding.



Foraminifera live in marine conditions; most are bottom living, but some are planktic. The planktic forms appear only since the Jurassic. During the Carboniferous-Permian, the large-shelled **fusulinids** were particularly important, but this group died out at the end of the Permian.

Vertebrates

Amphibians, like *Eryops*, continued to be prolific into the early Permian, but they were drastically reduced in numbers in the later parts of the period, perhaps due to increased competition with the reptiles that became the dominating group. The vertebrate fauna included also many primitive reptiles ('stem reptiles'), but was dominated by the mammal-like reptiles.



Mammal-like reptiles

Already during the late Carboniferous, the first synapsid mammal-like reptiles had evolved. The earliest forms belong to the familiar **'sail-backed reptiles',** the **pelycosaurs (Carboniferous-Permian),** like *Dimetrodon* (usually quite incorrectly sold in 'dinosaur' kits!). The most interesting characters of the mammal-like reptiles are the teeth, which unlike those of reptiles are varied in size and shape, including long mammal-like canine teeth for stabbing. The distinctive pelycosaur sail (which many of the pelycosaurs did not have) may have had a function for regulating the temperature of the animal.

Therapsids (Permian-Triassic) are mammal-like reptiles, some of which may have been **endothermic** ('hot-blooded') that is, they had the ability to control their body temperature. Some of the therapsids were large predatory animals with skulls 50-80 cm long, and sabre-tooth-like canines, but others were small and rat-like and may have had a hairy body. It is likely that the **true mammals** evolved from an ancestor within the latter group. Most of the mammal-like reptiles were wiped out in the Permian extinction.

THE AGE OF REPTILES – MESOZOIC

TRIASSIC

General

The first period of Mesozoic is the Triassic Period **(245-210 million years ago)**. Geologically it is a calm period, with no major orogenies. Pangea grew to its maximum size, divided by the **Tethys Sea** between the northern **Laurasia** and the southern **Gondwanaland** continents. The splitting up of Pangea may have started at the end of the period resulting in the separation of Laurasia and Gondwana. No polar glaciations occurred and the general climate was generally warm and dry.

The type area is in central Germany, where three distinct sedimentary stages are developed, the **Buntsandstein**, **the Muschelkalk**, and **the Keuper**. Of these the Muschelkalk is the only marine interval, comprising shales, dolomite and limestones. The Keuper is an arid interval with continental deposits of sands, fine clastics and locally evaporites. This tripartite division gave the period its name. In southern Europe, the Triassic consists solely of marine rocks, and was deposited in the northern Tethys with reefs of a more modern type than in the Palaeozoic.

On the American part of Pangea vulcanism occurred mainly in the west, facing the great ocean **Panthalassa**. This vulcanism with volcanic arcs colliding with the continent continued through the Mesozoic.

Scandinavia

Sediments of Triassic age are found in western Scania, and there are also some Late Triassic rocks on the island of Bornholm. In Scania, the Early Triassic deposition included fluvial sediments (mixtures of sand, silt and clay), whereas terrestrial conditions prevailed during mid-Triassic. The Late Triassic rocks comprise coarse arkoses and conglomerates, called the Kågeröd Beds. These turn into deltaic, lacustrine, and swamp-like conditions at the very latest stages of the Triassic in Scania resulting in clays and coal beds with numerous plant fossils.

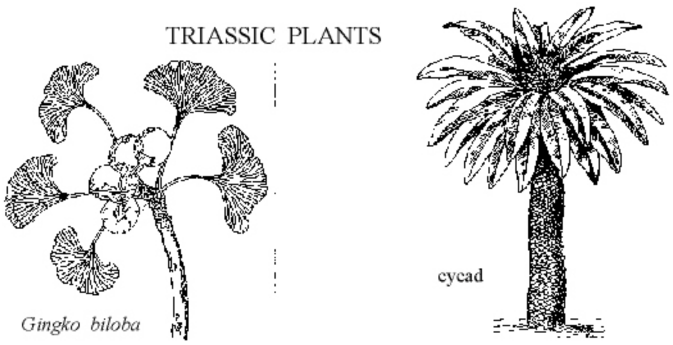
The Reptile Triumph & Dawn of the Dinosaurs

After the Permian extinction the recovery of the earth's fauna was fairly slow during the Triassic. In the land faunas, the much reduced, but still dominating synapsid therapsids show increasingly mammal-like features, while the diapsid reptiles gradually increase in diversity to become the dominating vertebrates during the later part of the period. Many of the labyrinthodont amphibians died out during late Triassic, and the first modern-type amphibians (frogs) appeared.

Typical Triassic Organisms

Plants

The land plants include many conifers and ferns along with the **cycads** **(Permian-Recent)**, which are palm-like trees, usually with short trunks, but some are up to 10 m high. The male and female flowers are placed in cones. The Recent cycads live in tropical and subtropical areas on the earth. The **ginkgo-trees** are first known from the Permian and are common



during the Triassic; some fossil ginkgos are very similar to the living species *G. biloba*.

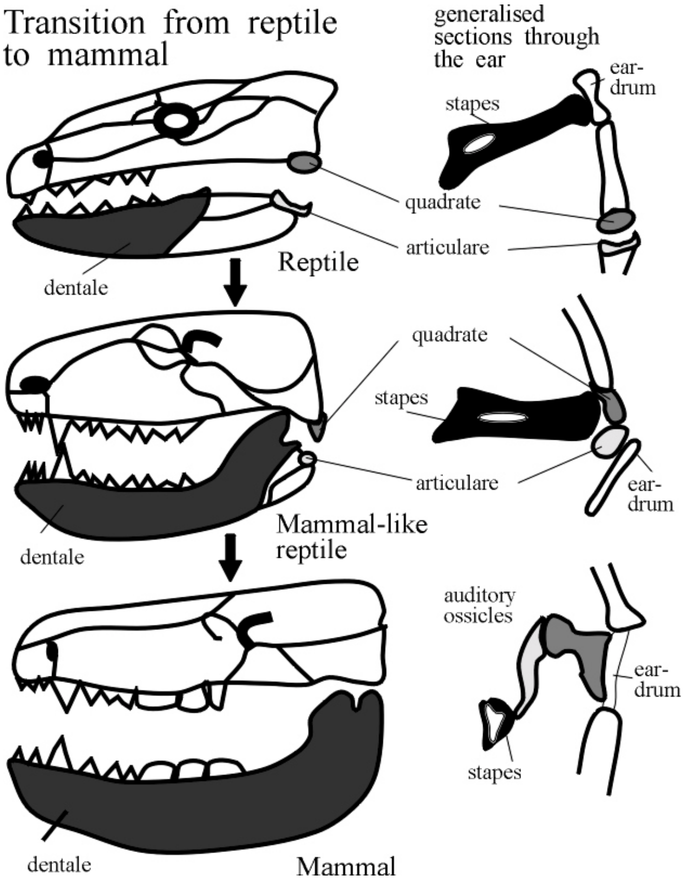
Invertebrates

Among the arthropods, the insects and the crustaceans became the dominating groups in the Mesozoic, and the latter replaced the trilobites in their habitats. Among the molluscs, the ammonoids were badly hit by the Permian extinction, but rapidly recovered to become a diverse and important group, which is important for biostratigraphy throughout the Mesozoic. Bivalves and gastropods also go through rapid diversification. Among the cnidarians, the modern-type corals replace the tabulate and rugose corals, the **scleractinians**.

The first mammals

The Recent mammals are characterized mainly by having: (1) mammary glands & care for their young, (2) endothermic thermoregulation, and (3) hairy body. However, these characters are generally not observable in fossils. The first true **mammals** **(Mammalia; Triassic-Recent)** are rat-sized forms from the late Triassic of Europe and China. It is almost certain that they evolved from a group of therapsid reptiles and the exact point at which they turned into mammals is usually decided on the basis of jaw structure.

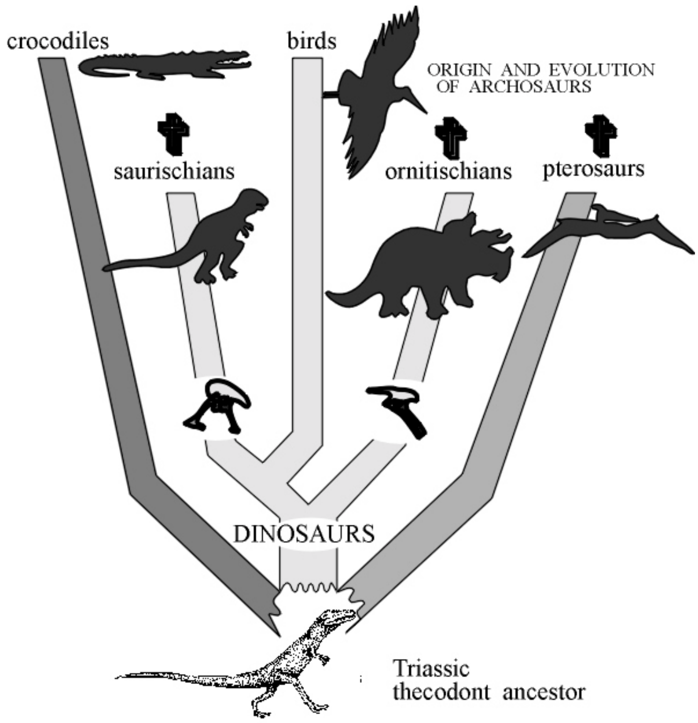
The lower reptilian jawbone is made up of several different bones, while that of the mammals consists of a single bone - the dentale. In the evolutionary transition from a reptilian to a mammalian jaw, the bones involved in forming the jaw joints change position and function in a gradualistic way. In the reptiles the lower jaw has the socket of the joint (articulare) receiving the tooth-like projection (quadrate) from the skull, whereas the mammalian joint consists of a socket (squamosal) in the skull and the tooth (dentale) projects from the lower jaw. In some transitional therapsid forms both joints seem to be functional, whereas in the true mammals, the two bones of the reptilian jaw joints have been transformed into the bones in the ear. During the entire Mesozoic, the mammals remained a small and fairly insignificant group, living as they were 'in the shadow of the dinosaurs'. It is likely that the three main groups, the **monotreme** (including the egg-laying Australian duck-billed platypus), **marsupial**, and **placental** mammals diverged from each other at an early stage, but the details



of this evolution are poorly understood.

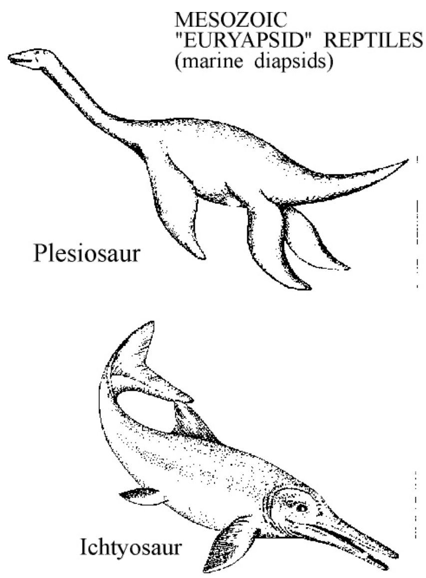
Diapsid reptiles - first dinosaurs

Although the earliest **diapsid reptiles** are known from the Carboniferous, they became dominant only since the late Triassic. The diapsid ancestors of the living **snakes** and **lizards** diverged from other diapsids - the **archosaurs** - already during the Permian. Some of the most important Triassic diapsids were the archosaur **'thecodonts'**, like *Eupakeria* - a small (about half a metre long) reptile that may have been able to run both on all four legs and upright. A 'thecodont' ancestor probably gave rise to the **crocodiles,** dinosaurs (and birds), as well as the **flying reptiles, the pterosaurs**. Some of the first dinosaurs (*Herrerasaurus* and *Coelophysis*) are known from the late Triassic of South and North America. In Europe, the best-known late Triassic dinosaur is the **prosauropod** *Plateosaurus* - a bipedal to quadruped form that may be related to the Jurassic-Cretaceous sauropods. In Sweden, Plateosaurus may have made late Triassic dinosaur footprints from Scania.



