



# An Introduction to Paleobiology

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## Chapter 1

# Paleobiology



Brachiopods and bryozoans in an Ordovician limestone, southern Minnesota.

**Paleobiology** (sometimes spelled **palaeobiology**) is a growing and comparatively new discipline which combines the methods and findings of the natural science biology with the methods and findings of the earth science paleontology. It is occasionally referred to as "geobiology."

Paleobiological research uses biological field research of *current* biota and of fossils *millions of years* old to answer questions about the molecular evolution and the evolutionary history of life. In this scientific quest, macrofossils, microfossils and trace fossils are typically analyzed. However, the 21st-century biochemical analysis of DNA and RNA samples offers much promise, as does the biometric construction of phylogenetic trees.

An investigator in this field is known as a *paleobiologist*.

### **Important research areas**

- Paleobotany applies the principles and methods of paleobiology to flora, especially green land plants, but also including the fungi and seaweeds (algae).
- Paleozoology uses the methods and principles of paleobiology to understand fauna, both vertebrates and invertebrates.
- Micropaleontology applies paleobiologic principles and methods to archaea, bacteria, protists and microscopic pollen/spores.
- Paleobiochemistry uses the methods and principles of organic chemistry to detect and analyze molecular-level evidence of ancient life, both microscopic and macroscopic.
- Paleoecology examines past ecosystems, climates, and geographies so as to better comprehend prehistoric life.
- Taphonomy analyzes the post-mortem history (for example, decay and decomposition) of an individual organism in order to gain insight on the behavior, death and environment of the fossilized organism.
- Paleoichnology analyzes the tracks, borings, trails, burrows, impressions, and other trace fossils left by ancient organisms in order to gain insight into their behavior and ecology.
- Stratigraphic paleobiology studies long-term secular changes, as well as the (short-term) bed-by-bed sequence of changes, in organismal characteristics and behaviors.
- Evolutionary developmental paleobiology examines the evolutionary aspects of the modes and trajectories of growth and development in the evolution of life – clades both extinct and extant.

## ***Paleobiologists***



Baron Nopcsa

The founder or "father" of modern paleobiology is said to be Baron Franz Nopcsa (1877 to 1933), a turn-of-the-century Hungarian scientist. He is also known as *Baron Nopcsa*, *Ferenc Nopcsa*, and *Franz Nopcsa von Felső-Szilvás*. He initially termed the discipline "paleophysiology."

However, credit for coining the word *paleobiology* itself should go to Professor Charles Schuchert. He proposed the term in 1904 so as to initiate "a broad new science" joining "traditional paleontology with the evidence and insights of geology and isotopic chemistry."

On the other hand, Charles Doolittle Walcott, a Smithsonian adventurer, has been cited as the "founder of Precambrian paleobiology." Although best-known as the discoverer of the mid-Cambrian Burgess shale animal fossils, in 1883 this American curator found the "first Precambrian fossil cells known to science" – a stromatolite reef then known as *Cryptozoon* algae. In 1899 he discovered the first acritarch fossil cells, a Precambrian algal phytoplankton he named *Chuarina*. Lastly, in 1914, Walcott reported "minute cells and chains of cell-like bodies" belonging to Precambrian purple bacteria.

Later 20th-century paleobiologists have also figured prominently in finding Archaean and Proterozoic eon microfossils: In 1954, Stanley A. Tyler and Elso S. Barghoorn described 2.1 billion-year-old cyanobacteria and fungi-like microflora at their Gunflint Chert fossil site. Eleven years later, Barghoorn and J. William Schopf reported finely-preserved Precambrian microflora at their Bitter Springs site of the Amadeus Basin, Central Australia.

Finally, in 1993, Schopf discovered O<sub>2</sub>-producing blue-green bacteria at his 3.5 billion-year-old Apex Chert site in Pilbara Craton, Marble Bar, in the northwestern part of Western Australia. So paleobiologists were at last homing in on the origins of the Precambrian "Oxygen catastrophe."

## Chapter 2

# Paleobotany

**Paleobotany**, also spelled as **palaeobotany** (from the Greek words *paleon* = old and "botany", study of plants), is the branch of paleontology or paleobiology dealing with the recovery and identification of plant remains from geological contexts, and their use for the biological reconstruction of past environments (paleogeography), and both the evolutionary history of plants, with a bearing upon the evolution of life in general. A synonym is **paleophytology**. Paleobotany includes the study of terrestrial plant fossils, as well as the study of prehistoric marine photoautotrophs, such as photosynthetic algae, seaweeds or kelp. A closely-related field is palynology, which is the study of fossilized and extant spores and pollen.

Paleobotany is important in the reconstruction of ancient ecological systems and climate, known as paleoecology and paleoclimatology respectively; and is fundamental to the study of green plant development and evolution. Paleobotany has also become important to the field of archaeology, primarily for the use of phytoliths in relative dating and in paleoethnobotany,

### ***Overview of the paleobotanical record***

Macroscopic remains of true vascular plants are first found in the fossil record during the Silurian Period of the Paleozoic era. Some dispersed, fragmentary fossils of disputed affinity, primarily spores and cuticles, have been found in rocks from the Ordovician Period in Oman, and are thought to derive from liverwort- or moss-grade fossil plants (Wellman et al., 2003).



An unpolished hand sample of the Lower Devonian Rhynie Chert from Scotland.

An important early land plant fossil locality is the Rhynie Chert, found outside the village of Rhynie in Scotland. The Rhynie chert is an Early Devonian sinter (hot spring) deposit composed primarily of silica. It is exceptional due to its preservation of several different clades of plants, from mosses and lycopods to more unusual, problematic forms. Many fossil animals, including arthropods and arachnids, are also found in the Rhynie Chert, and it offers a unique window on the history of early terrestrial life.

Plant-derived macrofossils become abundant in the Late Devonian and include tree trunks, fronds, and roots. The earliest tree is *Archaeopteris*, which bears simple, fern-like leaves spirally arranged on branches atop a conifer-like trunk (Meyer-Berthaud et al., 1999).

Widespread coal swamp deposits across North America and Europe during the Carboniferous Period contain a wealth of fossils containing arborescent lycopods up to 30 meters tall, abundant seed plants, such as conifers and seed ferns, and countless smaller, herbaceous plants.

Angiosperms (flowering plants) evolved during the Mesozoic, and flowering plant pollen and leaves first appear during the Early Cretaceous, approximately 130 million years ago.

## ***Plant fossils***

A plant fossil is any preserved part of a plant that has long since died. Such fossils may be prehistoric impressions that are many millions of years old, or bits of charcoal that are only a few hundred years old. Prehistoric plants are various groups of plants that lived before recorded history (before about 3500 BC).

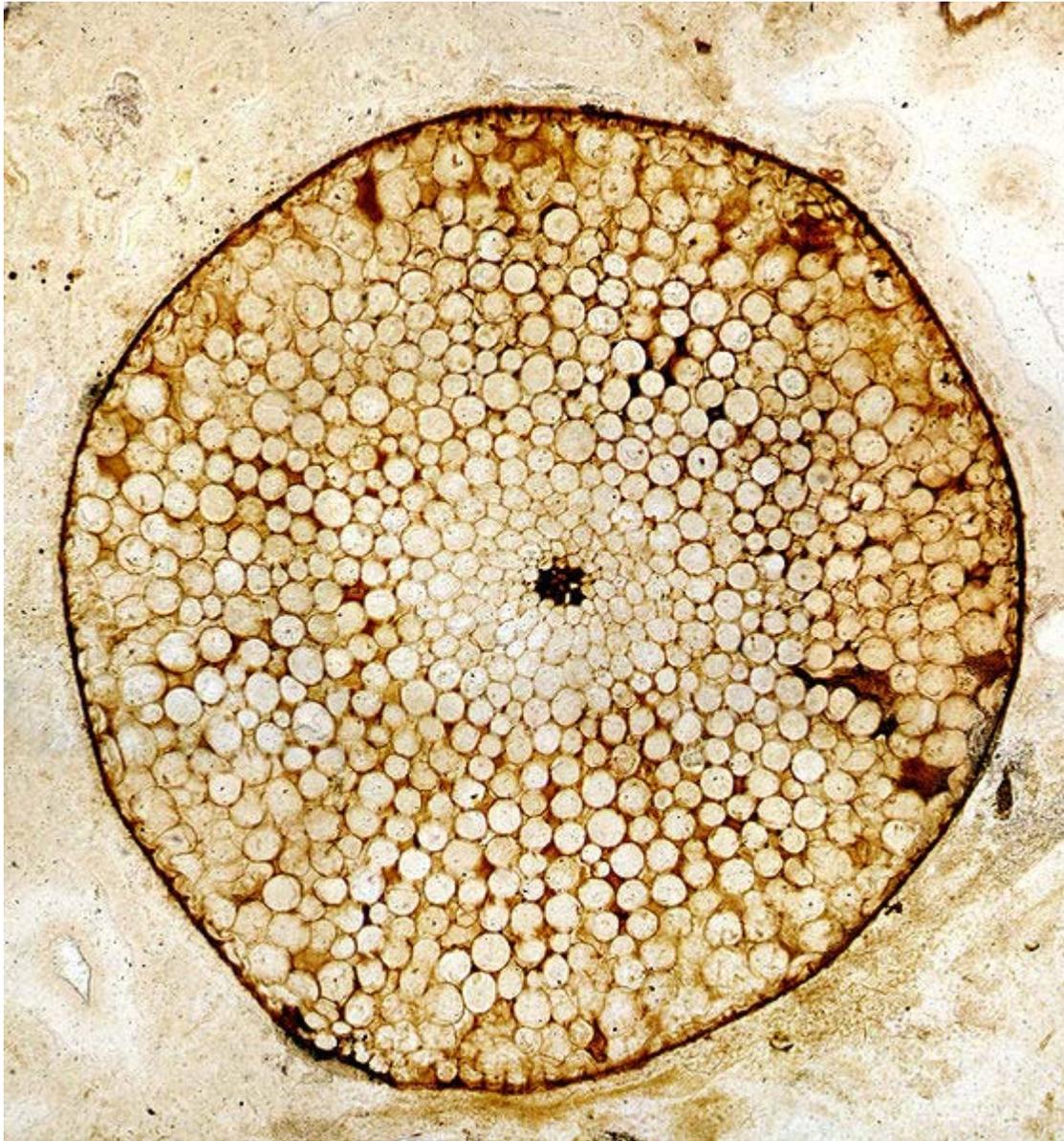
### **Preservation of plant fossils**



*Ginkgoites huttonii*, Middle Jurassic, Yorkshire, UK. Leaves preserved as compressions. Specimen in Munich Palaeontological Museum, Germany. Photo by Ghedoghedo

Plant fossils can be preserved in a variety of ways, each of which can give different types of information about the original parent plant. These modes of preservation are discussed in the general pages on fossils but may be summarised in a palaeobotanical context as follows.

1. **Adpressions (compressions - impressions).** These are the most commonly found type of plant fossil. They provide good morphological detail, especially of dorsiventral (flattened) plant parts such as leaves. If the cuticle is preserved, they can also yield fine anatomical detail of the epidermis. Little other detail of cellular anatomy is normally preserved.



*Rhynia*, Lower Devonian Rhynie Chert, Scotland, UK. Transverse section through a stem preserved as a silica petrifaction. Photo by Plantsurfer

2. **Petrifactions (permineralisations or anatomically preserved fossils).** These provide fine detail of the cell anatomy of the plant tissue. Morphological detail can also be determined by serial sectioning, but this is both time consuming and difficult.

3. **Moulds and casts.** These only tend to preserve the more robust plant parts such as seeds or woody stems . They can provide information about the three-dimensional form of the plant, and in the case of casts of tree stumps can provide evidence of the density of the original vegetation. However, they rarely preserve any fine morphological detail or cell anatomy. A subset of such fossils are **pith casts**, where the centre of a stem is either hollow or has delicate pith. After death, sediment enters and forms a cast of the central cavity of the stem. The best known examples of pith casts are in the Carboniferous Sphenophyta (*Calamites*) and cordaites (*Artisia*).



*Crossotheca hughesiana* Kidston, Middle Pennsylvanian, Coseley, near Dudley, UK. A lyginopteridalean pollen organ preserved as an authigenic mineralisation. Specimen in Sedgwick Museum, Cambridge, UK. Photo by Verisimilus.

4. **Authigenic mineralisations.** These can provide very fine, three-dimensional morphological detail, and have proved especially important in the study of reproductive structures that can be severely distorted in adpressions. However, as they are formed in mineral nodules, such fossils can rarely be of large size.

5. **Fusain.** Fire normally destroys plant tissue but sometimes charcoalfied remains can preserve fine morphological detail that is lost in other modes of preservation; some of the best evidence of early flowers has been preserved in fusain. Fusian fossils are delicate

and often small, but because of their buoyancy can often drift for long distances and can thus provide evidence of vegetation away from areas of sedimentation.

## **Fossil-taxa**

Plant fossils almost always represent disarticulated parts of plants; even small herbaceous plants are rarely preserved whole. Those few examples of plant fossils that appear to be the remains of whole plants in fact are incomplete as the internal cellular tissue and fine micromorphological detail is normally lost during fossilisation. An added complication is that, as explained above, plant remains can be preserved in a variety of ways, each revealing different features of the original parent plant.

Because of these difficulties, palaeobotanists usually assign different taxonomic names to different parts of the plant in different modes of preservation. For instance, in the subarborescent Palaeozoic sphenophytes, an impression of a leaf might be assigned to the genus *Annularia*, a compression of a cone assigned to *Palaeostachya*, and the stem assigned to either *Calamites* or *Arthroxyton* depending on whether it is preserved as a cast or a petrification. All of these fossils may have originated from the same parent plant but they are each given their own taxonomic name. This approach to naming plant fossils originated with the work of Brongniart (1822) and has stood the test of time; although non-palaeobotanist may find it a confusing system, it is generally regarded as the most practical way to overcome the special taphonomic difficulties encountered with plant fossils.