‘Euryapsid’ reptiles

The Triassic sea was dominated by various types of **‘Euryapsid’ reptiles** (having secondarily returned to life in water), including the earliest **ichthyosaurs** and **plesiosaurs**; both were predatory and became more abundant during the Jurassic and Cretaceous. The ichthyosaurs represent a typical example of convergent evolution, being similar in shape to both fish and dolphins; some late Triassic ichthyosaurs may be 15 m long. The plesiosaurs became dominant first in the Jurassic.



JURASSIC

General

The type area of the **Jurassic Period (210-145 million years ago)** is in the Jura Mountains, France. During this period, the supercontinent of Pangea began to disintegrate. The first rifting phases took place in the South Atlantic. The first phases of rifting between Africa and America occurred in the area of the Mexican Gulf region, associated with extensive evaporites in the Early and Middle Jurassic. By the middle and late part of the period, Laurasia and Gondwana were completely separated by the Tethys Sea. The climate generally became moister as compared with the Triassic but, during the early and middle parts, huge deserts covered many parts of Pangea. Warm climates may have extended almost into the polar regions.

During the Early Jurassic, sea levels started to rise and much of North America was again shallow seas. Bordering this sea deltas and swamps developed, now preserved as the Morrison Formation. In these environment dinosaurs and other Mesozoic land animals lived, and this is one of the riches localities for dinosaurs fossils.

In Europe, the Jurassic is divided into Liassic, Dogger and Malm. The Liassic consists mostly of shales and mudstones associated with a transgressive sequence usually containing a rich fossil fauna of Mesozoic marine life. The sea level was highly fluctuating in the Dogger, which is associated with sands and iron oolites (forming important iron ores). The Late Jurassic Malm, again is a transgressive sequence with numerous fossiliferous calcareous deposits

Scandinavia

In southern Scandinavian, there is a continuous succession across the Triassic-Jurassic boundary, i.e. the Triassic pattern of sedimentation with sand, mudstones and coal deposits continued into the Jurassic. The Jurassic deposits in Scania are mostly confined to the areas of Höganäs, Ängelholm and Fyledalen. Early Jurassic (Liassic) sediments are also known from Bornholm. Like in the rest of Europe the Middle Jurassic (Dogger) sometimes contains iron oolites. During the Middle Jurassic (Dogger), volcanic activity occurred in central Scania, with the formation of basalts. The Late Jurassic (Malm) is characterised by a mixed sedimentation in Scania and Denmark, with deposition of sands and shales in an environment with deltas and lakes.

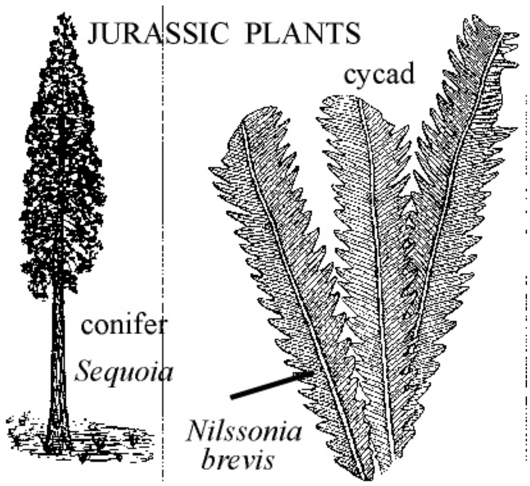
The Heyday of Dinosaurs

The Jurassic seas were teeming with marine reptiles including ichthyosaurs; the largest marine predators were the swan-necked plesiosaurs. Although the dinosaurs quickly became the dominating group of land living animals, we know relatively little about the early and middle Jurassic fauna, partly through lack of investigation and lack of exposures representing suitable environments.

Typical Jurassic Organisms

Plants

The Jurassic land plants include the same groups as during the Triassic but, the conifers (like *Sequoia*) and cycads are notable; some palaeobotanists call the Jurassic 'the age of cycads'. A typical Jurassic cycad (*Nilssonia brevis*) is known from the Höör Sandstone in Scania (the cathedral in Lund is built entirely of this type of rock).

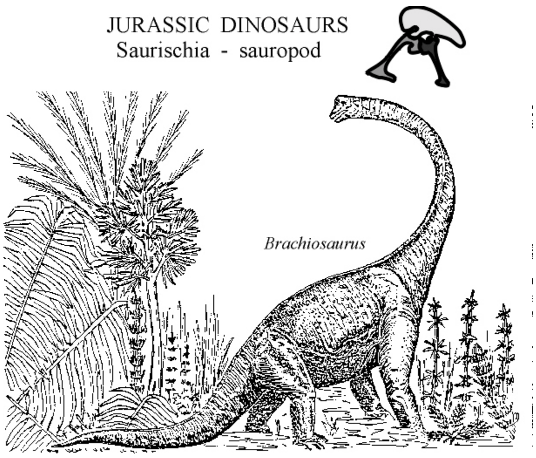


Dinosaurs

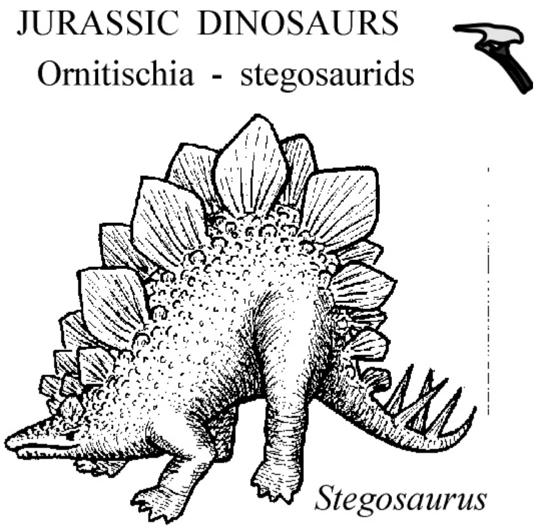
Most importantly, the **dinosaurs** **(Triassic-Cretaceous)** are distinguished from other reptiles mainly by their upright posture, where the limbs are held straight under the body. Living diapsid reptiles (like crocodiles) are all characterized by a sprawling gait, with the limbs held out from the body, but clearly this would not have been a workable solution for supporting gigantic land living dinosaurs. The dinosaurs are traditionally divided into two main groups: (1) the **Saurischia** **(Triassic-Cretaceous)** or **'lizard hips'**, having the three bones in the **pelvis** radiating in different directions like most lizards and (2) the **Ornithischia** **(Triassic-Cretaceous)** or **'bird hips'**, having the two lower pelvic bones parallel, pointing backwards like in the birds. The **saurischians** can be divided into two main groups: the **theropods** and **sauropods**.

The **theropods** or 'beast feet' were entirely predatory and bipedal dinosaurs most of which probably could run at some speed; they also may have had some of the most sophisticated brains of any dinosaur. During the Jurassic, great many different types of theropods existed, including the supposed 'poison-spitting' *Dilophosaurus* of 'Jurassic Park' fame! Other groups of theropods became even more important during the Cretaceous.

The **sauropods** or 'lizard feet' were entirely herbivorous and quadruped dinosaurs, and include the largest land living animals of all times, some, of which (*Brachiosaurus*) may have weighed around 55 tons (but unrealistic claims for as much as 190 tons have been made for other sauropods!), attaining lengths of 40 m. A stocky body supported by pillar-like legs with long tails and necks and a small, very lightly built skull characterizes them. Sauropod skulls are usually poorly preserved or not preserved at all - the skull of the Chinese *Eohelopus* in Uppsala is a rare example! For a long time the sauropods were considered to be aquatic animals since the legs supposedly could not have carried their weight. It is now clear, however, that all dinosaurs were land living animals, proven among other things by the finding of sauropod footprints. The sauropods reached their maximum diversity at around the Jurassic-Cretaceous transition with well-known forms like *Apatosaurus*, *Diplodocus* etc.



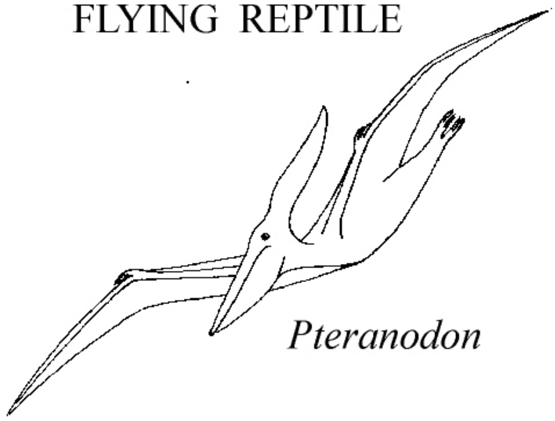
The **ornithischians** were entirely herbivorous dinosaurs, including both bipedal and quadruped forms. In the Jurassic, the ornithischians were comparatively rare. The most important were the bipedal **ornithopods** or 'bird feet'; the group originated during the early Jurassic and was some of the last dinosaurs to become extinct in the Cretaceous. Most early ornithopods were relatively small (around 1 m long) bipedal forms, some of which were probably good runners. The most famous Jurassic ornithischians are the **stegosaurids** including the late Jurassic *Stegosaurus* from North America. The stegosaurids are 'clumsy-looking' 6-7 m long quadruped animals with small skulls, supposedly having the smallest brains (size of a walnut!) of any dinosaur. On its back it had two rows of plates that may have had both defensive and thermoregulatory functions; in addition, it had intimidating spikes on the tail.



Flying reptiles

The **pterosaurs** **(Triassic-Cretaceous)** or 'winged reptiles' were probably derived from a thecodont ancestor, but the earliest evolution of the group is poorly known; they became common only after the Jurassic. The early pterosaurs had a long tail, which was reduced in later forms. The extremely elongated fourth finger supported the flight membranes of the wings. The skeleton was very light and thin with an enlarged skull; the short legs were poorly adapted for walking and it is now generally agreed that most if not all pterosaurs were active flyers. Moreover, some fossil findings indicate that some of them had a hairy body and may have been endothermic. The late Cretaceous pterosaurs include the largest flying organisms of all time, with the well-known *Pteranodon*, having a wingspan of up to 8 m and the less well-known *Quetzalcoatlus*, with a wingspan of perhaps 10 m (the size of small private plane!).

FLYING REPTILE

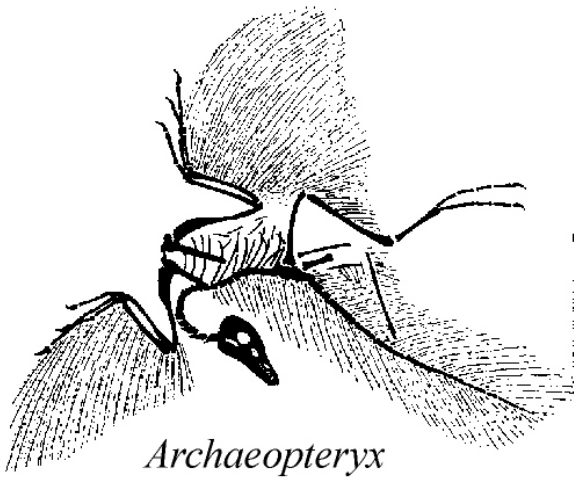


Pteranodon

The origin of birds

The earliest known **bird** **(Aves; Jurassic-Recent)** is ***Archaeopteryx*** from the late Jurassic (Solnhofen) of Germany; the six known skeletons (about the same size as a crow), some with preserved imprints of feathers, show a curious mix of reptile and bird-like characters, representing one of the best examples of a so-called 'missing link'. The bird-like characters include the feathers and the 'wishbone' (fused clavicles), whilst the teeth and the long tail are reptilian in appearance. It seems fairly certain that *Archaeopteryx* could fly, but the exact way in which flight may have originated is much disputed. There are also many contrasting views as to the origin of the birds, but for a long time it was generally thought that birds originated from an ancestor during the Triassic. Findings of small bird-like theropods (e.g. *Deinonychus*) with a light hollow skeleton have shifted the opinion of many scientists to support a dinosaur origin, but there is no general consensus on the matter. A Triassic finding of a supposed fossil bird would probably contradict the dinosaur origin, but these fossils are very poorly preserved and their interpretation is problematic. By the late Cretaceous many modern types of birds had originated and in Scania, flamingo-like forms have been found.

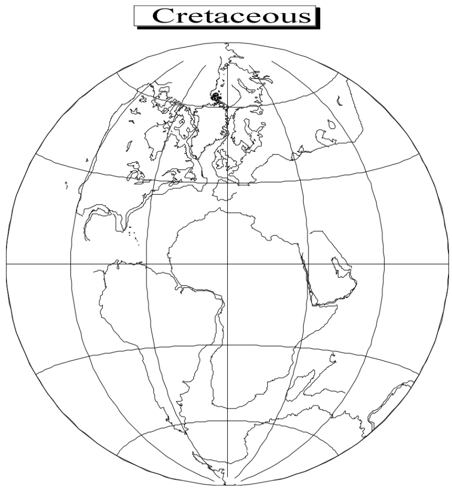
JURASSIC BIRD



Archaeopteryx

CRETACEOUS

General



The **Cretaceous Period** **(145-65 million years ago)** has the longest duration of all Phanerozoic periods. It was first defined on basis of sequences in the Paris Basin, France. As Gondwanaland was fragmented, the Atlantic Ocean started to form. The result was that land living animals no longer could spread across all continents. The climate generally became warmer and moister producing a greenhouse-type effect, resulting in the complete lack of polar ice caps and a general rise in the sea level. The global sea levels were the highest since the mid-Palaeozoic, and like then marine sediments became dominating on all continents. Epicontinental seas covered large areas of Europe, North Africa, Siberia, Australia and the interior of North America. The North American Sea was called "the interior seaway".

During the Cretaceous, Baltica and Laurentia were still connected in the north, but an open ocean basin existed in the mid Atlantic region. In the western part of Laurentia, orogenic movements occurred throughout the whole period. Chains of volcanic islands and "micro plates" were added to the western part of the Laurentian continent creating a series of orogenic episodes. The Cordillera Mountains formed as a result. The Gondwanaland continent continued to break up: the Indian continent drifted towards the north in the central Tethys. In the South Atlantic, the rift between South America and Africa widened. Antarctica and Australia were united still connected, but started to become separated from the main landmass of Gondwanaland.

In Europe, the Cretaceous can be divided into an Early and a Late part, with notable differences in sedimentation. The Early Cretaceous is dominated by continental sands, muddy sediments and marls, while the Late part of the period is dominated by the typical Cretaceous **chalk** limestones (from which the name of the period is derived), composed almost entirely of the microscopic tests of coccolithophores (see further below).

Scandinavia

In Sweden, Cretaceous sediments are only preserved in Scania. In Denmark, outcrops are limited to northern Jylland and Sjaelland. In the Early Cretaceous transgression, coastal deposits of sand, marls, and **greensand** (almost entirely made up of grains of dark green **glauconite**) are found in Höganäs, Bornholm, Kristianstad and east along the coast of Blekinge. During some of the Cretaceous transgressive episodes all of Scania and southern Halland were submerged. This was not entirely depending on eustasy, but also on tectonic block faulting. In the Late Cretaceous, the sea became deeper and the sedimentation of chalk limestone with flint (amorphic silica) started. In Denmark, the chalk now forms extensive erosional cliffs (=klint).

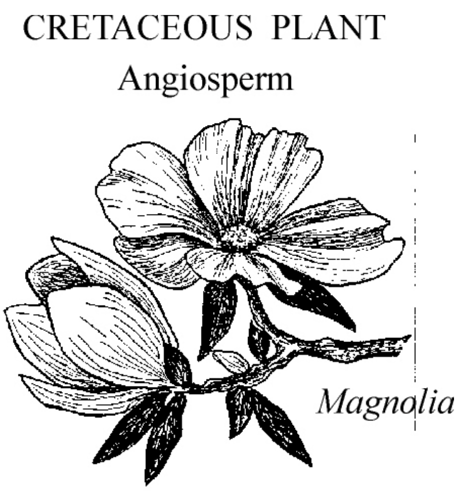
The Death of the Dinosaurs

The end of the period, coinciding with the end of the Mesozoic Era, is marked by the second largest but most famous extinction event in earth's history. On land all dinosaurs and pterosaurs became extinct along with some types of birds and some mammals, but it is difficult to find a corresponding pattern of extinction among the plants. In the seas, all the euryapsid plesiosaurs disappeared along with all the ammonoids and marine lizards, as well as several groups of protists, fish, and brachiopods; the ichthyosaurs had already become extinct earlier in the Cretaceous. However, most groups of molluscs, amphibians, turtles, and lizards apparently were not affected by the extinction event. The belemnites survived but became extinct during the early Tertiary. The cause of the so-called **K-T extinction** has been one of the most hotly debated questions in earth science and innumerable theories have been proposed. The more serious theories can be divided into two types: (1) catastrophic models, involving both extraterrestrial (meteorites) and terrestrial causes (like vulcanism), and (2) gradualistic models (decline from long-term climatic changes and ecological collapse). Most of the attention has naturally been concentrated around the extraterrestrial models, and a growing body of evidence indicates that a large meteorite may have hit the earth at around the K-T boundary. As with the Permian extinction, however, it is unlikely that the K-T event can be explained by a single factor.

Typical Cretaceous Organisms

Plants

Among the land plants, the seed ferns died out, but in general the early and mid-Cretaceous flora is similar to that of the Jurassic and dominated by cycads and ginkgos; the conifers also continue to be important. The most important event is the appearance of the flowering plants, the **angiosperms** in the early Cretaceous, and they go through an explosive diversification, and become dominant already by the late Cretaceous. Darwin called the rapid appearance and dominance of the flowering plants 'an abominable mystery'! This rapid diversification is almost certainly closely tied to the equally explosive diversification of the insects. At the end of the Cretaceous, the



angiosperms made up about 95% of the flora. The living Magnolia represents one of the oldest types of angiosperms, but trees like the oak and birch are also known from the Cretaceous.

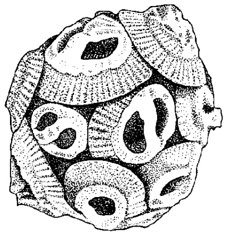
Algae

The Cretaceous Period derives its name from a type of sedimentary rock called 'chalk', essentially limestone made up almost entirely of the calcitic plates from a group of microscopic unicellular calcareous algae, the **coccolithophores**.

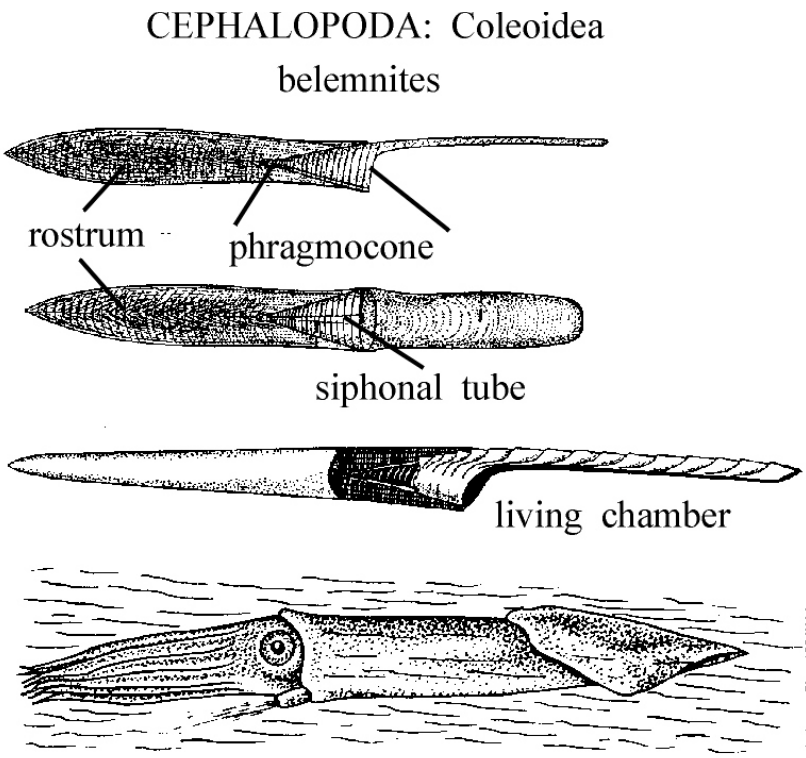
Belemnites

CALCAREOUS ALGAE

coccolith



The **belemnites (Carboniferous-Tertiary)** became abundant in the Cretaceous seas; they are considered to be members of the living cephalopod **subclass Coleoidea (Carboniferous-Recent)**. In the belemnites, the shell was not external like in the nautiloids and ammonoids, but entirely embedded in the soft tissues of the mantle. The shell consisted of an external cigar-shaped part called the **rostrum**. The anterior part of the rostrum contained a reduced chambered section, called the **phragmocone**, which corresponds to



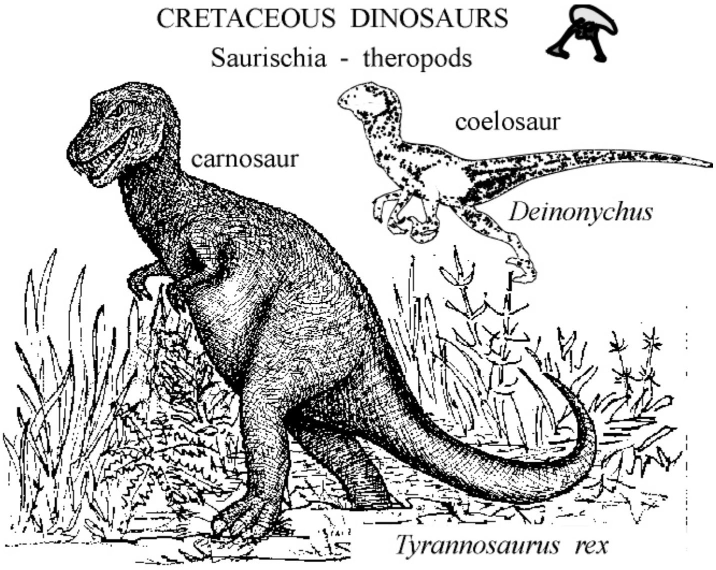
reconstruction of belemnite

the chambered shell of a nautiloid.