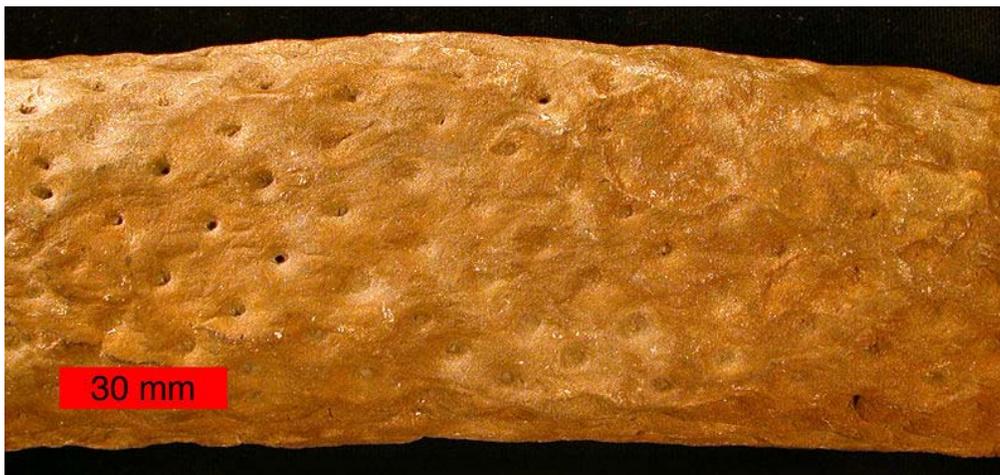
For many years this approach to naming plant fossils was tacitly accepted by palaeobotanists but not formalised within the *International Rules of Botanical Nomenclature* (e.g. Briquet, 1906). Eventually, Thomas (1935) and Jongmans et al. (1935) proposed a set of formal provisions, the essence of which was introduced into the first *International Code of Botanical Nomenclature* (Lanjou et al., 1952). These early provisions allowed fossils representing particular parts of plants in a particular state of preservation to be referred to organ-genera. In addition, a small subset of organ-genera, to be known as form-genera, were recognised based on the artificial taxa introduced by Brongniart (1822) mainly for foliage fossils. Over the years, the concepts and regulations surrounding organ- and form-genera became modified within successive *International Codes of Botanical Nomenclature*, reflecting a failure of the palaeobotanical community to agree on how this aspect of plant taxonomic nomenclature should work (a history reviewed by Cleal & Thomas, 2010). Eventually, the use of organ- and fossil-genera was abandoned with the *St Louis Code* (Greuter et al., 2000).

The situation in the current *Code* (McNeill et al., 2006) is that any plant taxon whose type is a fossil is referred to as a fossil-taxon. Such taxa can refer to a particular part of a plant preserved in a particular way, as defined in the diagnosis of that taxon. Otherwise, the names of fossil-taxa are subject to essentially the same regulations as control the nomenclature of living plants, notably that the names are fixed to a type specimen, and that competing names are chosen mainly on the basis of chronological priority of first publication. Although the name is always fixed to the type specimen, the circumscription

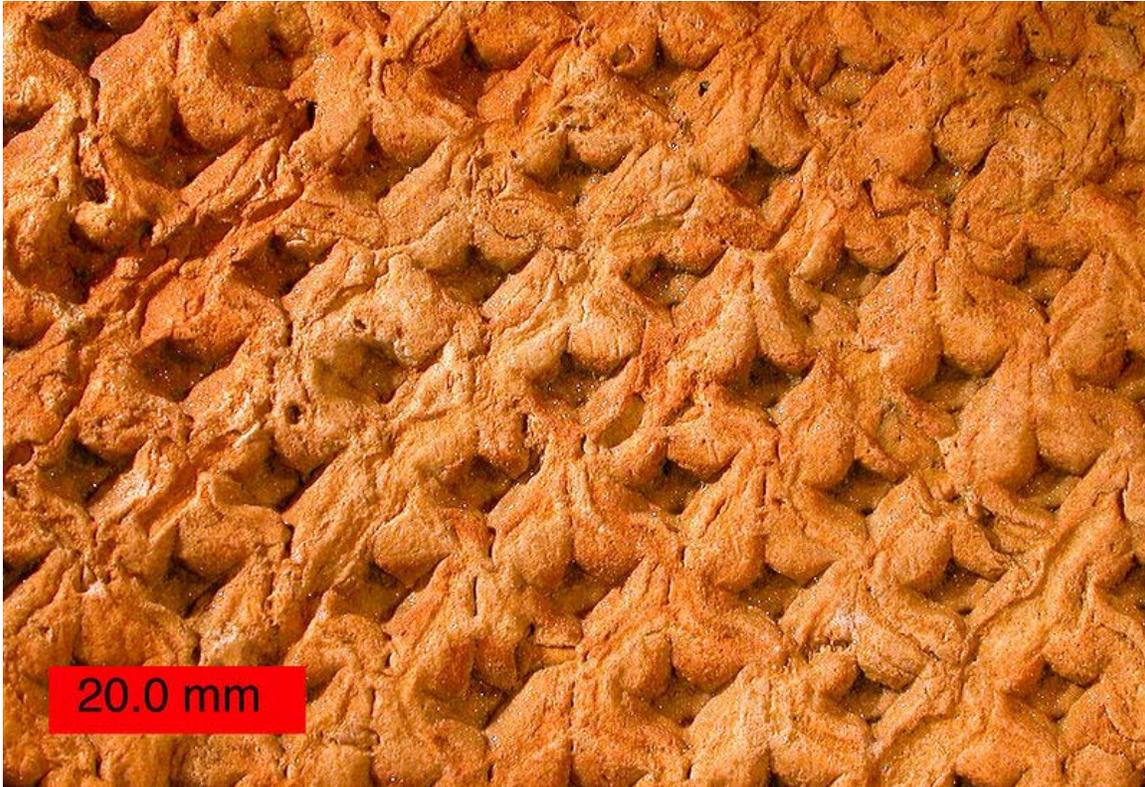
(i.e. range of specimens that may be included within the taxon) is defined by the diagnosis and can be changed by formal emendation. Such emendation could result in an expansion of the range of plant parts and/or preservation states that can be incorporated within the taxon. For instance, a fossil-genus originally based on compressions of ovules could be emended so that it also included the multi-ovulate cupules within which the ovules were originally borne. A complication can arise if, in this case, there was an already named fossil-genus for these cupules. If palaeobotanists were confident that the type of the ovule fossil-genus and of the cupule fossil-genus could be included within the newly emended genus, then the two names would compete as to being the correct one for the newly emended genus. However, this only happens if the actual type specimens (and not just specimens that are similar to the types) can be included within the newly revised taxon.

The current *Code* also refers to a specific subset of fossil-taxa that are known as morphotaxa. These differ from normal fossil-taxa in that they can only be used for fossils that represent the same part of the parent plant and that are preserved in the same way as the type specimen. Morphotaxa were introduced to try to overcome the issue of competing names that represented different plant parts and/or preservation states. What would you do if the species-name of a pollen-organ was pre-dated by the species name of the type of pollen produced by that pollen organ. It was argued that palaeobotanists would be unhappy if the pollen organs were named using the taxonomic name whose type specimen is a pollen grain. As pointed out by Cleal & Thomas (2010), however, the risk of the name of a pollen grain supplanting the name of a pollen organ is most unlikely. Palaeobotanists would have to be totally confident that the type specimen of the pollen species, which would normally be a dispersed grain, definitely came from the same plant that produced the pollen organ. We know from modern plants that closely related but distinct species can produce virtually indistinguishable pollen. It would seem that morphotaxa offer no real advantage to palaeobotanists over normal fossil-taxa and the concept is best abandoned.

### ***Fossil groups of plants***



*Stigmaria*, a common fossil tree root. Upper Carboniferous of northeastern Ohio.



External mold of *Lepidodendron* from the Upper Carboniferous of Ohio.

Some plants have remained remarkably unchanged throughout earth's geological time scale. Early ferns had developed by the Mississippian, conifers by the Pennsylvanian. Some plants of prehistory are the same ones around today and are thus living fossils, such as *Ginkgo biloba* and *Sciadopitys verticillata*. Other plants have changed radically, or have gone extinct entirely.

Examples of prehistoric plants are:

- *Araucaria mirabilis*
- *Archaeopteris*
- *Calamites*
- *Glossopteris*
- *Hymenaea protera*
- *Nelumbo aureavallis*
- *Protosalvinia*
- *Palaeoraphe*
- *Trochodendron nastae*
- *Dillhoffia*
- *Peltandra primaeva*

## ***Notable Paleobotanists***

- Edward W. Berry (1875–1945), paleoecology and phytogeography
- Constantin von Ettingshausen (1826–1897), Tertiary floras
- Dunkinfield Henry Scott (1854–1934), analysis of the structures of fossil plants
- Kaspar Maria von Sternberg (1761–1838), the "father of paleobotany"
- Franz Unger (1800–1870), pioneer in plant physiology, phytotomy and soil science
- Jack A. Wolfe (1936–2005) Tertiary paleoclimate of western North America.

## Chapter 3

# Paleozoology and Micropaleontology

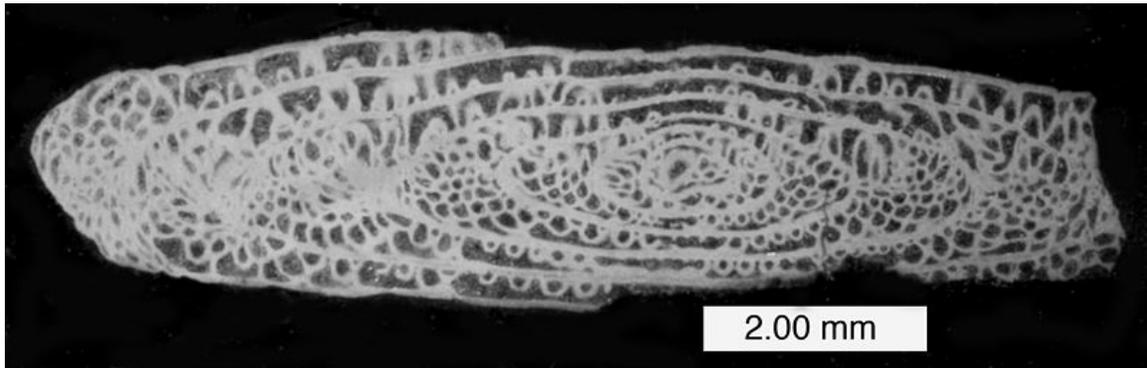
## Paleozoology

**Paleozoology**, also spelled as **palaeozoology**, is the branch of paleontology or paleobiology dealing with the recovery and identification of multicellular animal remains from geological (or even archeological) contexts, and the use of these fossils in the reconstruction of prehistoric environments and ancient ecosystems.

Definitive, macroscopic remains of these metazoans are found in the fossil record from the Ediacaran period of the Neoproterozoic era onwards, although they do not become common until the Late Devonian period in the latter half of the Paleozoic era.

Perhaps the best known macrofossils group is the dinosaurs. Other popularly known animal-derived macrofossils include trilobites, crustaceans, echinoderms, brachiopods, mollusks, bony fishes, sharks, Vertebrate teeth, and shells of numerous invertebrate groups. This is because hard organic parts, such as bones, teeth, and shells resist decay, and are the most commonly preserved and found animal fossils. Exclusively soft-bodied animals -- such as jellyfish, flatworms, nematodes, and insects -- are consequently rarely fossilized, as these groups do not produce hard organic parts.

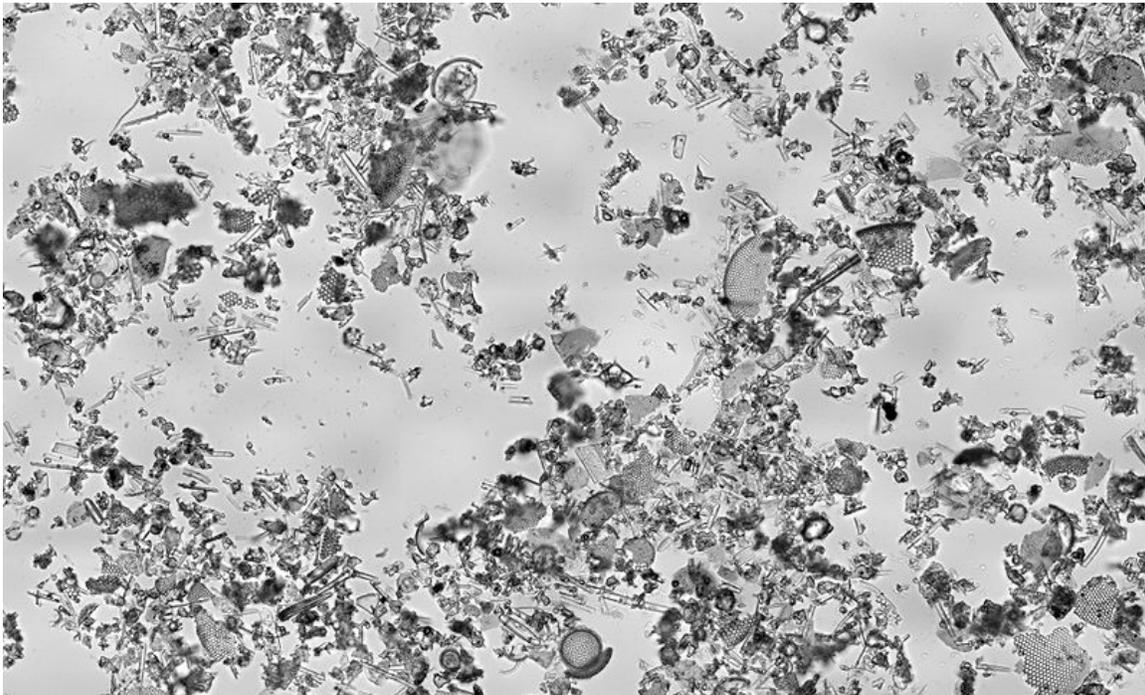
# Micropaleontology



Fusulinid (*Triticites*) from the Plattsmouth Chert, Red Oak, Iowa (Permian).