Dinosaurs

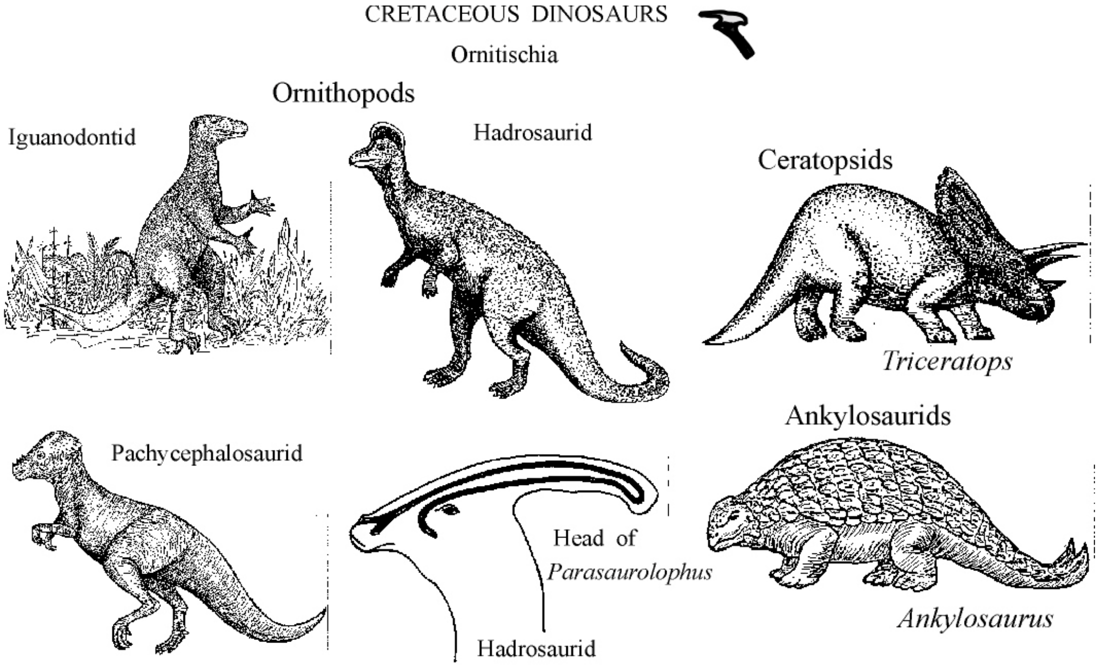
The Cretaceous predatory theropods include two groups, the **coelosaurs** and **carnosaurs**, both with a bipedal posture. The latter includes the most-famous-of-all-dinosaurs, the late

Cretaceous ***Tyrannosaurus rex***, attaining a length of 15 m and weighing about 15 tons. The skull of *T. rex* is extremely powerful with robust jaws and an impressive dentition. The strong hind legs are provided with three toes, but the front legs are small, and possibly of use mainly



in the process of regaining a bipedal position. *T. rex* is possibly the largest land living predator of all time! The coelosaurs are a group of mainly Cretaceous theropods that are lightly built and bird-like; they include the famous clawed 'raptors' like *Velociraptor* (from 'Jurassic Park') and *Deinonychus* (the name means 'terrible claw') that were important in the development of the idea that birds may have evolved from an ancestor within this group.

The ornithischians radiated and became very diverse in the Cretaceous. Common late Jurassic - early Cretaceous ornithopods include the well-known **iguanodontids** - *Iguanodon* was the first dinosaur to be described scientifically in 1825, and numerous complete skeletons have been found in Belgium; it is now one of the best-known dinosaurs. *Iguanodon* probably was mostly quadrupedal, with a very characteristic spiked thumb. Other ornithopods include the 'duck-bills', the **hadrosaurids** - a very diverse bipedal group that had flattened jaws, giving them their distinctive appearance; most hadrosaurs had very characteristic crests on their skulls, like the extremely elongate one of *Parasaurolophus*, containing canals from the nostrils. Uppsala palaeontologist Carl Wiman (1930) proposed that the shape of the crest and the canals might have been used for making sounds. Unique findings of hadrosaur nests (*Maiasaura*) indicate a previously unsuspected complex parental behaviour. The **pachycephalosaurids** are a small group of late Cretaceous bipedal ornithopods with characteristic thick skulls that may have been used in butting combats. The ornithischian **ceratopsids** (e.g. *Triceratops*) are also a late Cretaceous group that is mainly known from North America. The ceratopsids were mainly quadrupedal and are characterised by an enlarged skull; usually bearing pronounced horns and a bony frill. Another group of quadruped dinosaurs were the 'Mesozoic tanks' - the **ankylosaurids**. In the late Cretaceous, this group includes some extremely well protected forms like the 9-m long *Ankylosaurus* with its spinose back and powerful tail club.



Dinosaur biology

Since the dinosaurs are reptiles, they have usually been considered to be unable to control their body temperature internally - that is they were **ectotherms** ('cold-blooded'). During the past 20 years some scientists have argued that many or most dinosaurs were **endothermic** ('warm-blooded') like mammals and the possible direct ancestors of the dinosaurs - the birds. Most importantly the following evidence have been used in the debate: (1) the theoretical speed of some of the ornithopod raptors implies they may have been able to run much faster than any living cold-blooded reptile, (2) the bone histology of dinosaurs indicates that the rate of metabolism may have been higher than that of living reptiles, (3) the feathers in the earliest bird *Archaeopteryx*, indicate that it was endothermic and thus probably evolved from an endothermic dinosaur ancestor, (4) the findings of dinosaur nests indicates that the social behaviour was more complicated than that of living reptiles.

THE AGE OF MAMMALS - CENOZOIC

TERTIARY

General

Like the previous period, the **Tertiary** **(65-1.6 million years ago)** was also defined in the Paris Basin, and the name is a remnant of an older quadripartite geologic time scale (with primary, secondary, tertiary and quaternary). The Tertiary is a time of very intensive tectonic movements. Ocean basins are rapidly forming and orogenies are common as the continental plates gradually started to move to the positions they have today. The Atlantic Ocean widened. South America and Africa split apart in mid Cretaceous and in earliest Tertiary (Eocene); the rift zone between Scandinavia and Greenland became active. Intense vulcanism with basalts is known from Scotland, Greenland and Svalbard. On Iceland, the oldest rocks are also from the Eocene.

On the southern hemisphere, plate movements continued and during early Tertiary, the Australian and Antarctic plate was divided by a rift zone. The Antarctic plate rotated slightly but remained near the pole. The isolation of the Antarctic had severe climatic effects - glacial conditions developed in mid Tertiary. India and South America were isolated continents for tens of million of years during most of the Tertiary. In mid Tertiary time (Oligocene), the Indian continent collided with the Asian plate, creating the Himalayas and the high plateau of Tibet. This resulted in the closure of the eastern Tethys.

At the center of Gondwanaland, Africa moved to the north, pushing several micro plates in front (e.g. Turkey, parts of Italy and the Balkan). This movement closed the western Tethys at about 15 Ma, and resulted in several orogenies and the formation of several mountain chains (e.g. the Atlas). At the same time the Caucasus was raised as Turkey and the Iranian plates collided with southern Russia.

The latest Tertiary is named the Pliocene, and during this time the climate was very much the present one. The first modern ice ages may have begun in late Pliocene.

Scandinavia

The K-T boundary is clearly marked in the Scandinavian successions (and elsewhere) by a dark layer of clay (e.g. at Stevns Klint, Denmark). This clay contains Iridium, and as mentioned below this is a strong indicator for a meteoritic impact, which may have partly caused the mass extinction at this level. In Scandinavia, however, the deposition of chalk limestone continued in the early Tertiary (Danian).

In Denmark 75% of the outcrop area is of Tertiary age. During the period, Denmark was a part of the North Sea basin. The tertiary is a regressive period in Scandinavia, characterised by a subtropical climate. The Danian Sea retreated after a few million years and a continental sedimentation was established in southern Scandinavia, with mostly sands and marls being deposited. Volcanic ashes are frequent, originating from volcanism in the Atlantic and in northern Skagerack. The ashes and clays are rich in fossils of invertebrates, insects and fishes.

During Late Tertiary, swampy conditions existed on Jylland, where much of vegetation is preserved as deposits of brown coal. In central Europe similar deposits are found in eastern Germany and Poland.

The Rise of Modern Animals

With the death of the Mesozoic forms in the sea (such as ammonoids etc) the marine fauna of invertebrates and vertebrates became essentially modern in appearance. On land the mammals started to fill the ecological vacuum left by the extinction of the dinosaurs.

Typical Tertiary Organisms

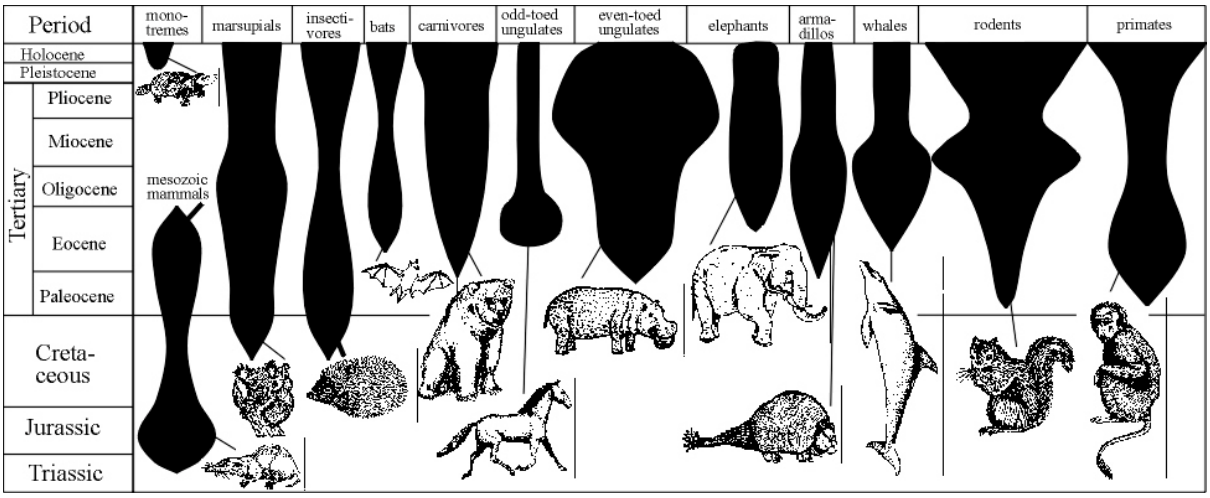
Plants

The earlier part of the Tertiary was still quite warm and most land areas were covered by lush vegetation. **Conifers** are particularly important and sometimes form coal deposits. A conifer, distributed mainly around the Baltic, produced the common deposits of amber with uniquely preserved organic remains of insects, plants etc. The angiosperms continued to radiate - the diversification of various types of grass probably was closely linked with the radiation of grass-eating mammals like horses etc. Towards the end of the Tertiary, the cooler climate resulted in a reduction in the distribution of forests.

Mammals

The two main groups of mammals both in the Tertiary and in the Recent are the **placental** and the **marsupial** mammals; the latter group gives birth to tiny live offspring that finish their development in a pouch. When the young marsupial is born it has a reptilian type of jaw, which is transformed into a mammalian jaw and three ear bones during development. In the placentals, the young are born at a much later developmental stage, and in many species the newly borns are able to fend for themselves almost directly after birth. In both fossil and Recent environments it is uncommon to find marsupials and placentals in the same geographic area - it seems that the marsupials usually were wiped out in the competition with placentals.