**Micropaleontology** (also sometimes spelled as **micropalaeontology**) is the branch of paleontology that studies microfossils.

## ***Microfossils***



Diatomaceous earth is a soft, siliceous, sedimentary rock made up of microfossils in the form of the frustules (shells) of single cell diatoms. This sample consists of a mixture of centric (radially symmetric) and pennate (bilaterally symmetric) diatoms. This image of diatomaceous earth particles in water is at a scale of 6.236 pixels/ $\mu\text{m}$ , the entire image covers a region of approximately 1.13 by 0.69 mm.

*Microfossils* are fossils generally not larger than four millimeters, and commonly smaller than one millimeter, the study of which requires the use of light or electron microscopy. Fossils which can be studied with the naked eye or low-powered magnification, such as a hand lens, are referred to as macrofossils. Obviously, it can be hard to decide whether or not some organisms should be considered microfossils, and so there is no fixed size boundary.

For example, some colonial organisms, such as bryozoa (especially the Cheilostomata) have relatively large colonies, but are classified on the basis of fine skeletal details of the tiny individuals of the colony. Most bryozoan specialists tend to consider themselves paleontologists, rather than micropaleontologists, but many micropaleontologists also study bryozoa.

In another example, many fossil genera of Foraminifera, which are protists, are known from shells (called "tests") that were as big as coins, such as the genus *Nummulites*.

Microfossils are a common feature of the geological record, from the Precambrian to the Holocene. They are most common in deposits of marine environments, but also occur in brackish water, fresh water and terrestrial sedimentary deposits. While every kingdom of life is represented in the microfossil record, the most abundant forms are protist skeletons or cysts from the Chrysophyta, Pyrrophyta, Sarcodina, acritarchs and chitinozoans, together with pollen and spores from the vascular plants.

### ***Areas of study***

Micropaleontology can be roughly divided into four areas of study on the basis of microfossil composition: (a) calcareous, as in coccoliths and foraminifera, (b) phosphatic, as in the study of some vertebrates, (c) siliceous, as in diatoms and radiolaria, or (d) organic, as in the pollen and spores studied in palynology.

This division reflects differences in the mineralogical and chemical composition of microfossil remains (and therefore in the methods of fossil recovery) rather than any strict taxonomic or ecological distinctions. Most researchers in this field, known as **micropaleontologists**, are typically specialists in one or more taxonomic groups.

## Calcareous microfossils



Fossil nummulitid foraminiferans showing microspheric and megalospheric individuals; Eocene of the United Arab Emirates; scale in mm.

Calcareous [ $\text{CaCO}_3$ ] microfossils include Coccoliths, Foraminifera, Calcareous dinoflagellates, and Ostracods (seed shrimp).

## Phosphatic microfossils

Phosphatic microfossils include Conodonts (tiny oral structures of an extinct chordate group), some scolecodonts ("worm" jaws), Shark spines and teeth, and other Fish remains (collectively called "ichthyoliths").

## Siliceous microfossils

Siliceous microfossils include Diatoms, Radiolaria, Silicoflagellates, phytoliths, some scolecodonts ("worm" jaws), and spicules.

## Organic microfossils

The study of organic microfossils is called palynology. Organic microfossils include pollen, spores, Chitinozoans (thought to be the egg cases of marine invertebrates), Scolecodonts ("worm" jaws), Acritarchs, Dinoflagellate cysts, and fungal remains.

## **Methods**

Sediment or rock samples are collected from either cores or outcrops, and the microfossils they contain extracted by a variety of physical and chemical laboratory techniques, including sieving, density separation by centrifuge, and chemical digestion of the unwanted fraction. The resulting concentrated sample of microfossils is then mounted on a slide for analysis, usually by light microscope. Taxa are then identified and counted. The very large numbers of microfossils that a small sediment sample can often yield allows the collection of statistically robust datasets which can be subjected to multivariate analysis. A typical microfossil study will involve identification of a few hundred specimens from each of ten to a hundred samples.

## **Applications of micropaleontology**

Microfossils are especially noteworthy for their importance in biostratigraphy. Since microfossils are often extremely abundant, widespread, and quick to appear and disappear from the stratigraphic record, they constitute ideal index fossils from a biostratigraphic perspective. In addition, the planktonic and nektonic habits of some microfossils gives them the added bonus of appearing across a wide range of facies or paleoenvironments, as well as having near-global distribution, making biostratigraphic correlation even more powerful and effective.

Microfossils also provide some of the most important records of global environmental change on long-timescales, particularly from deep-sea sediments. Across vast areas of the ocean floor, the shells of planktonic micro-organisms sinking from surface waters provide the dominant source of sediment, and they continuously accumulate (typically at rates of 20-50 million per million years). Study of changes in assemblages of microfossils and of changes in their shell chemistry (e.g., oxygen isotope composition) are fundamental to research on climate change in the geological past.

In addition to providing an excellent tool for sedimentary rock-body dating and for paleoenvironmental reconstruction – heavily used in both petroleum geology and paleoceanography – micropaleontology has also found a number of less orthodox applications, such as its growing role in forensic police investigation or in determining the provenance of archaeological artefacts.

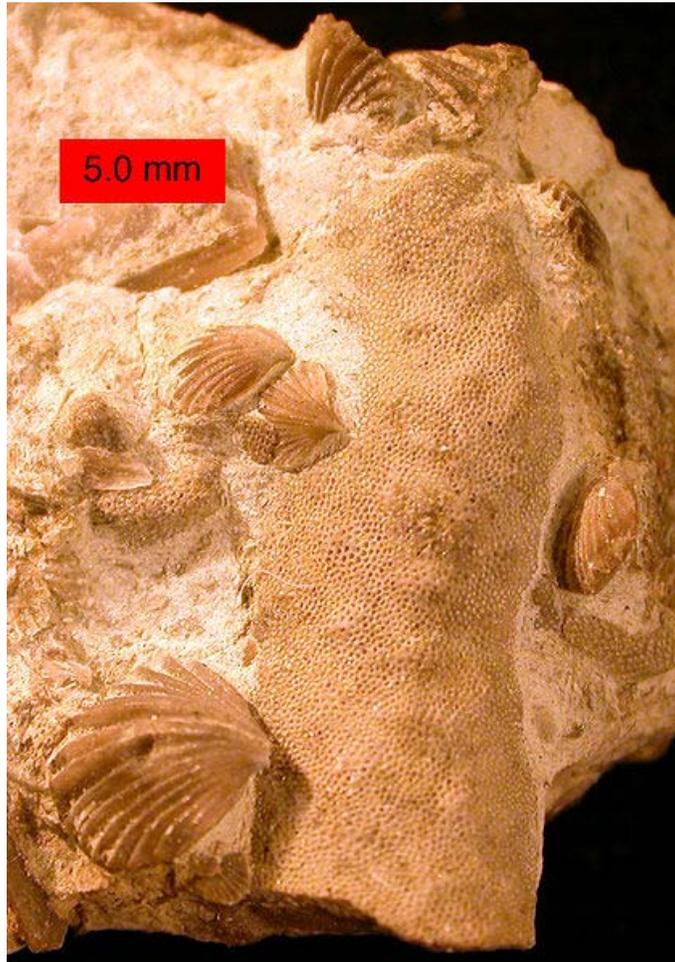
Micropaleontology is also a tool of Geoarchaeology used in archaeological reconstruction of human habitation sites and environments. Changes in the microfossil population abundance in the stratigraphy of current and former water bodies reflect changes in environmental conditions. Naturally occurring Ostracods in freshwater bodies are impacted by changes in salinity and pH due to human activities. When correlated with other dating techniques, prehistoric environments can be reconstructed. Work on Lake Tanganyika provided a profile of human induced environmental changes of a 4,000 year period.

Similar work in the arid American Southwest has provided information on irrigation canals used by prehistoric peoples from 2100 B.C. to 500 B.C. Other archaeological work in arid climates throughout the Americas has incorporated Micropaleontological analysis to build a more complete picture of prehistoric climate and human activity.

## Chapter 4

# Paleoecology and Ichnology

## Paleoecology



*Zygospira modesta*, spiriferid brachiopods, preserved in their original positions on a trepostome bryozoan; Cincinnatiian (Upper Ordovician) of southeastern Indiana.

**Paleoecology** uses data from fossils and subfossils to reconstruct the ecosystems of the past. It involves the study of fossil organisms and their associated remains, including their life cycle, living interactions, natural environment, and manner of death and burial to reconstruct the paleoenvironment.

The fossil record has been studied to try and clarify the relationship animals have to their environment, in part to help understand the current state of biodiversity. A close link has been found between vertebrate taxonomic and ecological diversity, that is the diversity of animals and the niches they occupy.

### ***Reconstruction and Measurement***

Paleoecology's aim is therefore to build the most detailed model possible of the life environment of previously living organisms found today as fossils. Such reconstruction takes into consideration complex interactions among environmental factors such as temperatures, food supplies, and degree of solar illumination. Often much of this information is lost or distorted by the fossilization process or diagenesis of the enclosing sediments, making interpretation difficult.

The environmental complexity factor is normally tackled through statistical analysis of the available numerical data (quantitative paleontology or paleostatistics), while the study of post-mortem processes is known as the field of taphonomy.

### ***Quaternary***

Much paleoecological research focuses on the last two million years (the Quaternary period) because older environments are less well-represented in the fossil timeline of evolution. Indeed, many studies concentrate on the Holocene epoch (the last 11,000 years), or the last glacial stage of the Pleistocene epoch (the Wisconsin/Weichsel/Devensian/Würm glaciation of the ice age, from 50,000 to 10,000 years ago). Such studies are useful for understanding the dynamics of ecosystem change and for reconstructing pre-industrialization ecosystems. Many public policy decision-makers have pointed to the importance of using paleoecological studies as a basis for choices made in conservation ecology.

# Ichnology



Dinosaur footprints, preserved at Dinosaur Ridge

**Ichnology** is the branch of geology that deals with traces of organismal behavior, such as burrows and footprints. It is generally considered as a branch of paleontology; however, only one division of ichnology, paleoichnology, deals with trace fossils, while neoichnology is the study of modern traces. Parallels can often be drawn between modern traces and trace fossils, helping scientists to decode the possible behavior and anatomy of the trace-making organisms even if no body fossils can be found. An **ichnologist** is a scientist whose area of study and research is ichnology.

Ichnologic studies are based on the discovery and analysis of biogenic structures: features caused by living organisms. Thus, burrows, trackways, trails and borings are all examples of biogenic structures, but not casts or molds of dead shells or other bodily remains. To keep body and trace fossils nomenclatorially separate, ichnospecies are erected for trace fossils. Ichnotaxa are classified somewhat differently in zoological nomenclature than taxa based on body fossils.

Examples include:

- Late Cambrian trace fossils from intertidal settings include *Protichnites* and *Climactichnites*, amongst others
- Mesozoic dinosaur footprints including ichnogenera such as *Grallator*, *Atreipus* and *Anomoepus*
- Triassic to Recent termite mounds, which can encompass several square kilometers of sediment

## Chapter 5

# Biostratigraphy

**Biostratigraphy** is the branch of stratigraphy which focuses on correlating and assigning relative ages of rock strata by using the fossil assemblages contained within them. Usually the aim is correlation, demonstrating that a particular horizon in one geological section represents the same period of time as another horizon at some other section. The fossils are useful because sediments of the same age can look completely different because of local variations in the sedimentary environment. For example, one section might have been made up of clays and marls while another has more chalky limestones, but if the fossil species recorded are similar, the two sediments are likely to have been laid down at the same time.



The first reef builder is a worldwide index fossil for the Lower Cambrian

Ammonites, graptolites, archeocyathids, and trilobites are index fossils that are widely used in biostratigraphy. Microfossils such as acritarchs, chitinozoans, conodonts, dinoflagellate cysts, pollen, spores and foraminiferans are also frequently used. Different fossils work well for sediments of different ages; trilobites, for example, are particularly useful for sediments of Cambrian age. To work well, the fossils used must be widespread geographically, so that they can occur in many different places. They must also be short lived as a species, so that the period of time during which they could be incorporated in the sediment is relatively narrow. The longer lived the species, the poorer the stratigraphic precision, so fossils that evolve rapidly, such as ammonites, are favoured over forms that evolve much more slowly, like nautiloids. Often biostratigraphic correlations are based on a fauna, not an individual species, as this allows greater precision. Further, if only one species is present in a sample, it can mean that (1) the strata were formed in the known fossil range of that organism; (2) that the fossil range of the organism was incompletely known, and the strata extend the known fossil range. For instance, the presence of the fossil *Treptichnus pedum* was used to define the base of the Cambrian period, but it has since been found in older strata.

Fossil assemblages were traditionally used to designate the duration of periods. Since a large change in fauna was required to make early stratigraphers create a new period, most of the periods we recognise today are terminated by a major extinction event or faunal turnover.

## ***Fossils as a basis for stratigraphic subdivision***

### **Concept of stage**

A stage is a major subdivision of strata, each systematically following the other each bearing a unique assemblage of fossils. Therefore, stages can be defined as a group of strata containing the same major fossil assemblages. French palaeontologist Alcide d'Orbigny is credited for the invention of this concept. He named stages after geographic localities with particularly good sections of rock strata that bear the characteristic fossils on which the stages are based.

### **Concept of zone**

In 1856 German palaeontologist Albert Oppel introduced the concept of zone (also known as biozones or Oppel zone). A zone includes strata characterised by the overlapping range of fossils. They represent the time between the appearance of species chosen at the base of the zone and the appearance of other species chosen at the base of the next succeeding zone. Oppel's zones are named after a particular distinctive fossil species, called an index fossil. Index fossils are one of the species from the assemblage of species that characterise the zone.