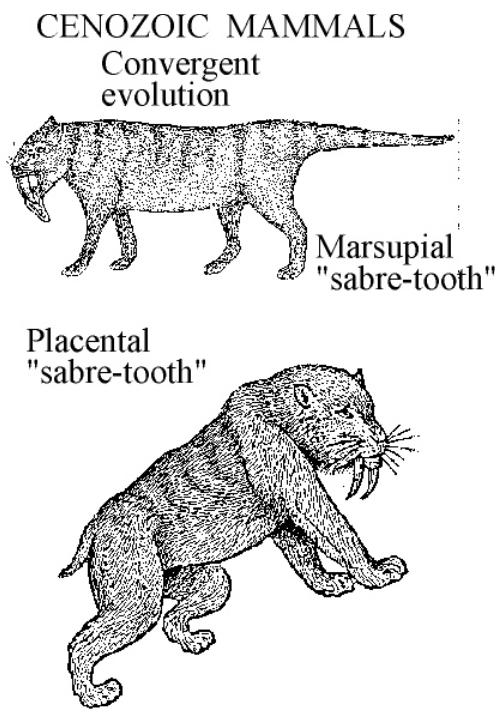
The high metabolic rate of mammals requires large amounts of food; thus, it is not surprising that they exhibit many adaptations for increasing and making the intake of food more effective. In particular, the morphology of the jaw and teeth show many adaptations for rather specialised types of food, but the rest of the body also shows these adaptations. The most primitive mammals were probably insectivores, like the living hedgehogs. Convergent adaptations to a more specialised insectivore life habit like that of the ant-eater have appeared many times in several monotreme, marsupial and placental lineages. Most mammals are herbivores and this feeding habit has resulted in a number of important adaptations; the digestion of plan materials cannot be accomplished entirely in the stomach, but the mechanical degradation by use of teeth is important. The mammalian herbivores frequently have teeth that grow continuously as they are worn down.



Mammalian evolution during the Tertiary took place mainly in isolation on the individual continents; many endemic faunas with a local distribution are known. The rise of the placental mammals in the early part of the Tertiary - the Palaeocene - is the typical example of an adaptive radiation. This radiation took place mainly in the closely connected Europe, North America, and Asia, where the number of mammal families increased from around 10-20 in the early Palaeocene to about 70-80 in the early Eocene, including many groups of insectivores, carnivores, and herbivores.

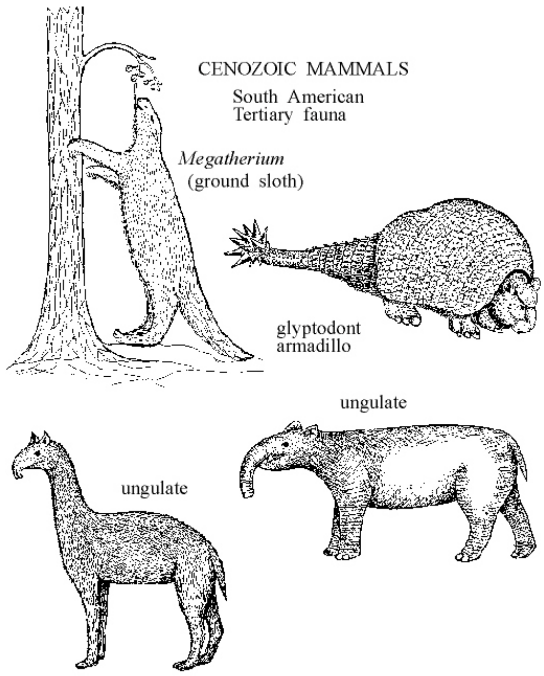
An important group of herbivores are the **hoofed mammals** - the **ungulates**, first known from the Cretaceous. The group was not common during the Palaeocene, but during the early Eocene, the ungulates rapidly radiated into two main groups: (1) the **odd-toed** (with 1, 3, or 5 toes) like horses, tapirs, and rhinoceroses, and (2) the **even-toed** (2 or 4 toes), including pigs, cattle, deer, sheep, and camels. The supposed 'progressive' evolution of the horse from the earliest small 'terrier-sized' (*Hyracotherium*) Eocene horse, through larger and larger forms with fewer and fewer toes during the Tertiary up to the large one-toed Recent horse (*Equus*) is one of the classic examples of 'gradualistic' evolution; 'Darwin's Bulldog' T.H. Huxley used it as one of the main proofs for the reality of Darwin's evolutionary theories. However, it is now realised that the evolution of the horse was more complicated than the usual picture, and there was certainly more than one evolutionary lineage from the Eocene to the present. However, there seems to be a trend towards larger and larger size among the mammals (although small forms persist as well); this trend is termed '**Cope´s law**' after the famous American dinosaur hunter. The changes in the horse are also related to changes in life and feeding habits. The horse originated in North America, where most of its evolution also took place. There were several periods of migration into Eurasia and South America, and eventually the American horses became extinct during the Quaternary, while the Eurasian form survived, and could ironically be used in the conquest of the Americas. The elephants and their relatives - the **proboscideans** - may be related to the ungulates; they appear in Africa at around the late Eocene. Their closest relatives are found in the marine mammal group - the seacows - a group that also is first known from the Eocene.

The **carnivores** include the dogs, cats, hyenas, bears, and seals, all having a pair of canine teeth on each side of the jaw; these teeth are generally long and used in puncturing the skin. The most extreme development of the canines is found in the sabre-toothed forms that have appeared independently several times in mammal evolution. The hyenas have a special type of broad premolar teeth used for crushing bones. The earliest carnivores are known from the late Palaeocene; the origin of the group is uncertain. The modern groups began to diverge in the Eocene. Some carnivores went back into the seas to form the seals, sea lions, and walruses; the first of this group is known from the Miocene. Some carnivore groups have secondarily become adapted to an **omnivore** life habit, like the bears, first appearing in the Oligocene.



Almost half of the living mammals belong to the **rodents**, including rats, mice, and squirrels that are characterised by deep-rooted incisor teeth, which grow throughout their life. The group is first known from the Palaeocene. Although most living rodents are small, some Miocene and Pliocene forms reached the size of a rhinoceros.

The whales and their relatives - the **cetaceans** - have returned to a marine life; the group includes the largest animals to have lived on Earth, and it is still uncertain from which group they originated. The oldest whale is from the Eocene and has carnivore teeth and rather well developed limbs, whereas a later Eocene form (*Basilosaurus*) was obviously entirely aquatic. In post-Eocene times, the whales diverged into a toothed group including the dolphins and the baleens, including the blue whale.



The first possible marsupial mammals are known from the Cretaceous of North America, and the group then spread into South America and Australasia, where their main radiation took place. South America was an isolated continent for most of the Tertiary Period, and here the marsupials included many examples of evolutionary convergence in their morphology and life habits, such as the look-alike **marsupial carnivores** 'sabre-toothed tiger' and 'hyena'. The South American Tertiary fauna is one of the few examples of marsupials and placentals living together; the placental fauna included many endemic species that were found by Darwin (during his 'Beagle' voyage). This fauna was dominated by forms like the gigantic **ground sloth** (*Megatherium*), 6 m long and the equally gigantic **glyptodont armadillos**, as well as anteaters, and **ungulates** that are not known anywhere else. When the Central American land bridge between South and North America became established in the late Tertiary, the endemic fauna in South America was severely hit by the invading species and the marsupials and large placentals became extinct.

In Australia, the marsupials were the dominant mammals for a long time and this explains the variation and diversity shown by them, including many examples of convergence. The earliest Australian marsupial fauna is poorly known from the fossil record.

QUATERNARY

The Rise of Man

The first part of the **Quaternary Period** - the **Pleistocene (1.6 million - 10.000 years ago)** - was a time of extensive glaciations causing a general lowering of the sea level. During the glacial periods, a fauna of specially adapted mammals lived in Eurasia, including the mammoths, woolly rhinoceros, giant deer, cave bears etc. all of which are now extinct. In Africa, primate evolution resulted in the rise of Man. During the last part of the period - the **Holocene (10.000 years ago - present)** the glaciers retreated and were replaced by a warmer period with stable temperatures that probably was important for the rise of civilisation.

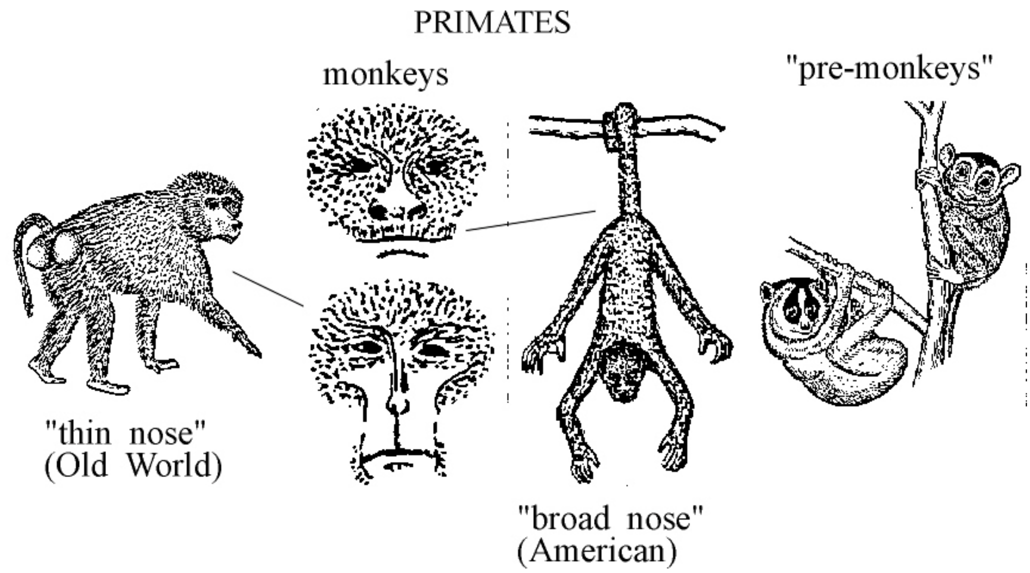
Typical Quaternary Organisms

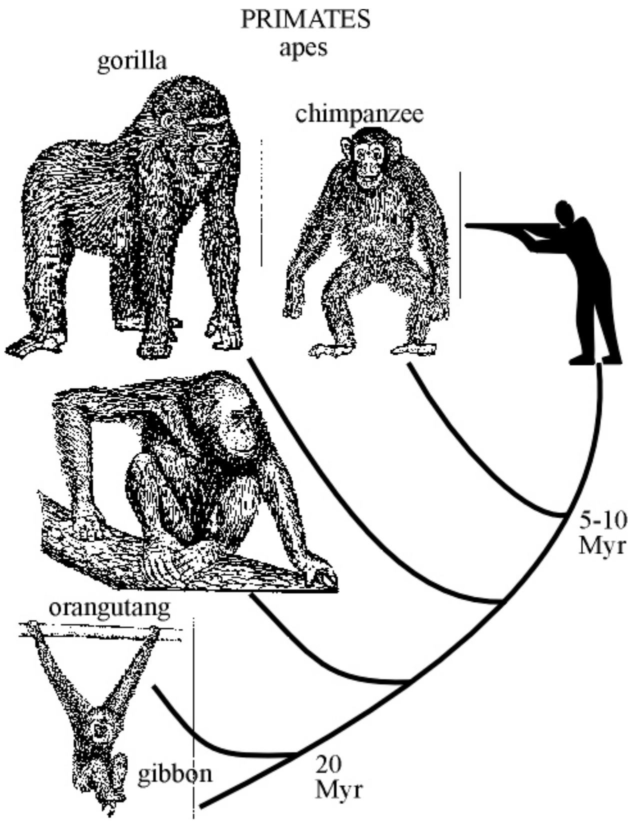
Primates and human evolution

The **primates** ('supreme animals') are characterised by showing adaptations for a tree-dwelling life habit, including: (1) large brains in proportion to their body size, (2) good eye sight with stereoscopic vision, (3), extended parental care, usually with one young at a time. These characters are important in the active and highly mobile life led by the primates, in which good eyesight and estimation of distance as well as intelligence would be important for survival. Moreover, the tree-dwelling life makes it impractical to have more offspring than can be easily carried whilst moving around.

During primate evolution the tree-dwelling life habit has been lost in some lineages that became terrestrial, like in that leading to the hominids. Perhaps long periods of drought have been involved in this development since the reduction of the tropical forests may have forced some primates to leave life in the trees. On account of their life habit, fossil of primates are not common; the oldest known possible primate is a squirrel-like animal from the late Cretaceous, but many scientists doubt this interpretation. The main primate radiation took place during the Eocene when many squirrel-like **'pre-monkeys'** existed; these fossil forms seem to be related to pre-monkeys like, e.g., the lemurs that today are restricted to Madagascar.

The true **monkeys** may be divided into two separately evolving groups: (1) the American monkeys - the so-called **'broad noses'**, where the nostrils are far apart, and (2) the Old World monkeys - the **'thin noses'**, having closely-spaced nostrils. Most forms of both these groups are entirely tree dwelling and the earliest forms of both groups are known from the Oligocene. The Old World Monkeys seem to be ancestral to the apes and humans. Molecular data indicates that they share a last common ancestor with the apes and humans, about 30 million years ago, in the Oligocene. Although most Old World Monkeys are tree-dwellers, several types (like baboons) have become terrestrial, while terrestrial forms are unknown among the American monkeys. The oldest findings of Old World Monkeys are from the Eocene of Egypt.





Apart from the humans, the apes include the living Asian tree-living gibbons and the orangutang as well as the more terrestrial African gorilla and chimpanzee. All apes are characterised by the lack of a tail. The gorilla and chimp are both quadruped and knuckle-walkers. They may walk upright for short distances, whilst only humans are fully bipedal. The gibbons split off from the other lineages at around the early Miocene, and molecular studies indicate that the orangutang and gorillas diverged somewhat later, whereas chimpanzees and humans shared a common ancestor that lived about 5-10 million years ago at the end of the Miocene. The latter date was previously considered to be contradicted by the fossil evidence, indicating a final split between the great apes and humans at around 14-25 million years ago; however, reconsideration of existing fossils as well as new findings are in agreement with a late Miocene split.

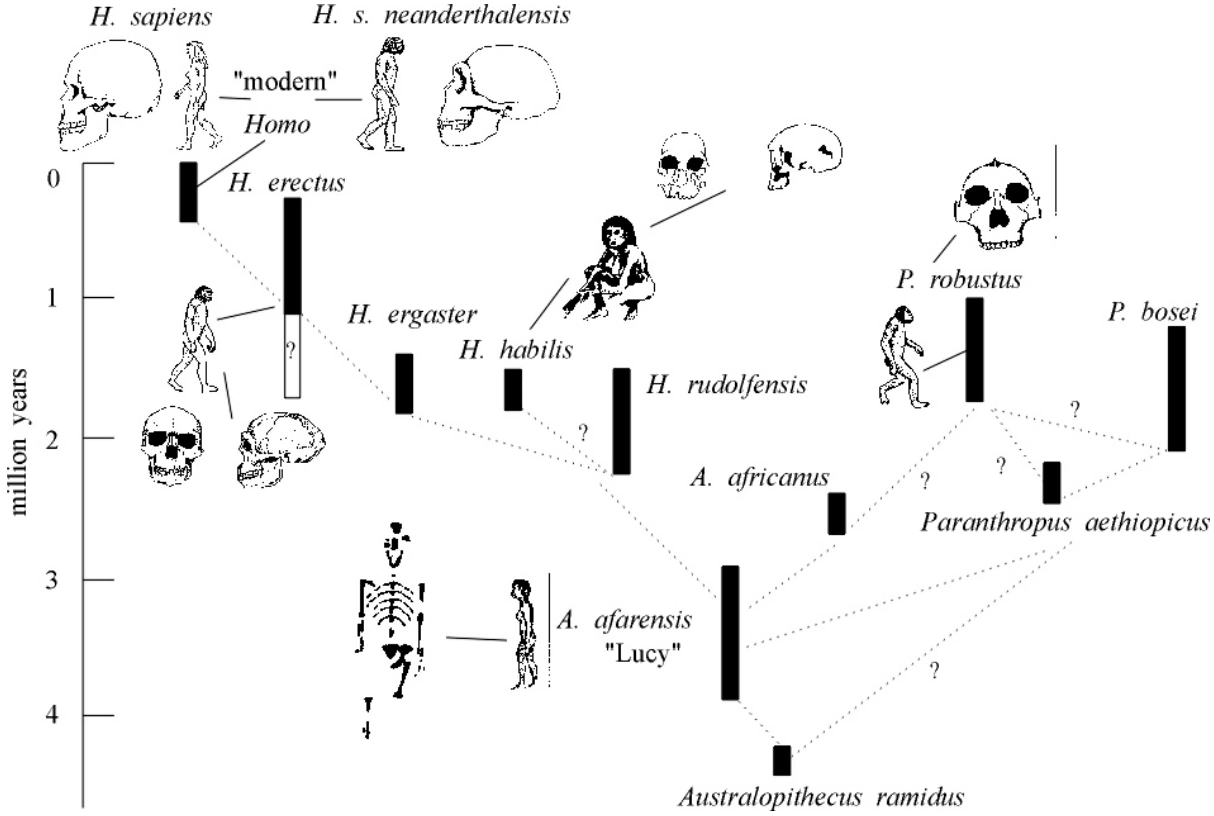
One of the best-known Miocene apes include the quadruped African ***Proconsul***, lacking a tail and having a fairly large brain; together with later Miocene forms like Asian ***Sivapithecus*** (including *Ramapithecus*) and ***Gigantopithecus***. Some of these forms were previously considered to be early representatives of the hominid lineage, but are now thought to be more closely related to orangutangs. *Gigantopithecus* is a large Gorilla-like form with huge grinding teeth; it is first found in the Miocene, but survived well into the Pleistocene, and may have been seen by modern humans (perhaps causing the 'yeti/abominable snow man myths').

The ancestry of our own group, the **hominids** **(Family Hominidae; Pliocene-Recent)** is very uncertain because of a lack of fossils; the hominid family includes mainly two genera - ***Homo*** ('know thyself') and ***Australopithecus*** (literally 'southern ape'). The latter genus is the oldest, with the first possible representative (*A. ramidus*) from around 4.4 million years ago, but the earliest well-known fossils are the 3 million years old, almost complete skeleton of ***A. afarensis*** - that is, 'Lucy' (named by her discoverer, Donald Johanson, after the Beatles tune 'Lucy in the Sky with Diamonds') from Hadar, Ethiopia. The hominids are characterised by true bipedal walking, resulting in: (1) the backbone became somewhat S-shaped so that the centre of gravity is placed directly above the hips, (2) the forelimbs became shortened, (3) the pelvis became short and broad so that it supports the guts, and (4) the foot became flattened to ease the balance. The fact that *Australopithecus* was walking upright is also proved by the findings of roughly contemporary (3.5 million years old) footprints in an ash layer at Laetoli, Tanzania. *Australopithecus* was a relatively small hominid with a weight of up to 50 kg, with a relative brain size about half of ours; the teeth are ape-like, indicating that it was a plant eater. There are several species of *Australopithecus* in the late Pliocene and beginning of Pleistocene (3-2 million years ago); the 'robust' forms of *Australopithecus* are placed by some scientists in the genus *Paranthropus*.

The earliest representatives of our own genus ***Homo habilis*** ('the handy man') appear at around 2-1.6 million years ago, and were first found in Kenya (Olduvai Gorge) in 1961 by Louis Leaky. The relationship between *Homo* and *Australopithecus* is one of the most hotly debated problems in human evolution. *H. habilis* was about 1.5 m tall and had a relative brain size that almost equals ours. The hands of *H. habilis* are very similar to those of humans; the first traces of stone tools are found in the same beds. At around 1.6 million years ago, an even more human-like hominid first appears in Africa - ***Homo erectus***; this hominid differs from Recent humans, mainly in having more pronounced eyebrow ridges, a stronger built jaw and in the lack of a chin. The species was first found on Java in the 1890s and from about 1 million years ago, *H. erectus* can be found distributed widely across Africa, Asia ('Peking Man' and 'Java Man'), and Europe. Caves inhabited by 'Peking Man' and associated elaborate stone tools indicate that human-type culture had started to emerge.

The last phase in human evolution - the appearance of essentially 'modern humans' took place from around 300.000 - 100.000 years ago. The question as to where and when the first modern humans evolved is also much debated, but molecular and fossil evidence seem to support the 'Out of Africa' model. The **Neanderthal Man** was discovered in a cave in Germany (Neander Valley) in the late 1850s; in contrast to the widely spread *H. erectus*, the Neanderthals are restricted to Europe and the Middle East, where they are represented by a rich fossil material. The affinity of *Homo neanderthalensis*, as it was first named in the

1860s, was hotly debated at the time, and is debated still; they differ from *H. sapiens* mainly by having more robust eyebrow ridges as well as larger teeth, and the Neanderthals are frequently considered to form a subspecies of our own species. The Neanderthals vanished from sight at around before the last glaciation some 35.000-30.000 years ago, associated with the appearance of the so-called **Cro-Magnon Man**. This event has led to much speculation (and several best-selling novels and movies). It is possible that the Neanderthals were killed by the invading more fierce and brutal 'Rambo-like' Cro-Magnon Man, essentially having the morphological (and psychological?) characteristics of modern humans.



GEOLOGIC TIMESCALE

		Time Divisions		Began (MA)
PHANEROZOIC	CENOZOIC	Quaternary		
			Holocene	0.01
			Pleistocene	1.6
		Tertiary		
			Pliocene	5
			Miocene	23
			Oligocene	35
			Eocene	56
			Paleocene	65
	MESOZOIC		Cretaceous	145
			Jurassic	210
			Triassic	245
	PALEOZOIC		Permian	290
			Carboniferous	360
			Devonian	410
			Silurian	440
			Ordovician	505
			Cambrian	540
	PRECAMBRIAN		Proterozoic	2500
			Archaean	3800
			(Age of Earth)	(4600)