The zone is the fundamental biostratigraphic unit. Its thickness range from a few to hundreds of metres, and its extant range from local to worldwide. Biostratigraphic units are divided into six principal kinds of biozones:

- *Taxon range biozone* represent the known stratigraphic and geographic range of occurrence of a single taxon.
- *Concurrent range biozone* include the concurrent, coincident, or overlapping part of the range of two specified taxa.
- *Interval biozone* include the strata between two specific biostratigraphic surfaces. It can be based on lowest or highest occurrences.
- *Lineage biozone* are strata containing species representing a specific segment of an evolutionary lineage.
- *Assemblage biozones* are strata that contain a unique association of three or more taxa.
- *Abundance biozone* are strata in which the abundance of a particular taxon or group of taxa is significantly greater than in the adjacent part of the section.

### Index fossils



*Amplexograptus*, a graptolite index fossil, from the Ordovician near Caney Springs, Tennessee.

To be useful in stratigraphic correlation index fossils should be:

- Independent of their environment

- Geographically widespread (provincialism/isolation of species should be avoided as much as possible)
- Rapidly evolving
- Abundant (easy to find in the rock record)
- Easy to preserve (Easier in low-energy, non-oxidized environment)
- Easy to identify

## Chapter 6

# Taphonomy



Sponge borings (*Entobia*) and serpulid worm encrustations on a modern shell of the bivalve *Mercenaria* in North Carolina.

**Taphonomy** is the study of decaying organisms over time and how they become fossilized (if they do). The term taphonomy, was introduced to paleontology in 1940 by Russian scientist Ivan Efremov to describe the study of the transition of remains, parts, or products of organisms, from the biosphere, to the lithosphere, *i.e.* the creation of fossil assemblages.

Taphonomists study such phenomena as biostratinomy, decomposition, diagenesis, and encrustation and bioerosion by sclerobionts. (Sclerobionts are organisms which dwell on hard substrates such as shells or rocks.)

One motivation behind the study of taphonomy is to better understand biases present in the fossil record. Fossils are ubiquitous in sedimentary rocks, yet paleontologists cannot draw the most accurate conclusions about the lives and ecology of the fossilized organisms without knowing about the processes involved in their fossilization. For example, if a fossil assemblage contains more of one type of fossil than another, one can either infer that that organism was present in greater numbers, or that its remains were more resistant to decomposition.

During the late twentieth century, taphonomic data began to be applied to other paleontological subfields such as paleobiology, paleoceanography, ichnology (the study of trace fossils) and biostratigraphy. By coming to understand the oceanographic and ethological implications of observed taphonomic patterns, paleontologists have been able to provide new and meaningful interpretations and correlations that would have otherwise remained obscure in the fossil record.



An articulated wombat skeleton in Imperial-Diamond cave (Jenolan Caves).



The La Brea tar pits represent an unusual depositional environment for their epoch (Pleistocene) and location (southern California).

Archaeologists study taphonomic processes in order to determine how plant and animal (as well as human) remains accumulate and differentially preserve within archaeological sites. This is critical to determining whether these remains are associated with human activity. In addition, taphonomic processes may alter biological remains after they are deposited at a site. Some remains survive better than others over time, and can therefore bias an excavated collection.

Forensic taphonomy is concerned with the study of the decomposition of human remains, particularly in the context of burial sites.

Experimental taphonomy *testing* usually consists of exposing the remains of organisms to various altering processes, and then examining the effects of the exposure.

### **Research areas**

Taphonomy has undergone an explosion of interest since the 1980s, with research focussing on certain areas.

- microbial, biogeochemical, and larger-scale controls on the preservation of different tissue types; in particular, exceptional preservation in Konservat-lagerstätten. Covered within this field is the dominance of biological versus physical agents in the destruction of remains from all major taxonomic groups (plants, invertebrates, vertebrates)
- processes that concentrate biological remains; especially the degree to which different types of assemblages reflect the species composition and abundance of source faunas and floras
- the spatio-temporal resolution and ecological fidelity of species assemblages, particularly the relatively minor role of out-of-habitat transport contrasted with the major effects of time-averaging
- the outlines of megabiases in the fossil record, including the evolution of new bauplans and behavioral capabilities, and by broad-scale changes in climate, tectonics, and geochemistry of Earth surface systems.

### ***Taphonomic biases in the fossil record***

Because of the very select processes that cause preservation, not all organisms have the same chance of being preserved. An organism has a much greater chance of being preserved if it, say, has hard parts (e.g. most mollusks); this represents a bias in the fossil record towards organisms with hard parts. It is thus arguably the most important goal of taphonomy to identify the scope of such biases such that they can be quantified to allow correct interpretations of the relative abundances of organisms that make up a biota.

Sources of bias result from relative eases of preservation due to many different factors. Each variable that affects preservation is a source of bias, which are listed below.

#### **Spatial fidelity**

A sedimentary deposit may have experienced a mixing of noncontemporaneous remains within single sedimentary units via physical or biological processes; i.e. a deposit could be ripped up and redeposited elsewhere, meaning that an deposit may contain a large amount of fossils from another place (an **allochthonous** deposit, as opposed to the usual autochthonous). Thus, a question that is often asked of fossil deposits is to what extent does the fossil deposit record the true biota that originally lived there? Many fossils are obviously autochthonous, such as rooted fossils like crinoids, and many fossils are intrinsically obviously allochthonous, such as the presence of photoautotrophic plankton in a benthic deposit that must have sunk to be deposited. A fossil deposit may thus become biased towards exotic species (i.e. species not endemic to that area) when the sedimentology is dominated by gravity driven surges, such as mudslides, or may become biased if there is very little endemic organisms to be preserved. This is a particular problem in palynology.

## Temporal resolution

Because population turnover rates of individual taxa are much less than net rates of sediment accumulation, the biological remains of successive, noncontemporaneous populations of organisms may be admixed within a single bed, known as **time-averaging**. Because of the slow and episodic nature of the geologic record, two apparently contemporaneous fossils may have actually lived centuries, or even millennia, apart. Moreover, the *degree* of time averaging in an assemblage may vary. The degree varies on many factors, such as tissue type, the habitat, the frequency of burial events and exhumation events, and the depth of bioturbation within the sedimentary column relative to net sediment accumulation rates. Like biases in spatial fidelity, there is a bias towards organisms that can survive reworking events, such as shells. An example of a more ideal deposit with respect to time-averaging bias would be a volcanic ash deposit, which captures an entire biota caught in the wrong place at the wrong time (e.g. the Silurian Herefordshire lagerstätte).

## Compositional fidelity

This perhaps represents the biggest source of bias in the fossil record. First and foremost, biomineralizing organisms have a far greater chance of being represented in the fossil record than an entirely soft bodied organism. We know from habitats around the world that soft bodied organisms may form 30% to 100% of the biota, however most fossil assemblages preserve none of this unseen diversity. This bias thus acts at a very great taxonomic level, with entire phyla of animals cut out of the fossil record due to a lack of hard parts. Many animals that moult, on the other hand, are overrepresented, as one animal may leave multiple fossils due to its discarded body parts.

## Completeness of time series

The geological record is very discontinuous, and deposition is episodic at all scales. At the largest scale, a sedimentological high-stand period may mean that no deposition may occur for tens of thousands of years and, in fact, erosion of the deposit may occur. Such a hiatus is called an unconformity. Conversely, a catastrophic event such as a mudslide may overrepresent a time period. At a shorter scale, scouring processes such as the formation of ripples and dunes and the passing of turbidity currents may cause layers to be removed. Thus the fossil record is biased towards periods of greatest sedimentation; periods of time that have less sedimentation are consequently less well represented in the fossil record.

A related problem is the slow changes that occur in the depositional environment of an area; a deposit may experience periods of poor preservation to, for example, a lack of biomineralizing elements. This causes the taphonomic or diagenetic obliteration of fossils, producing gaps and condensation of the record.

## **Consistency in preservation over Geologic time**

Major shifts in intrinsic and extrinsic properties of organisms, including morphology and behavior in relation to other organisms-or shifts in the global environment, can cause secular or long-term cyclic changes in preservation (megabiases).

## **Human biases**

Much of the incompleteness of the fossil record is due to the fact that only a small amount of rock is ever exposed at the surface of the Earth, and not even most of that has been explored. Our fossil record relies on the small amount of exploration that has been done on this. Unfortunately, paleontologists as humans can be very biased in their methods of collection; a bias that must be identified. Potential sources of bias include,

- **Search images.** Field experiments have shown that paleontologists working on, say fossil clams are better at collecting clams than anything else, because their search images has been shaped to bias them in favour of clams.
- **Relative ease of extraction.** Fossils that are easy to obtain (such as many phosphatic fossils that are easily extracted en masse by dissolution in acid) are overabundant in the fossil record.
- **Taxonomic bias.** Fossils with easily discernable morphologies will be easy to distinguish as separate species, and will thus have an inflated abundance (this happened with the SSF).

## ***Preservation of biopolymers***

The taphonomic pathways involved in relatively inert substances such as calcite (and to a lesser extent bone) are relatively obvious, as such body parts are stable and change little through time. However, the preservation of "soft tissue" is more interesting, as it requires more peculiar conditions. While usually only biomineralised material survives fossilisation, the preservation of soft tissue is not as rare as sometimes thought.



Although chitin exoskeletons of arthropods are subject to decomposition, they often maintain shape during permineralization, especially if they are already somewhat mineralized.

Both DNA and proteins are unstable, and rarely survive more than hundreds of thousands of years before degrading. Polysaccharides also have low preservation potential, unless they are highly cross-linked; this interconnection is most common in structural tissues, and renders them resistant to chemical decay. Such tissues (resistant chemical in brackets) include wood (lignin), spores and pollen (sporopollenin), the cuticles of plants (cutan) and animals, the cell walls of algae (algaenan), and potentially the polysaccharide layer of some lichens. This interconnectedness makes the chemicals less prone to chemical decay, and also means they are a poorer source of energy so less likely to be digested by scavenging organisms. After being subjected to heat and pressure, these

cross-linked organic molecules typically 'cook' and become kerogen or short (<17 C atoms) aliphatic/aromatic carbon molecules. Other factors affect the likelihood of preservation; for instance scleritisation renders the jaws of polychaetes more readily preserved than the chemically equivalent but non-sclerotised body cuticle.

It was thought that only tough, cuticle type soft tissue could be preserved by Burgess shale type preservation, but an increasing number of organisms are being discovered that lack such cuticle, such as the probable chordate *Pikaia* and the shellless *Odontogriphus*.

It is a common misconception that anaerobic conditions are necessary for the preservation of soft tissue; indeed much decay is mediated by sulfate reducing bacteria which can only survive in anaerobic conditions. Anoxia does, however, reduce the probability that scavengers will disturb the dead organism, and the activity of other organisms is undoubtedly one of the leading causes of soft-tissue destruction.

Plant cuticle is more prone to preservation if it contains cutan, rather than cutin.

Plants and algae produce the most preservable compounds, which are listed according to their preservation potential by Tegellaar.

## Chapter 7

# Evolutionary Developmental Biology

**Evolutionary developmental biology (evolution of development** or informally, **evo-devo**) is a field of biology that compares the developmental processes of different organisms to determine the ancestral relationship between them, and to discover how developmental processes evolved. It addresses the origin and evolution of embryonic development; how modifications of development and developmental processes lead to the production of novel features, such as the evolution of feathers; the role of developmental plasticity in evolution; how ecology impacts in development and evolutionary change; and the developmental basis of homoplasy and homology.

Although interest in the relationship between ontogeny and phylogeny extends back to the nineteenth century, the contemporary field of evo-devo has gained impetus from the discovery of genes regulating embryonic development in model organisms. General hypotheses remain hard to test because organisms differ so much in shape and form.

Nevertheless, it now appears that just as evolution tends to create new genes from parts of old genes (molecular economy), evo-devo demonstrates that evolution alters developmental processes to create new and novel structures from the old gene networks (such as bone structures of the jaw deviating to the ossicles of the middle ear) or will conserve (molecular economy) a similar program in a host of organisms such as eye development genes in molluscs, insects, and vertebrates. Initially the major interest has been in the evidence of homology in the cellular and molecular mechanisms that regulate body plan and organ development. However more modern approaches include developmental changes associated with speciation.

### ***Basic principles***

Charles Darwin's theory of evolution is based on three principles: natural selection, heredity, and variation. At the time that Darwin wrote, the principles underlying heredity and variation were poorly understood. In the 1940s, however, biologists incorporated Gregor Mendel's principles of genetics to explain both, resulting in the modern synthesis. It was not until the 1980s and 1990s, however, when more comparative molecular

sequence data between different kinds of organisms was amassed and detailed, that an understanding of the molecular basis of the developmental mechanisms has arisen.

Currently, it is well understood how genetic mutation occurs. However, developmental mechanisms are not understood sufficiently to explain which kinds of phenotypic variation can arise in each generation from variation at the genetic level. Evolutionary developmental biology studies how the dynamics of development determine the phenotypic variation arising from genetic variation and how that affects phenotypic evolution (especially its direction). At the same time evolutionary developmental biology also studies how development itself evolves.

Thus, the origins of evolutionary developmental biology come from both an improvement in molecular biology techniques as applied to development, and the full appreciation of the limitations of classic neo-Darwinism as applied to phenotypic evolution. Some evo-devo researchers see themselves as extending and enhancing the modern synthesis by incorporating into it findings of molecular genetics and developmental biology. Others, drawing on findings of discordances between genotype and phenotype and epigenetic mechanisms of development, are mounting an explicit challenge to neo-Darwinism.

Evolutionary developmental biology is not yet a unified discipline, but can be distinguished from earlier approaches to evolutionary theory by its focus on a few crucial ideas. One of these is modularity: as has been long recognized, plants and animal bodies are modular: they are organized into developmentally and anatomically distinct parts. Often these parts are repeated, such as fingers, ribs, and body segments. Evo-devo seeks the genetic and evolutionary basis for the division of the embryo into distinct modules, and for the partly independent development of such modules.

Another central idea is that some gene products function as switches whereas others act as diffusible signals. Genes specify proteins, some of which act as structural components of cells and others as enzymes that regulate various biochemical pathways within an organism. Most biologists working within the modern synthesis assumed that an organism is a straightforward reflection of its component genes. The modification of existing, or evolution of new, biochemical pathways (and, ultimately, the evolution of new species of organisms) depended on specific genetic mutations. In 1961, however, Jacques Monod, Jean-Pierre Changeux and François Jacob discovered within the bacterium *Escherichia coli* a gene that functioned only when "switched on" by an environmental stimulus. Later, scientists discovered specific genes in animals, including a subgroup of the genes which contain the homeobox DNA motif, called Hox genes, that act as switches for other genes, and could be induced by other gene products, morphogens, that act analogously to the external stimuli in bacteria. These discoveries drew biologists' attention to the fact that genes can be selectively turned on and off, rather than being always active, and that highly disparate organisms (for example, fruit flies and human beings) may use the same genes for embryogenesis (e.g., the genes of the "developmental-genetic toolkit", see below), just regulating them differently.

Similarly, organismal form can be influenced by mutations in promoter regions of genes, those DNA sequences at which the products of some genes bind to and control the activity of the same or other genes, not only protein-specifying sequences. In addition to providing new support for Darwin's assertion that all organisms are descended from a common ancestor, this finding suggested that the crucial distinction between different species (even different orders or phyla) may be due less to differences in their content of gene products than to differences in spatial and temporal *expression* of conserved genes. The implication that large evolutionary changes in body morphology are associated with changes in gene regulation, rather than the evolution of new genes, suggested that the action of natural selection on promoters responsive to Hox and other "switch" genes may play a major role in evolution.

Another focus of evo-devo is developmental plasticity, the basis of the recognition that organismal phenotypes are not uniquely determined by their genotypes. If generation of phenotypes is conditional, and dependent on external or environmental inputs, evolution can proceed by a "phenotype-first" route, with genetic change following, rather than initiating, the formation of morphological and other phenotypic novelties. The case for this was argued for by Mary Jane West-Eberhard in her 2003 book *Developmental plasticity and evolution*.

## **History**

An early version of recapitulation theory, also called the *biogenetic law* or *embryological parallelism*, was put forward by Étienne Serres in 1824–26 as what became known as the "Meckel-Serres Law" which attempted to provide a link between comparative embryology and a "pattern of unification" in the organic world. It was supported by Étienne Geoffroy Saint-Hilaire as part of his ideas of idealism, and became a prominent part of his version of Lamarckism leading to disagreements with Georges Cuvier. It was widely supported in the Edinburgh and London schools of higher anatomy around 1830, notably by Robert Edmond Grant, but was opposed by Karl Ernst von Baer's embryology of divergence in which embryonic parallels only applied to early stages where the embryo took a general form, after which more specialised forms diverged from this shared unity in a branching pattern. The anatomist Richard Owen used this to support his idealist concept of species as showing the unrolling of a divine plan from an archetype, and in the 1830s attacked the transmutation of species proposed by Lamarck, Geoffroy and Grant. In the 1850s Owen began to support an evolutionary view that the history of life was the gradual unfolding of a teleological divine plan, in a continuous "ordained becoming", with new species appearing by natural birth.

In *On the Origin of Species* (1859), Charles Darwin proposed evolution through natural selection, a theory central to modern biology. Darwin recognised the importance of embryonic development in the understanding of evolution, and the way in which von Baer's branching pattern matched his own idea of descent with modification:

“ We can see why characters derived from the embryo should be of equal importance with those derived from the adult, for a natural classification of course includes all ages. ”

Ernst Haeckel (1866), in his endeavour to produce a synthesis of Darwin's theory with Lamarckism and Naturphilosophie, proposed that "ontogeny recapitulates phylogeny," that is, the development of the embryo of every species (ontogeny) fully repeats the evolutionary development of that species (phylogeny), in Geoffroy's linear model rather than Darwin's idea of branching evolution. Haeckel's concept explained, for example, why humans, and indeed all vertebrates, have gill slits and tails early in embryonic development. His theory has since been discredited. However, it served as a backdrop for a renewed interest in the evolution of development after the modern evolutionary synthesis was established (roughly 1936 to 1947).

Stephen Jay Gould called this approach to explaining evolution as *terminal addition*; as if every evolutionary advance was added as new stage by reducing the duration of the older stages. The idea was based on observations of neoteny. This was extended by the more general idea of heterochrony (changes in timing of development) as a mechanism for evolutionary change.

D'Arcy Thompson postulated that differential growth rates could produce variations in form in his 1917 book *On Growth and Form*. He showed the underlying similarities in *body plans* and how geometric *transformations* could be used to explain the variations.

Edward B. Lewis discovered homeotic genes, rooting the emerging discipline of evo-devo in molecular genetics. In 2000, a special section of the Proceedings of the National Academy of Sciences (PNAS) was devoted to "evo-devo", and an entire 2005 issue of the Journal of Experimental Zoology Part B: Molecular and Developmental Evolution was devoted to the key evo-devo topics of evolutionary innovation and morphological novelty.

### ***The developmental-genetic toolkit***

**The developmental-genetic toolkit** consists of a small fraction of the genes in an organism's genome whose products control its development. These genes are highly conserved among Phyla. Differences in deployment of toolkit genes affect the body plan and the number, identity, and pattern of body parts. The majority of toolkit genes are components of signaling pathways, and encode for the production of transcription factors, cell adhesion proteins, cell surface receptor proteins, and secreted morphogens, all of these participate in defining the fate of undifferentiated cells, generating spatial and temporal patterns, which in turn form the body plan of the organism. Among the most important of the toolkit genes are those of the **Hox** gene cluster, or complex. Hox genes, transcription factors containing the more broadly distributed homeobox protein-binding DNA motif, function in patterning the body axis. Thus, by combinatorial specifying the identity of particular body regions, Hox genes determine where limbs and other body

segments will grow in a developing embryo or larva. A paragon of a toolbox gene is *Pax6/eyeless*, which controls eye formation in all animals. It has been found to produce eyes in mice and *Drosophila*, even if mouse *Pax6/eyeless* was expressed in *Drosophila*.

This means that a big part of the morphological evolution undergone by organisms is a product of variation in the genetic toolkit, either by the genes changing their expression pattern or acquiring new functions. A good example of the first is the enlargement of the beak in Darwin's Large Ground-finch (*Geospiza magnirostris*), in which the gene *BMP* is responsible for the larger beak of this bird, relative to the other finches.

The loss of legs in snakes and other squamates is another good example of genes changing their expression pattern. In this case the gene *Distal-less* is very under-expressed, or not expressed at all, in the regions where limbs would form in other tetrapods. This same gene determines the spot pattern in butterfly wings, which shows that the toolbox genes can change their function.

Toolbox genes, as well as being highly conserved, also tend to evolve the same function convergently or in parallel. Classic examples of this are the already mentioned *Distal-less* gene, which is responsible for appendage formation in both tetrapods and insects, or, at a finer scale, the generation of wing patterns in the butterflies *Heliconius erato* and *Heliconius melpomene*. These butterflies are Müllerian mimics whose coloration pattern arose in different evolutionary events, but is controlled by the same genes. The previous supports Kirschner and Gerhardt's theory of Facilitated Variation, which states that morphological evolutionary novelty is generated by regulatory changes in various members of a large set of conserved mechanisms of development and physiology.

### ***Development and the origin of novelty***

Among the more surprising and, perhaps, counterintuitive (from a neo-Darwinian viewpoint) results of recent research in evolutionary developmental biology is that the diversity of body plans and morphology in organisms across many phyla are not necessarily reflected in diversity at the level of the sequences of genes, including those of the developmental genetic toolkit and other genes involved in development. Indeed, as Gerhart and Kirschner have noted, there is an apparent paradox: "where we most expect to find variation, we find conservation, a lack of change".

Even within a species, the occurrence of novel forms within a population does not generally correlate with levels of genetic variation sufficient to account for all morphological diversity. For example, there is significant variation in limb morphologies amongst salamanders and in differences in segment number in centipedes, even when the respective genetic variation is low.

A major question then, for evo-devo studies, is: If the morphological novelty we observe at the level of different clades is not always reflected in the genome, where does it come from? Apart from neo-Darwinian mechanisms such as mutation, translocation and duplication of genes, novelty may also arise by mutation-driven changes in gene

regulation. The finding that much biodiversity is not due to differences in genes, but rather to alterations in gene regulation, has introduced an important new element into evolutionary theory. Diverse organisms may have highly conserved developmental genes, but highly divergent regulatory mechanisms for these genes. Changes in gene regulation are "second-order" effects of genes, resulting from the interaction and timing of activity of gene networks, as distinct from the functioning of the individual genes in the network.

The discovery of the homeotic Hox gene family in vertebrates in the 1980s allowed researchers in developmental biology to empirically assess the relative roles of gene duplication and gene regulation with respect to their importance in the evolution of morphological diversity. Several biologists, including Sean B. Carroll of the University of Wisconsin–Madison suggest that "changes in the cis-regulatory systems of genes" are more significant than "changes in gene number or protein function". These researchers argue that the combinatorial nature of transcriptional regulation allows a rich substrate for morphological diversity, since variations in the level, pattern, or timing of gene expression may provide more variation for natural selection to act upon than changes in the gene product alone.

Epigenetic alterations of gene regulation or phenotype generation that are subsequently consolidated by changes at the gene level constitute another class of mechanisms for evolutionary innovation. Epigenetic changes include modification of the genetic material due to methylation and other reversible chemical alteration, as well as nonprogrammed remodeling of the organism by physical and other environmental effects due to the inherent plasticity of developmental mechanisms. The biologists Stuart A. Newman and Gerd B. Müller have suggested that organisms early in the history of multicellular life were more susceptible to this second category of epigenetic determination than are modern organisms, providing a basis for early macroevolutionary changes.

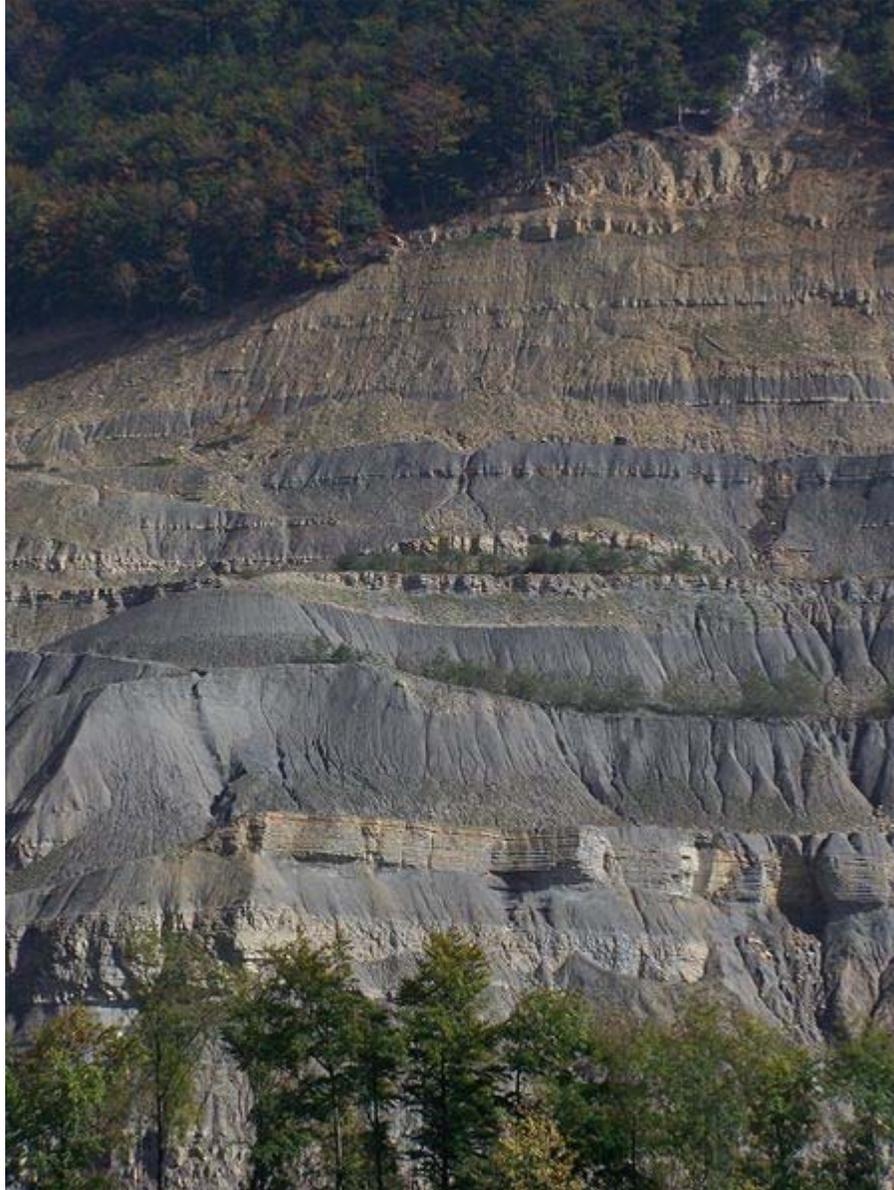
## Chapter 8

# Eonothem and Megabias

## Eonothem



Horseshoe Canyon Formations exposed in Horseshoe Canyon near Drumheller, Alberta.



Oxfordian (Upper Jurassic) cyclic sediments at Péry-Reuchenette, near Tavannes, kanton Bern, Switzerland. Alternating layers are limestone (light, more competent) and marl/clay; dominant cycle is the 200000 year-cycle.