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GLOSSARY

Absolute dating – numerisk datering.
Acanthod (Acanthodii) – akantod, taggpansarhaj.
Acritarch – akritark, organiskt mikrofossil.
Actinopterygii – strålfenig benfisk.
Adductor – adduktor, brachiopodernas slutarmuskel.
Agnathan (Agnatha) – agnat, käklös fisk.
Algae – alger.
Allochthonous – allokton, sammansatt av transporterat material
Alum shale – alunskiffer, svart, bituminös lerskiffer, som innehåller kolväten
Amber – bärnsten, fossil kåda.
Amino acid - aminosyra, organisk molekyl ($CH(NH_2)COOH$) , beståndsdel i protein
Ammonite (Ammonoidea) – ammonit, utdöd bläckfisk.
Amnion – amnion, fosterhinna.
Amniote – amniot, fosterhinnedjur (reptiler, däggdjur, fåglar).
Amphibians (Amphibia) – amfibie, groddjur.
Anaerobic (anoxic) - anaerob, syrefri
Analogous – analogier, karaktärer som ej påvisar släktskap.
Anapsid – anapsid, reptiler som saknar skallöppning bakom ögat.
Angiosperm – angiosperm, gömfröiga växter.
Angular unconformity – diskordans, kontaktyta där lagren ligger i vinkel mot varandra.
Anhydrite – anhydrit, ortorombiskt evaporitmineral ($CaSO_4$).
Animalia (Kingdom) – djurriket, flercelliga djur.
Ankylosaurid – ankylosaurid, pansardinosaurier.
Anthozoa – anthozo, koralldjur.
Anthracite – antracit, den renaste formen av stenkol, som är svart & hård.
Anthraconite (”stink stone”) – orsten.
Apatite – apatit, en grupp mineral bestående av framförallt kalciumfosfat ($Ca_5(PO_4CO_3)_3(FOHCL)$)
Aquatic – akvatisk, bildad i vatten.
Aragonite – aragonit, ortorombiskt kalciumkarbonat ($CaCO_3$)
Archaean – arkeikum, den äldsta eonen inom prekambrium.
Archaebacteria – arker, arkebakterier.
Archaeocyatha – arkeocyather, utdöda svampdjur.
Archaeopteryx – urfågeln från jura.
Archosaur – arkosaurie, “härskarödlor” (inkl fåglar, krokodiler, flygödlor, dinosaurier)
Arenite – arenit, bergart bestående av sandstora partiklar.
Arkose – arkos, sandsten som innehåller kantiga osoterade bergartsfragment.
Arthropoda – artropoder, leddjur.
Articulata – artikulater, brachiopoder med lås.
Asteroidea – sjöstjärnor.
Atoll – atoll, ringformat korallrev, med central lagun.
Australopithecus – “sydapa”, ett viktigt fossilt hominidsläkte.
Autochthonous – autokton, sammansatt av partiklar som bildats på platsen.
Autotheca – autotheka, stora öppningar för individen hos dendroida graptoliter.
Autotroph - autotrof, organism som själv binder energi genom fotosyntes eller kemosyntes
Aves – fåglar (“flygande dinosaurier”).
Bahamitic sediments – bahamitiska sediment, vanlig typ av nutida karbonater.
Baltoscandia – Baltoskandia, geografisk benämning på Skandinavien och de baltiska staterna.
Banded Iron Formation (BIF) – prekambriska bandade järnformationer.
Barrier reef – barriärrev, långsträckt korallrev parallelt med stranden.
Belemnite – belemnit, utdöd bläckfisk.
Benthic - bentisk, bottenlevande.
Bentonite – bentonit, mjuk, plastisk vulkanisk lera.
Biofacies – biofacies, facies enligt fossilinnehåll.
Biogenic – biogen, bildad genom ngn form av biologisk aktivitet.
Biostratigraphy – biostratigrafi, stratigrafi baserad på fossil.
Bioturbation – bioturbation, orsakas av grävande organismer.
Biozone – biozon, biostratigrafisk enhet.
Bitheca – bitheka, små öppningar för individen hos dendroida graptoliter.
Bituminous – bituminös, innehållande kolväten.
Bivalve – bivalvie, mussla.
Bone – ben, vertebraternas innerskelett består av kalciumfosfat.
Brachial (dorsal) – brakial, ryggskalet hos brachiopoder.
Brachidium – lofoforstöd hos brachiopoder.
Brachiopod – brachiopod, “armfoting”.
Breccia – breccia, grovkornig, klastisk bergart med kantiga fragment.
Brown coal – brunkol, kol av låg kvalitet (omvandlad torv).
Byssal thread – byssystråd, blåmusslans vidhäftningsstruktur.
Caecilian – “maskgroddjur”.
Calcareous mud mound – “kalkslamhög”, revliknande strukturer utan organiskt ramverk.
Calcareous ooid – kalkooid.
Calcilutite – kalcilutit, kalksten uppbyggd av mikrit (kalkslam).
Calcite – kalcit, hexagonalt kalciumkarbonat ($CaCO_3$).
Calcium carbonate – kalciumkarbonat ($CaCO_3$).
Calcium phosphate – kalciumfosfat ($Ca_5(PO_4)_3OH$).
Cambrian – kambrium
Cambrian explosion – kambriska explosionen, snabba

diversifieringen av liv i början av kambrium..
Camerae – kammare, t ex hos nautiloida bläckfiskar.
Carbonate platform – karbonatplattformar, t ex Bahamas.
Carbonates – karbonater.
Carboniferous – karbon
Carbonization – förkolning, tafonomisk process där de flyktiga organiska molekylerna försvinner och lämnar en hinna av kol (t ex växtfossil).
Carnivore – rovdjur.
Carnosaur – karnosaurie, köttätande dinosaurier.
Cartilage – brosk.
Cast – avgjutning, positiv replik av ett fossil.
Catastrophism – Katastrofläran, geologiska/biologiska förändringar orsakas av plötsliga katastrofer.
Cement – cement, bindemedel mellan korn i en sedimentär bergart.
Cementation – cementering, sammanbindning av sedimentkorn genom kemisk utfällning av mineral.
Cenozoic – kenozoikum.
Cenozoic – kenozoikum.
Cephalocordates – cefalokordater, ryggsträngsdjur inkl lansettfisken.
Cephalon – huvud.
Cephalopod – cephalopod, "huvudfoting", bläckfisk.
Ceratopsid – ceratopsid, noshornsödlor.
Cetacean – val.
Chalk – kritkalksten, ren kalcilutit bildad av huvudsakligen kokkoliter.
Chamosite – chamosit, viktigt järnmineral bl a i oolitmalm.
Chelicerata – chelicerater, spindeldjur.
Chemosyntesis - kemosyntes,- syntes av organiska föreningar med hjälp av kemisk energi, (t ex reduktion av svavel till svavelväte
Chitinozoan – kitinozo, organiskt mikrofossil.
Chondrichthyes – hajfiskar.
Chordates (Chordata) – kordater, ryggsträngsdjur.
Chronostratigraphy – kronostratigrafi.
Chronozone – kronozon, den maximala tidsmässiga utbredningen av en biozon.
Cladistics – kladistik, fylogenetisk analysmetod.
Cladogram – kladogram, fylogenetiskt släktskapsträd.
Clastic – klastisk, bestående av fragment som bildats genom vittring.
Clay mineral – lermineral, grupp av aluminiumrika silikatmineral bestående av små platta partiklar, som bildas genom vittring av fältspater och andra silikatmineral.
Claystone – lersten, terrigen klastisk bergart bestående av övervägande lermineral.
Club mosses – lummerväxter.
Cnidaria – nässeldjur.
Cnidoblast – nässelcell.
Coccolith – kokkolit, mikroskopisk planktisk alg med kalkplåtar (bildar kritkalksten).
Coelacanth – kvastfenig fisk.
Coleoidea – bläckfiskar inkl de utdöda belemniterna.
Collagen – kollagen, fibrösa organiska fibrer.
Comb-gills – kamgälar, filtrerapparat hos musslor.
Compound eye – lansettöga.
Concretion – konkretion, hård kompakt rund bildning av mineral inuti en sedimentär bergart, bildad genom kemisk utfällning (t ex orsten).
Conformity – konformitet, lagring utan luckor.
Conifer – barrträd.
Conodont – konodont, tandlikt fosfatiskt mikrofossil.
Continental shelf – kontinentalsockel.
Coprolite – koprolit, fossil exkrement.
Coquina – skalgruskalk.
Cordaite – kordait, utdöd typ av gymnosperm.
Correlation – korrelation, fastställande av likåldrighet av lager mellan olika platser.
Cretaceous – krita.
Crinoid – krinoide, sjölilja.
Cross-bedding – korsskiktning, upprepad skevavlagring i ett terrigent klastiskt sediment (t ex i deltan)
Crustacea – kräftdjur.
Cuticle – kutikula, icke-sellulärt skyddande yttre hinna.
Cyanobacteria – cyanobakterier (tidigare "blå-gröna alger").
Cycads – kottepalmer.
Cyclothem – cyklotem, serie av strata bildade under en upprepad sedimentationscykel, t ex de karbonska kolförekomsterna.
Cystoid – cystoide, "kristalläpple", utdöd tagghuding.
Deltaic – deltaisk, delta-avlagrad.
Dendroidea – dendroida graptoliter.
Deuterostomia – deuterostomier, djur med radiärklyvning.
Devonian – devon.
Diagenesis – diagenes, alla processer i ett sediment efter avsättningen.
Diapsids– diapsid, reptiler med två skallöppningar bakom ögat.
Diductor – diduktor, slutarmuskel hos brachiopoder.
Dinosaur – dinosaurie, "skräcködla".
Dipnoi – lungfiskar.
Disconformity – diskonformitet, parallella lager åtskilda genom en erosionsyta.
Discontinuity surface – diskontinuitetsyta, korrosionsyta mellan två lager.
Dolostone (dolomite) – dolomit ($CaMg(CO_3)_2$, kalkbergart bestående av mineralet dolomit.
Dorsal – dorsal, ryggsidan.
Echinodermata – echinodermater, tagghudingar.
Echinoid – echinoide, sjöborre.
Endosymbiosis - endosymbios, symbios inuti en annan organism
Endothermic – endoterm, jämnvarma djur (t ex däggdjur).
Environmental facies – sedimentär facies, ett sediments bildningsaspekt, t ex eolisk, fluvial etc.
Eolian – eolisk, vindtransporterad.
Epicontinental sea – epikontinentalhav, hav som ligger på kontinentalblocken.
Eubacteria (Kingdom) – eubakterier, "vanliga" bakterier.
Eukaryote - eukaryot, organism vars celler har kärna.
Euryapsid – euryapsid, marina reptiler.
Eurypterid (sea scorpion) – eurypterid, sjöskorpion.
Eurypterids – eurypterider, "havsskorpioner".
Eustacy – eustasi, världsvida variationer i havsnivån, bl a