In stratigraphy and geology, an **eonothem** is the totality of rock strata laid down in the stratigraphic record deposited during a certain eon of the continuous geologic timescale. The Eonothem is not to be confused with the eon itself, which is a corresponding division of geologic time spanning a specific amount of (millions of) years, during which rocks were formed that are classified within the eonothem. In practice, the rock column is discontinuous:

“ Technically, a complete geologic record doesn't occur anywhere. For such a record to develop would require the area to have been receiving sedimentary deposits continually ever since the origin of the earth. Nowhere is such a situation known to exist. If it did exist, we could not effectively look at the strata because they would still be buried, and modern strata would continue to be deposited on top of them.

The earth's surface has been far too dynamic to allow that to occur anywhere. No area has been in such a static condition throughout the earth's long history. Areas that have had sediment deposited on them at one time are later uplifted and eroded. In some places this has occurred many times. There is ample evidence to prove such a sequence of events.

”

Eonothems, despite discontinuities (locally missing strata or unconformities), can be compared to others where the rock record is more complete and by correlation of points of correspondence be fixed appropriately within the eon. Eonothems are therefore useful as a broad chronostratigraphic unit, specifying approximate age within the timelines within the rock column.

Eonothems are subdivided into erathems and their smaller subdivisions within geology and paleobiology and their sub-fields, and a whole system of cross-disciplinary classification by strata is in place with oversight by the International Commission on Stratigraphy. Since oldest rocks are deposited first and lowest in a stratigraphic section, whether one is discussing the rock record is usually clear in context. (A fossil or feature present in the "upper Phanerozoic" eonothem (strata) would be discussed as being dated within the "later Phanerozoic" eon, whereas something found in the middle Phanerozoic could be discussing a layer, stage or the relative time.)

Eonothems are not often used in practice as expert dating estimates can be and usually are specified into the more refined timelines of smaller chronostratigraphic units, which can be subdivided in turn down to the many defined stages, the smallest units used in dating.

Eonothems have the same names as their corresponding eons, which means during the history of the Earth only four eonothems were formed. Oldest to newest these are the Hadean, Archean, Proterozoic, and Phanerozoic.

### ***Dating standards***

GSSAs are defined by the International Commission on Stratigraphy and are used primarily for time dating rock layers older than 630 million years ago (mya), before a good fossil record exists. The record becomes spotty at about 542 mya, and the ICS may well have resort to defining additional GSSA's between the two dates.

For more recent periods, a Global Boundary Stratotype Section and Point (GSSP), largely based on research progress in geobiology and improved methods of fossil dating is used to define such boundaries. In contrast to GSSAs, GSSPs are based on important events and transitions within a particular stratigraphic section. In older sections, there is insufficient fossil record or well preserved sections to identify the key events necessary for a GSSP so GSSAs are defined based on fixed dates.

## Megabias

A **megabias**, or a **taphonomic megabias** is a large scale pattern in the quality of the fossil record that affects paleobiologic analysis at provincial to global levels and at timescales usually exceeding ten million years. It can result from major shifts in intrinsic and extrinsic properties of organisms, including morphology and behaviour in relation to other organisms, or shifts in the global environment, which can cause secular or long-term cyclic changes in preservation

### ***Introduction***

The fossil record exhibits bias at many different levels. At the most basic level, there is a global bias towards biomineralizing organisms, because biomineralized body parts are more resistant to decay and degradation. Due to the principle of uniformitarianism, there is a basic assumption in geology that the formation of rocks has occurred by the same naturalistic processes throughout history, and thus that the reach of such biases remains stable over time. A megabias is a direct contradiction of this, whereby changes occur in large scale paleobiologic patterns. This includes

- Changes in diversity and community structure over tens of millions of years
- Variation in the quality of the fossil record between mass and background extinction times
- Variation among different climate states, biogeographic provinces, and tectonic settings.

It is generally assumed that the quality of the fossil record decreases globally and across all taxa with increasing age, because more time is available for the diagenesis and destruction of both fossils and enclosing rocks, and thus the term "megabias" is usually used to refer to global trends in preservation. However it has been noted that the fossil record of some taxa actually *improves* with greater age. Examples such as this, and other related paleobiological trends, clearly indicate the action of a megabias, but only within one particular taxon. Hence, it is necessary to define four classes of megabias related to the reach of the bias, first defined by Kowalewski and Flessa.

### ***Within-taxon megabias***

A change in the quality of a single taxon's record. It may happen whenever evolutionary, environmental, or geologic trends affect the taxon's fossilization potential.

## ***Among-taxon static megabias***

This occurs when the fossilization potential varies from group to group. Among-taxon megabiases include both static and dynamic distortions. A static megabias is constant through time. For example, flatworms have always had a poor record relative to mollusks because mollusks as a taxon are almost always biomineralizing, whereas flatworms are almost never biomineralizing.

## ***Among-taxon dynamic megabias***

A dynamic megabias occurs when the fossilization potential of one group relative to that of another group changes through time. For example, lingulide brachiopods had a lower fossilization potential than articulate brachiopods, but only in the early Paleozoic. This has changed through time, governed by changes in bathymetry and lateral shifts in lithofacies associated with basin evolution. By the Middle Ordovician, articulates had diversified to become important components of all marine environments except the deep basin; inarticulates were most important in offshore and basinal settings. By moving away from the main taphonomic window, the inarticulates sacrificed their fossilization potential whilst not necessarily decreasing their biological diversity.

## ***Global megabias***

A global megabias is one that occurs over the whole world, though not necessarily in all depositional environments. There are numerous documented examples of this, many of which concern the Cambrian explosion and the Ediacaran fauna, both divisive subjects within the paleobiological community. Darwin commented on the Cambrian Explosion, it being a great problem in his eyes, and speculated that it may be due to a increased propensity for preservation in the Cambrian and a reduced potential beforehand.

## **Cambrian reduction of phosphatization**

Many fossils, such as the Cambrian Small Shelly Fauna (SSF) are preserved through secondary phosphatization. Such preservation can boost the diversity estimates in three ways:

- By preserving fossils that might otherwise be destroyed
- By preserving fine anatomical structures that enhance taxonomic resolution. Small anatomical details will show differences between two specimens that would otherwise be lumped within the same group; in this way, an inflated measure of diversity is given
- By allowing easy collection. Phosphatized organisms are incredibly easily to extract by acid maceration, allowing large numbers of specimens to be collected with ease.

The number of phosphatic facies deposits decreases significantly from the early- to mid-Cambrian. Most probably, this is the cause for the pattern of SSF diversity decline after

the Botomian extinction. Whilst there may well have been a significant extinction worldwide of small shelly fossils, a significant decrease in the abundance of phosphatized facies may have caused the decline in SF diversity to appear much more severe than it really was.

### **Overabundance of Konzervat-Lagerstätten**

It has been noted after the last 20 years that Exceptional Faunas, a particular class of Konzervat-Lagerstätten exemplified by Burgess shale deposits, are statistically overabundant considering their age and style of preservation. This problem is also known as the "Post-Cambrian closure of the deep-water slope-basin taphonomic window". It seems that the cause of this may have been ecological, at least in the root cause; a post-Cambrian changes in the amount of bioturbation in deeper-water low oxygen environments increased sedimentary porosity and thus enhanced microbial activity and accelerated rates of decay. These higher rates of decay after the Cambrian meant that many soft bodied organisms were destroyed before the opportunity for preservation arose.

## Chapter 9

# Stage (Stratigraphy) and System (Stratigraphy)

## Stage (stratigraphy)

Units in geochronology and stratigraphy		
Segments of rock (strata) in chronostratigraphy	Periods of time in geochronology	Notes
Eonothem	Eon	4 total, half a billion years or more
Erathem	Era	12 total, several hundred million years
System	Period	
Series	Epoch	tens of millions of years
<b>Stage</b>	Age	millions of years
Chronozone	Chron	smaller than an age/stage, not used by the ICS timescale

In chronostratigraphy, a **stage** is a succession of rock strata laid down in a single age on the geologic timescale, which usually represents millions of years of deposition. A given stage of rock and the corresponding age of time will by convention have the same name, and the same boundaries.

Rock series are divided into stages, just as geological epochs are divided into ages. Stages can be divided into smaller stratigraphic units called chronozones.

The term **faunal stage** is sometimes used, referring to the fact that the same fauna (animals) are found throughout the layer (by definition).

## ***Defining***

Stages are primarily defined by a consistent set of fossils (biostratigraphy) or a consistent magnetic polarity in the rock. Usually one or more index fossils that are common, found worldwide, easily recognized, and limited to a single, or at most a few, stages are used to define the stage's bottom.

Thus, for example, in the (still used) local North American subdivision paleontologist finding fragments of the trilobite *Olenellus* would identify the beds as being from the Waucoban Stage whereas fragments of a later trilobite such as *Elrathia* would identify the stage as Albertan.

Stages were very important in the 19th and early 20th century as they were the major tool available for dating rock beds until the development of seismology and radioactive dating in the second half of the 20th Century. Microscopic analysis of the rock (petrology) is also sometimes useful in confirming that a given segment of rock is from a particular age.

Originally, faunal stages were only defined regionally; however as additional stratigraphic tools, and especially geochronological ones, were developed, stages were defined over broader and broader areas. More recently, the adjective "faunal" has been dropped as regional and global correlations of rock sequences have become relatively certain and there is less need for faunal labels to define the age of formations. A tendency developed to use European and, to a lesser extent, Asian, stage names for the same time period world wide, even though the faunas in other regions often had little in common with the stage as originally defined.

## ***International standardization***

Boundaries and names are established by the International Commission on Stratigraphy (ICS) of the International Union of Geological Sciences. As of 2008, the ICS is nearly finished a task begun in 1974, subdividing the Phanerozoic eonothem into internationally accepted stages using two types of benchmark. For younger stages, a Global Boundary Stratotype Section and Point (GSSP), a physical outcrop clearly demonstrates the boundary. For older stages, a Global Standard Stratigraphic Age (GSSA) is an absolute date. The benchmarks will give a much greater certainty that results can be compared with confidence in the date determinations, and such results will have farther scope than any evaluation based solely on local knowledge and conditions.

In many regions around the world local subdivisions and classification criteria are still used along with the newer internationally coordinated uniform system, but once the

research establishes a more complete international system, it is expected that local systems will be abandoned.

### ***Stages and lithostratigraphy***

Stages can include many lithostratigraphic units (for example formations, beds, members, etc.) of differing rock types that were being laid down in different environments at the same time. In the same way, a lithostratigraphic unit can include a number of stages or parts of them.

## **System (stratigraphy)**

A **system** in the natural sciences and stratigraphy is an idealized composite unit of the geologic record made up of a succession of rock layers that were laid down together within a certain corresponding geological time span, and are used in turn to date things to a certain corresponding geologic period. The system is thus a unit of the geologic record or rock column, pieced together using the Law of Superposition and mapped to its corresponding period—the associated continuous chronostratigraphical time unit, a relative metric that science committees have determined solid dating for as organized on the geologic time scale. A system is therefore a unit of chronostratigraphy, unrelated to lithostratigraphy, which subdivides rock layers on their lithology. Systems are subdivisions of erathems and are themselves divided into series, epochs and stages.

System is a term defining a unit of rocklayers formed in a certain time interval; it is in theory equivalent to the term *period* defining the interval of time itself, but unlike the system of time units, a system in many locations may be interrupted and incomplete as geologic forces alternately uplift or depress a region, bend the landscape and so expose a terrain feature once accumulating rock to weathering and vice versa. The overall rock record has been piecewise constructed throughout each physical system, series, et al. using superposition, and is treated in practice as one large continuous rock column, the whole matching the corresponding period. For this reason, the two words are sometimes confused in informal literature.

### ***Systems in the geological timescale***

The systems of the Phanerozoic eonothem were defined during the 19th century, beginning with the Cretaceous (by Belgian geologist Jean d'Omalius d'Halloy in the Paris Basin) and the Carboniferous (by British geologists William Conybeare and William Phillips) in 1822. The Paleozoic and Mesozoic erathems were divided into the currently used systems before the second half of the 19th century, except for a minor revision when the Ordovician system was added in 1879.

The Cenozoic has recently seen some revisions by the International Commission on Stratigraphy; it will most probably be divided into three systems (Paleogene, Neogene and Quaternary) while older (and currently still better known) names are now series (Paleocene, Eocene, Oligocene, Miocene and Pliocene) or abandoned (Tertiary).

Another recent development is the official division of the Proterozoic eonothem into systems, which was decided in 2004.

## Chapter 10

# Cenomanian

The **Cenomanian** is, in the ICS' geological timescale the oldest or earliest age of the Late Cretaceous epoch or the lowest stage of the Upper Cretaceous series. An age is a unit of geochronology: it is a unit of time; the stage is a unit in the stratigraphic column deposited during the corresponding age. Both age and stage bear the same name.

As a unit of geologic time measure, the Cenomanian age spans the time between  $99.6 \pm 0.9$  Ma and  $93.5 \pm 0.8$  Ma (million years ago). In the geologic timescale it is preceded by the Albian and is followed by the Turonian.

The Cenomanian is coeval with the Woodbinian of the regional timescale of the Mexican Gulf and the Eaglefordian of the regional timescale of the US eastcoast.

At the end of the Cenomanian an anoxic event took place, called the Cenomanian-Turonian boundary event or the "Bonarelli Event", that is associated with a minor extinction event for marine species.

### ***Stratigraphic definitions***

The Cenomanian was introduced in scientific literature by French palaeontologist Alcide d'Orbigny in 1847. Its name comes from the New Latin name of the French city of Le Mans (département Sarthe), *Cenomanum*.

The base of the Cenomanian stage (which is also the base of the Upper Cretaceous series) is placed at the first appearance of foram species *Rotalipora globotruncanoides* in the stratigraphic record. An official reference profile for the base of the Cenomanian (a GSSP) is located in an outcrop at the western flank of Mont Risou, near the village of Rosans in the French Alps (département Hautes-Alpes, coordinates:  $44^{\circ}23'33''\text{N}$ ,  $5^{\circ}30'43''\text{E}$ ). The base is, in the reference profile, located 36 meters below the top of the Marnes Bleues Formation.

The top of the Cenomanian (the base of the Turonian) is at the first appearance of ammonite species *Watinoceras devonense*.

Important index fossils for the Cenomanian are the ammonites *Calycocheras naviculare*, *Acanthoceras rhotomagense* and *Mantelliceras mantelli*.

## Sequence stratigraphy and palaeoclimatology

The late Cenomanian represents the highest mean sea-level observed in the Phanerozoic eon, the past six hundred million years (approximately one hundred and fifty meters above present day sea-levels). A corollary is that the highlands were at all time lows, so the landscape on Earth was one of warm broad shallow seas inundating low lying land areas on the precursors to today's continents. What few lands rose above the waves were made of old mountains and hills, upland plateaus, all much weathered. Tectonic mountain building was minimal and most continents were isolated by large stretches of water. Without highlands to brake winds, the climate would have been windy and waves large, adding to the weathering and fast rate of sediment deposition.

## Palaeontology

### †Belemnites

#### Belemnites of the Cenomanian

Taxa	Presence	Location	Description	Images
<i>Hibolites</i>				

### †Ankylosauria

#### Ankylosaurs of the Cenomanian

Taxa	Presence	Location	Description	Images
<ul style="list-style-type: none"> <li><i>Acanthopholis</i></li> </ul>	Albian or Aptian to Cenomanian	Upper Greensand Group, Cambridgeshire, England	A nodosaurid with an armor of oval plates set almost horizontally into the skin, with spikes protruding from the neck and shoulder area, along the spine. Its size has been estimated to be in the range of 3 to 5.5 meters (10 to 18 ft) long and approximately 380 kilograms (840 lb) in	 <p><i>Acanthopholis</i></p>

- Animantarx* Cenomanian to Turonian Cedar Mountain Formation, Utah, USA weight. thought of as a nodosaurid ankylosaur, although its precise relationships within that family are uncertain. A nodosaurid ankylosaur about 4 to 6 meters (13 to 20 feet) long with bony dermal plates covering the top of its body. It may have had spikes along its side as well. It had four short legs, five-toed feet, a short neck, and a long, stiff, clubless tail.
- Nodosaurus* Wyoming, Kansas, USA
- Stegopelta* Late Albian to early Cenomanian Frontier Formation, Wyoming, USA A poorly known genus of nodosaurid
- Tsagantegia* Baynshiree Svita Formation, Dzun-Bayan, Mongolia An ankylosaurid known from the remains of its skull
- Zhejiangosaurus* Chaochuan Formation, Zhejiang, China Nodosaurid
- Zhongyuansaurus* Ruyang, Henan, China Nodosaurid

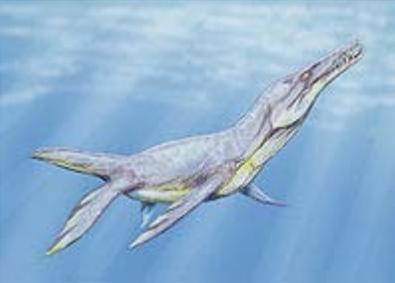
## †Ornithopoda

Ornithopods of the Cenomanian				
Taxa	Presence	Location	Description	Images
<i>Anabisetia</i>		Cerro Lisandro Formation, Neuquén, Argentina	A small bipedal herbivore, almost seven feet (2 meters) long	
<i>Bihariosaurus</i>		Bihor, Romania	An iguanodont similar to Camptosaurus	
<i>Eolambia</i>	Albian-	Utah, USA	An iguanodont	

<i>Gadolosaurus</i>	Cenomanian	Mongolia	
<i>Notohypsilophodon</i>	Cenomanian-Turonian	Bajo Barreal Formation, Chubut, Argentina	A hypsilophodontid or other basal ornithopod, <i>Notohypsilophodon</i> would have been a bipedal herbivore. Its size has not been estimated
<i>Oryctodromeus</i>		Blackleaf Formation, Montana, and Wayan Formation, Idaho, USA	A burrowing hypsilophodont
<i>Protohadros</i>		Flower Mound, Texas, USA	A primitive hadrosauroid, <i>Protohadros</i> reached 6 m (19.5 ft) in length and had many hadrosaur-like features
<i>Shuangmiaosaurus</i>	Cenomanian-Turonian	China	A poorly known iguanodont

## †Plesiosauria

### Plesiosaurs of the Cenomanian

Taxa	Presence	Location	Description	Images
<i>Plesioleurodon</i>		Belle Fourche Shale, Wyoming, USA	A pliosaurid characterized by a moderately long symphysis bearing 8 pairs of teeth, teeth that are nearly circular in cross-section and which are smooth on the outer surface (except near the base), ribs of the neck vertebrae being single-headed (double-headed in Jurassic pliosaurs), and a long slender interpectoral bar on the coracoid	 <p><i>Plesioleurodon</i></p>

## †Sauropoda

### Sauropods of the Cenomanian

Taxa	Presence	Location	Description	Images
<i>Argentinosaurus</i>		Río Limay Formation, Neuquén, Argentina		 <p><i>Argentinosaurus</i></p>
<i>Brachiosaurus</i>	? <i>Brachiosaurus nougaredi</i>	Wargla, Algeria		

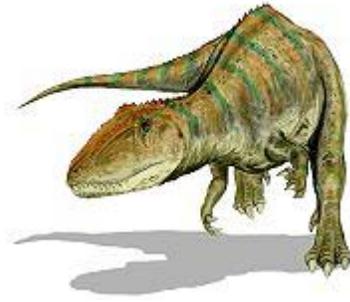
*Brachiosaurus*

## Theropoda

### Theropods of the Cenomanian

Taxa	Presence	Location	Description
<i>Bahariasaurus</i>		Bahariya Oasis, Egypt; Niger	
<i>Carcharodontosaurus</i>		Morocco; Niger	
<i>Deltadromeus</i>		Morocco	
<i>Giganotosaurus</i>		Rio Limay, Argentina	
<i>Mapusaurus</i>		Huincul Formation, Argentina	
<i>Oxalaia</i>		Brasil	
<i>Siamosaurus</i>		Thailand	
<i>Sigilmassasaurus</i>		Tafilalt, Morocco	
<i>Spinosaurus</i>		Bahariya Oasis, Egypt; Tunisia; Morocco	
<i>Unenlagia</i>		Comahue, Argentina	

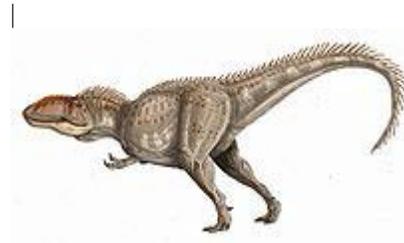
### Images



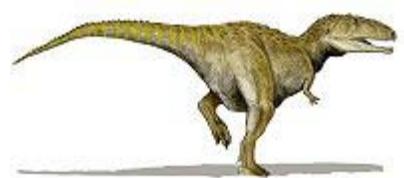
*Carcharodontosaurus*



*Deltadromeus*



*Giganotosaurus*



*Mapusaurus*  
File:Spinosaurus BW.jpg  
*Spinosaurus*

unnamed  
enantiornithine bird

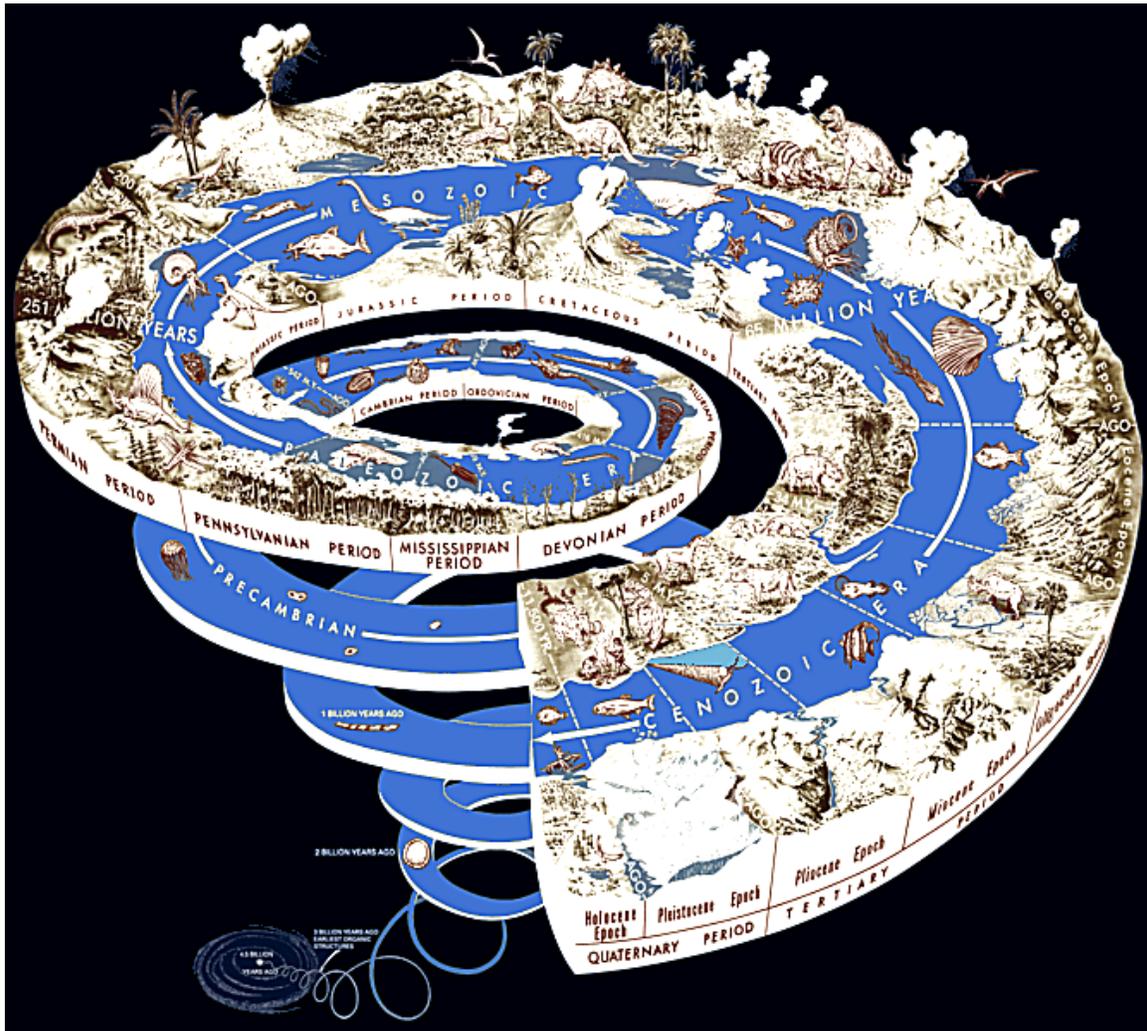
Nammoura, Ouadi al  
Gabour, Lebanon



*Unenlagia*

# Chapter 11

# Paleontology



Paleontology investigates the entire history of life on Earth.



A paleontologist at work at John Day Fossil Beds National Monument



The preparation of the fossilized bones of *Europasaurus holgeri*

**Paleontology** is the study of prehistoric life, including organisms' evolution and interactions with each other and their environments (their paleoecology). As a "historical science" it tries to explain causes rather than conduct experiments to observe effects. Paleontological observations have been documented as far back as the 5th century BC. The science became established in the 18th century as a result of Georges Cuvier's work on comparative anatomy, and developed rapidly in the 19th century. Fossils found in China since the 1990s have provided new information about the earliest evolution of animals, early fish, dinosaurs and the evolution of birds and mammals. Paleontology lies on the border between biology and geology, and shares with archaeology a border that is difficult to define. It now uses techniques drawn from a wide range of sciences, including biochemistry, mathematics and engineering. As knowledge has increased, paleontology has developed specialized subdivisions, some of which focus on different types of fossil organisms while others study ecological and environmental history, such as ancient climates.

Body fossils and trace fossils are the principal types of evidence about ancient life, and geochemical evidence has helped to decipher the evolution of life before there were organisms large enough to leave fossils. Estimating the dates of these remains is essential but difficult: sometimes adjacent rock layers allow radiometric dating, which provides absolute dates that are accurate to within 0.5%, but more often paleontologists have to rely on relative dating by solving the "jigsaw puzzles" of biostratigraphy. Classifying ancient organisms is also difficult, as many do not fit well into the Linnean taxonomy that is commonly used for classifying living organisms, and paleontologists more often use cladistics to draw up evolutionary "family trees". The final quarter of the 20th century saw the development of molecular phylogenetics, which investigates how closely organisms are related by measuring how similar the DNA is in their genomes. Molecular phylogenetics has also been used to estimate the dates when species diverged, but there is controversy about the reliability of the molecular clock on which such estimates depend.

Use of all these techniques has enabled paleontologists to discover much of the evolutionary history of life, almost all the way back to when Earth became capable of supporting life, about 3,800 million years ago. For about half of that time the only life was single-celled micro-organisms, mostly in microbial mats that formed ecosystems only a few millimeters thick. Earth's atmosphere originally contained virtually no oxygen, and its oxygenation began about 2,400 million years ago. This may have caused an accelerating increase in the diversity and complexity of life, and early multicellular plants and fungi have been found in rocks dated from 1,700 to 1,200 million years ago. The earliest multicellular animal fossils are much later, from about 580 million years ago, but animals diversified very rapidly and there is a lively debate about whether most of this happened in a relatively short Cambrian explosion or started earlier but has been hidden by lack of fossils. All of these organisms lived in water, but plants and invertebrates started colonizing land from about 490 million years ago and vertebrates followed them about 370 million years ago. The first dinosaurs appeared about 230 million years ago and birds evolved from one dinosaur group about 150 million years ago. During the time of the dinosaurs, mammals' ancestors survived only as small, mainly nocturnal insectivores, but after the non-avian dinosaurs became extinct in the Cretaceous–Tertiary

extinction event 65 million years ago mammals diversified rapidly. Flowering plants appeared and rapidly diversified between 130 million years ago and 90 million years ago, possibly helped by coevolution with pollinating insects. Social insects appeared around the same time and, although they have relatively few species, now form over 50% of the total mass of all insects. Humans evolved from a lineage of upright-walking apes whose earliest fossils date from over 6 million years ago, and anatomically modern humans appeared under 200,000 years ago. The course of evolution has been changed several times by mass extinctions that wiped out previously dominant groups and allowed other to rise from obscurity to become major components of ecosystems.