orsakade av nedisningar och plattrörelser.
Evaporite – evaporit, bergart bildad genom utfällning ur hypersalint vatten (t ex gips, stensalt etc).
Even-toed – partåiga hovdjur.
Evolutionary faunas – evolutionära faunor.
Exoskeleton – exoskelett, ytterskelett.
External mould – yttre avtryck.
Extinction – utdöende.
Facies – facies, ett sediments eller bergarts karaktär och utseende.
Facies – facies, utbildning, karaktären av ett sediment eller bergart.
Fennoscandian Border Zone – Fennoskandiska randzonen, gränszon mellan fennoskandiska urbergsskölden och Tornquistlinjen.
Fennoscandian Shield (Baltic Shield) – Fennoskandiska skölden.
Fern – ormbunke.
Filter-feeding – filtrerare.
Fissility – skiffrighet, graden av lätthet som en skiffer kan delas längs skiktytorna.
Fluvial – fluvial, flodtransporterad.
Foraminifer – foraminifer, "skalamöba".
Formation, formation, grundläggande litostratigrafisk enhet. Skall vara karterbar i fält genom litologiska egenskaper
Fossilization – fossilisering.
Frame-builder – rambyggare, kalkutsöndrande organismer som bygger upp rev.
Framework – ramverk, den vågresistenta kärnan av rambyggarnas skelett.
Fringing reef – randrev, korallrev beläget längs stranden.
Fungi (Kingdom) – svampar.
Ga – Ga, förkortning för giga-annum, miljard år.
Gaia- teorin att jorden representerar ett självreglerande system
Gastrolith – gastrolit, magstenar.
Gastropod – gastropod, snäcka.
Ginkgos – ginkgoväxter.
Glacial striation – isräffla.
Glauconite – glaukonit, grönfärgat glimmermineral, som bildas i marina miljöer med långsam sedimentation.
Gnathostome – gnatostomier, käkförsedda ryggradsdjur.
Gondwanaland – Gondwanaland, den södra delen av superkontinenten Pangea.
Graded bedding – graderad skiktning, gradvis minskande kornstorlek uppåt.
Greensand – grönsand, glaukonitisk sand.
Greywacke – gråvacka, hård omogen sandsten, vanligen med graderad skiktning.
Gymnosperms – gymnospermer, nakenfröiga växter.
Gypsum – gips, hydrerat kalciumsulfat ($CaSO_4$ 2 H_2O), typiskt evaporitmineral.
Hadean – hadeikum, äldsta prekambrium från vilken bevarade bergarter saknas.
Hadrosaurid – hadrosaurie, anknäbbsdinosaurier.
Halite – halit, natriumklorid (NaCl), det vanligaste evaporitmineralet.
Hematite - hematit, rött järnmineral (Fe_2O_3), viktigt i järnmalmer.
Hemichordata – hemikordater, t ex graptoliter.
Hercynian – hercynsk, orogenes under karbon-perm i Europa och Ural.
Heterochrony – heterokroni, "olika tid", viktig makroevolutionär mekanism.
Heterotroph - heterotrof, organism som är beroende av organisk föda producerad av andra organismer.
Hiatus – hiatus, avbrott i sedimentationen.
Hinge – låsrand t ex hos brachiopoder.
Homologous – homologier, karaktärer som tyder på släktskap.
Horsetails – fräkenväxter.
Iapetus sea – Iapetushavet (protoatlanten), djuphav mellan Europa och Nordamerika.
Ichthyosaur – ichtyosaurie, fisködla.
Ichthyostega – "fyrfota fisken", en av de tidigaste tetrapoderna.
Immature – omogen, instabil sedimentbergart, bildad genom kortvarig vittring och transport.
Inarticulata – inartikulater, brachiopoder som saknar lås.
Index fossil – ledfossil, fossil med stratigrafisk användbarhet.
Internal mould – stenkärna, inre avgjutning.
Jurassic – jura.
Key bed (marker bed) – ledlager, t ex ett bentonitlager.
Kingdom – rike, den högsta taxonomiska enheten (t ex Animalia).
K-T extinction – krita-tertiär utdöendet.
Labyrinthodont – labyrintodonter, primitiv typ av fossila groddjur.
Lacustrine – lakustrin, bildad på sjöbotten.
Laurasia – Laurasien, norra delen av superkontinenten Pangea.
Ligament – ligament, elastiskt band som öppnar skalen hos musslor.
Limonite – limoni, grupp brunfärgade amorfa järnhydroxider.
Lingulate (Lingulata) – fosfatskaliga brachiopoder.
Lithification – litifiering, slutstadiet i konsolideringsprocessen.
Lithofacies – litofacies, ett sediments litologiska karaktär.
Lithology – litologi, bergartstyp.
Lithostratigraphy – litostratigrafi, bergartsstratigrafi, baserad på litologin hos sedimentära bergarter.
Living chamber – boningskammare.
Living fossil – levande fossil, djurgrupp som uppvisar långsam evolutionär hastighet.
Lophophore – lofofor, filtrerande organ hos brachiopoder.
Ma – Ma, förkortning för mega-annum, miljon år.
Mature – mogen, stabil sedimentbergart, bildad genom långvarig vittring och transport.
Macroevolution – makroevolution, evolution över artnivån.
Mammalia – däggdjur.
Mammal-like reptile – däggdjurslika reptil.
Mantle – mantel, mjukdel som utsöndrar skalet hos t ex brachiopoder och musslor.
Marl – märgel.
Marsupial – pungdjur.
Mesozoic – mesozoikum.

Micrite – mikrit (kalkslam), finkornig aragonit el. Kalcit.
Microevolution – mikroevolution, evolution på artnivån.
Monera (Kingdom) – bakterieriket.
Monophyletic – monofyletisk, grupp som härstammar från en gemensam stamförfader.
Monotremes – kloakdjur (t ex näbbdjuret).
Mosasaur – mosasaurie, marin varan.
Mould – avtryck, negativ replik av ett fossil.
Moult – skalömsning (hos leddjur).
Mud cracks – torksprickor, polygonala sprickor bildade genom uttorkning av sediment.
Mudstone – slamsten.
Mummification – mumifiering.
Nautiloidea – nautiloida bläckfiskar.
Nektic – nektisk, simmande.
Neural chord – nervsträng.
Notochord – korda, ryggsträng.
Odd-toed – uddatåiga hovdjur.
Offlap – offlap, lagerföljd vid regression.
Omnivore – omnivor, allätare.
Onlap – onlap, lagerföljd vid transgression.
Ooid – ooid, sfäriskt karbonat eller järnkorn, koncentriskt uppbyggd kring en kärna, bildad genom kemisk utfällning av karbonat eller järn under agitering.
Oolite – bergart bestående av ooider.
Order – ordning.
Ordovician – ordovicium.
Ornithischians (“brid hips”) – fågelhöftade dinosaurier (ej släkt med fåglar).
Ornithopods – fågeltåiga dinosaurier.
Orogeny – orogenes, bergskedjeveckning.
Oscillation ripples – böljeslagsmärken, bildade genom vågrörelser.
Ostracod – ostrakod, musselkräfta.
Pachycephalosaur – pachycephalosaurier, tjockskalle dinosaurier.
Paleozoic – paleozoikum.
Panspermia – panspermi, livet kan ha uppstått i universum och förts till jorden (små gröna män?) Panthalassa – Panthalassa, havet som omgav superkontinenten Pangea.
Paraconformity – parakonformitet, osynlig lucka i lagerföljden.
Paralic – paralisk, växling mellan marin, brackvattens, och kontinental miljö (associerad med kolbildning).
Paraphyletic – parafyletisk, grupp som härstammar från en gemensam förfader men inte inkluderar alla (t ex reptiler, som ej inkluderar fåglar).
Peat – torv, mjuk träskavlagring, förstadium till kol.
Pedicle – pedikel, fastsättningsorgan hos brachiopoder.
Pellet – pellet, ovalt rundat korn av mikrokristallin kalcit, exkrement från organismer.
Pelvis – bäcken.
Pelycosaurs – pelykosaurier, segelödlor, en typ av däggdjurslik reptil
Permian – perm.
Phanerozoic – fanerozoikum, delen av jordens historia med “synligt liv”.
Phosphorite – fosforit, bergart bestående av mest fosfat.
Phyletic gradualism – fyletisk gradulalism, långsam gradvis artbildning.
Phylogeny - fylogeni, eng. phylogeny - organismers inbördes släktskapsförhållanden
Phylum – fylum.
Placental – placentalie, moderkaksdäggdjur.
Placoderm – plakoderm, armpansarhajar.
Plantae (Kingdom) – landväxter.
Plesiosaur – plesiosaurie, svanödla.
Polyphyletic – polyfyletisk, grupp som ej härstammar från en gemensam stamförfader.
Prebiotic broth (primordial soup) – “ursoppa”, den organiska blandning ur vilken livet uppstod enl en teori.
Precambrian – prekambrium, delen av jordens historia före kambrium.
Progymnosperm – förfröväxter.
Prokaryote - prokaryot, - organism där cellerna saknar kärna.
Proterozoic – proterozoikum, “gömt liv”, den yngre eonen inom prekambrium.
Pterosaur – pterosaurie, flygödla.
Punctuated equilibrium – punkterad jämnvikt, snabb artbildning utan mellanstadier.
Pygidium – bakkropp.
Quartzarenite – kvartsarenit, kvartssandsten.
Quaternary – kvartär.
Recrystallization – rekristallisering, omkristallisering.
Regression – regression, tillbakadragande av hav från landområden, d v s strandförskjutning i riktning mot havet.
Replacement – ersättning, diagenetisk/tafonomisk process varvid ett minerall utlöses och ersätts av ett annat.
Reptilian – reptil.
Rhyniophyt- ryniofyt, de mest primitiva landväxterna.
Rugose coral – rugos korall, “bägarkorall”.
Russian Platform (East European Platform) – ryska plattformen (östeuropeiska plattformen).
Sandstone – sandsten.
Saurischian – ödlehöftad dinosaurie.
Sauropod – sauropod ödlefötot, långhalsade jättedinosaurier.
Scavenging – asätare.
Sedimentary rock – sedimentbergart, bergart som bildats vid litifiering av löst vittrat material.
Seed fern – fröormbunke.
Septae – septa, väggar, t ex mellan bläckfiskens kammrar.
Sessile – sessil, fastsittande.
Shale – skiffer, laminerad slambergart, lätt delbar längs skiktytorna.
Shield – sköld, den del av en kraton som varit stabil sedan prekambrium.
Shield – urbergssköld.
Silica – kisel (SiO_2).
Silicification – förkisling, diagenetisk/tafonomisk process där kiseldioxid utfälls.
Siltstone – siltsten.
Silurian – silur.
Siphon – sifon, tubformat utskott från manteln hos infauna mollusker.

Siphonal tube (siphuncle) – sifonalrör, sammanbinder kammrar hos bläckfiskar.
Sockets – låsgropar hos artikulata brachiopoder.
Sorting – sortering, graden av sedimentkornens variation inom en dominerande fraktion.
Spar – spat, färglöst karbonatcement med liten kristallstorlek.
Special preservation – unik bevaring, t ex mjukdelsbevaring.
Species – art.
Stegosaurid – stegosaurid, taködledinosaurier.
Stem reptile – stamreptil.
Stolon – stolon, smalt inre rör hos graptoliter.
Stratigraphy – stratigrafi, studiet av lagrade bergarter och deras inbördes förhållande.
Stromatolite – stromatolit, laminerad struktur bildad av bakteriemattor.
Stylolite – stylolit, oregelbunden utlösningsyta, med tandat utseende.
Suture – sutur, kontakten mellan kammare och ytterskal hos bläckfiskar, t ex ammoniter.
Swim bladder – simblåsa.
Synapsid – synapsid, däggdjurslika reptiler och däggdjur med en stor skallöppning bakom ögat.
Tabulae – “golv” hos tabulata koraller.
Tabulate coral – tabulat korall.
Taconic – Takonsk, fas av den kaledonska veckningen.
Taphonomy – tafonomi, studiet av vad som händer organismer efter döden.
Taxon – taxon, taxonomiska enheter (arter, familjer etc.)
Taxonomy – taxonomi, vetenskap som behandlar organismernas uppdelning och släktskap.
Temporal openings – skallöppningar bakom ögat.
Terrigenous – terrigen, material från land, bildat genom vittring ovan havsytan.
Tertiary – tertiär.
Tethys sea – Tethyshavet, det hav som avdeladeGondwanaland från Eurasien.
Tetrapod – tetrapod, fyrfota djur.
Thorax – mellankropp.
Tillite – tillit, litifierad morän, isavlagrad osorterad grovkornig.
Trace fossil – spårfossil, spår av en organisms aktivitet.
Transgression – transgression, havets framryckning över ett landområde, d v s landförskjutning mot land.
Triassic – trias
Tunicata – tunikater, sjöpungar.
Turbidite – turbidit, suspensionsström, sedimentlavin.
Turtle – sköldpadda.
Unconformity – diskonformitet.
Uniformitarianism – likformighetsläran, geologiska/biologiska processer fortgår på samma sätt idag som under jordens tidigare historia.
Wacke – vacka, t ex gråvacka
Vascular plant – kärlväxt.
Ventral – ventral, buksidan
Vertebrata – vertebrat, ryggradsdjur.
Yolk – gula.

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Illustrations have been re-drawn from the following sources

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Mutvei, H. & Stuenes, S. 1982. Paleontologi – kompendium för grundkurs i geovetenskap. Uppsala Universitet.

Torsvik, T. H. & Smethurst, M.A. 1989-1997. GMAP32 – Geographic Mapping and Reconstruction System, Geological Survey of Norway. http://www.ngu.no/geophysics/soft32.htm

Some useful links

http://www.ucmp.berkeley.edu/

http://phylogeny.arizona.edu/tree/phylogeny.html

http://www.science.ubc.ca/~geol313/links/links.htm

http://www.nhm.ac.uk/hosted_sites/paleonet/

http://www.sepm.org/sepm.html

http://www.le.ac.uk/geology/map2/PalAss/

http://www.sedimentology.geo.uu.se/palaeo/Mainpages/Links.html