***Definition***



A paleontologist carefully chips rock from a column of dinosaur vertebrae.

The simplest definition is "the study of ancient life". Paleontology seeks information about several aspects of past organisms: "their identity and origin, their environment and evolution, and what they can tell us about the Earth's organic and inorganic past".

## **A historical science**

Paleontology is one of the historical sciences, along with archaeology, geology, biology, astronomy, cosmology, philology and history itself. This means that it aims to describe phenomena of the past and reconstruct their causes. Hence it has three main elements: description of the phenomena; developing a general theory about the causes of various types of change; and applying those theories to specific facts.

When trying to explain past phenomena, paleontologists and other historical scientists often construct a set of hypotheses about the causes and then look for a "smoking gun", a piece of evidence which indicates that one of the hypotheses is a better explanation than the others. Sometimes the "smoking gun" is discovered by a fortunate accident during other research, for example the discovery by Luis Alvarez and Walter Alvarez of an iridium-rich layer at the Cretaceous–Tertiary boundary made asteroid impact and volcanism the most favored explanations for the Cretaceous–Tertiary extinction event.

The other main type of science is experimental science, which is often said to work by conducting experiments to *disprove* hypotheses about the workings and causes of natural phenomena – note that this approach cannot prove a hypothesis is correct, since some later experiment may disprove it. However, when confronted with totally unexpected phenomena, such as the first evidence for invisible radiation, experimental scientists often use the same approach as historical scientists: construct a set of hypotheses about the causes and then look for a "smoking gun".

## **Related sciences**

Paleontology lies on the boundary between biology and geology since paleontology focuses on the record of past life but its main source of evidence is fossils, which are found in rocks. For historical reasons paleontology is part of the geology departments of many universities, because in the 19th century and early 20th century geology departments found paleontological evidence important for estimating the ages of rocks while biology departments showed little interest.

Paleontology also has some overlap with archaeology, which primarily works with objects made by humans and with human remains, while paleontologists are interested in the characteristics and evolution of humans as organisms. When dealing with evidence about humans, archaeologists and paleontologists may work together – for example paleontologists might identify animal or plant fossils around an archaeological site, to discover what the people who lived there ate; or they might analyze the climate at the time when the site was inhabited by humans.



Analyses using engineering techniques show that *Tyrannosaurus* had a devastating bite, but raise doubts about how fast it could move.

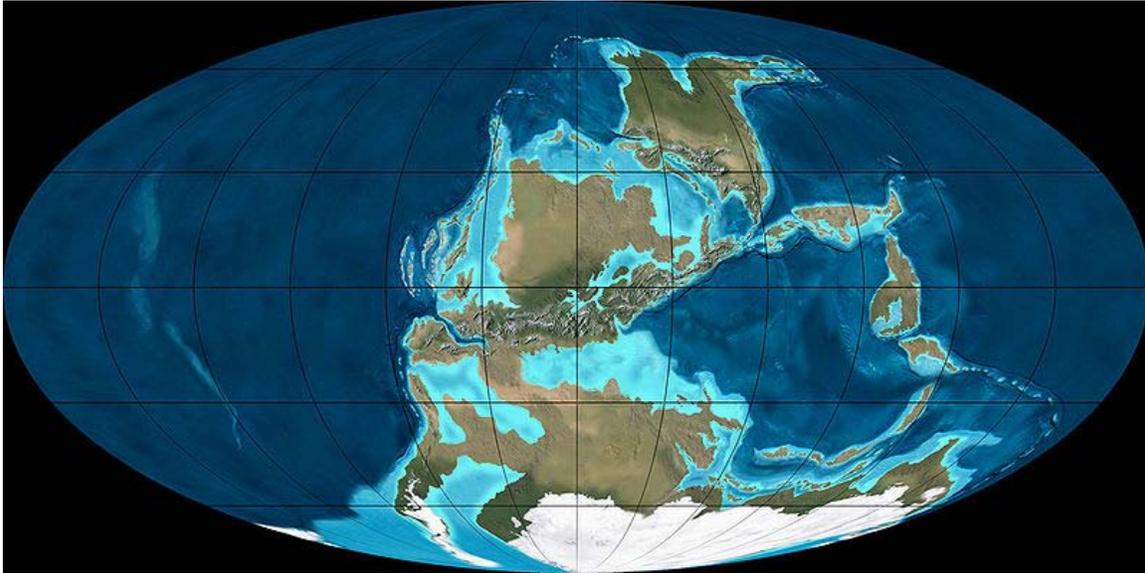
In addition paleontology often uses techniques derived from other sciences, including biology, ecology, chemistry, physics and mathematics. For example geochemical signatures from rocks may help to discover when life first arose on Earth, and analyses of carbon isotope ratios may help to identify climate changes and even to explain major transitions such as the Permian–Triassic extinction event. A relatively recent discipline, molecular phylogenetics, often helps by using comparisons of different modern organisms' DNA and RNA to re-construct evolutionary "family trees"; it has also been used to estimate the dates of important evolutionary developments, although this approach is controversial because of doubts about the reliability of the "molecular clock". Techniques developed in engineering have been used to analyse how ancient organisms might have worked, for example how fast *Tyrannosaurus* could move and how powerful its bite was.

Paleontology even contributes to astrobiology, the investigation of possible life on other planets, by developing models of how life may have arisen and by providing techniques for detecting evidence of life.

## **Subdivisions**

As knowledge has increased, paleontology has developed specialised subdivisions. Vertebrate paleontology concentrates on fossils of vertebrates, from the earliest fish to the immediate ancestors of modern mammals. Invertebrate paleontology deals with

fossils of invertebrates such as molluscs, arthropods, annelid worms and echinoderms. Paleobotany focuses on the study of fossil plants, but traditionally includes the study of fossil algae and fungi. Palynology, the study of pollen and spores produced by land plants and protists, straddles the border between paleontology and botany, as it deals with both living and fossil organisms. Micropaleontology deals with all microscopic fossil organisms, regardless of the group to which they belong.



In the Carboniferous period, the continents were not in the same places as they are today, and there was extensive glaciation.

Instead of focusing on individual organisms, paleoecology examines the interactions between different organisms, such as their places in food chains, and the two-way interaction between organisms and their environment – for example the development of oxygenic photosynthesis by bacteria hugely increased the productivity and diversity of ecosystems, and also caused the oxygenation of the atmosphere, which in turn was a prerequisite for the evolution of the most complex eucaryotic cells, from which all multicellular organisms are built. Paleoclimatology, although sometimes treated as part of paleoecology, focuses more on the history of Earth's climate and the mechanisms which have changed it – which have sometimes included evolutionary developments, for example the rapid expansion of land plants in the Devonian period removed more carbon dioxide from the atmosphere, reducing the greenhouse effect and thus helping to cause an ice age in the Carboniferous period.

Biostratigraphy, the use of fossils to work out the chronological order in which rocks were formed, is useful to both paleontologists and geologists. Biogeography studies the spatial distribution of organisms, and is also linked to geology, which explains how Earth's geography has changed over time.

## Sources of evidence

### Body fossils



This *Marrella* specimen illustrates how clear and detailed the fossils from the Burgess Shale lagerstätte are.

Fossils of organisms' bodies are usually the most informative type of evidence. The most common types are wood, bones, and shells. Fossilisation is a rare event, and most fossils are destroyed by erosion or metamorphism before they can be observed. Hence the fossil record is very incomplete, increasingly so further back in time. Despite this, it is often adequate to illustrate the broader patterns of life's history. There are also biases in the fossil record: different environments are more favorable to the preservation of different types of organism or parts of organisms. Further, only the parts of organisms that were already mineralised are usually preserved, such as the shells of molluscs. Since most animal species are soft-bodied, they decay before they can become fossilised. As a result, although there are 30-plus phyla of living animals, two-thirds have never been found as fossils.

Occasionally, unusual environments may preserve soft tissues. These lagerstätten allow paleontologists to examine the internal anatomy of animals that in other sediments are represented only by shells, spines, claws, etc. – if they are preserved at all. However, even lagerstätten present an incomplete picture of life at the time. The majority of organisms living at the time are probably not represented because lagerstätten are

restricted to a narrow range of environments, e.g. where soft-bodied organisms can be preserved very quickly by events such as mudslides; and the exceptional events that cause quick burial make it difficult to study the normal environments of the animals. The sparseness of the fossil record means that organisms are expected to exist long before and after they are found in the fossil record – this is known as the Signor-Lipps effect.

### Trace fossils



Cambrian trace fossils including *Rusophycus*, made by a trilobite

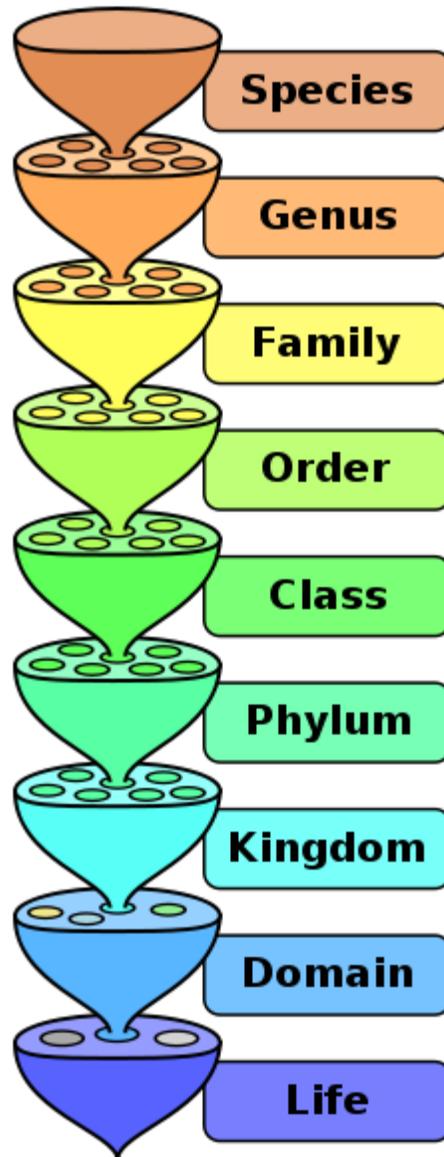
Trace fossils consist mainly of tracks and burrows, but also include coprolites (fossil feces) and marks left by feeding. Trace fossils are particularly significant because they represent a data source that is not limited to animals with easily-fossilized hard parts, and which reflects organisms' behaviour. Also many traces date from significantly earlier than the body fossils of animals that are thought to have been capable of making them. Whilst exact assignment of trace fossils to their makers is generally impossible, traces may for example provide the earliest physical evidence of the appearance of moderately complex animals (comparable to earthworms).

### Geochemical observations

Geochemical observations may help to deduce the global level of biological activity, or the affinity of a certain fossil. For example geochemical features of rocks may reveal

when life first arose on Earth, and may provide evidence of the presence of eucaryotic cells, the type from which all multicellular organisms are built. Analyses of carbon isotope ratios may help to explain major transitions such as the Permian–Triassic extinction event.

### ***Classifying ancient organisms***



Levels in the Linnean taxonomy

Naming groups of organisms in a way that is clear and widely agreed is important, as some disputes in palaeontology have been based just on misunderstandings over names. Linnean taxonomy is commonly used for classifying living organisms, but runs into difficulties when dealing with newly-discovered organisms that are significantly different from known ones. For example: it is hard to decide at what level to place a new higher-

level grouping, e.g. genus or family or order; this is important since the Linnean rules for naming groups are tied to their levels, and hence if a group is moved to a different level it has to be renamed.

Paleontologists generally use approaches based on cladistics, a technique for working out the evolutionary "family tree" of a set of organisms. It works by the logic that, if groups B and C have more similarities to each other than either has to group A, then B and C are more closely related to each other than either is to A. Characters that are compared may be anatomical, such as the presence of a notochord, or molecular, by comparing sequences of DNA or proteins. The result of a successful analysis is a hierarchy of clades – groups that share a common ancestor. Ideally the "family tree" has only two branches leading from each node ("junction"), but sometimes there is too little information to achieve this and paleontologists have to make do with junctions that have several branches. The cladistic technique is sometimes fallible, as some features, such as wings or camera eyes, evolved more than once, convergently – this must be taken into account in analyses.

Evolutionary developmental biology, commonly abbreviated to "Evo Devo", also helps paleontologists to produce "family trees". For example the embryological development of some modern brachiopods suggests that brachiopods may be descendants of the halkieriids, which became extinct in the Cambrian period.

### ***Estimating the dates of organisms***

Paleontology seeks to map out how living things have changed through time. A substantial hurdle to this aim is the difficulty of working out how old fossils are. Beds which preserve fossils typically lack the radioactive elements needed for radiometric dating. This technique is our only means of giving rocks greater than about 50 million years old an absolute age, and can be accurate to within 0.5% or better. Although radiometric dating requires very careful laboratory work, its basic principle is simple: the rates at which various radioactive elements decay are known, and so the ratio of the radioactive element to the element into which it decays shows how long ago the radioactive element was incorporated into the rock. Radioactive elements are common only in rocks with a volcanic origin, and so the only fossil-bearing rocks that can be dated radiometrically are a few volcanic ash layers.

Consequently, paleontologists must usually rely on stratigraphy to date fossils. Stratigraphy is the science of deciphering the "layer-cake" that is the sedimentary record, and has been compared to a jigsaw puzzle. Rocks normally form relatively horizontal layers, with each layer younger than the one underneath it. If a fossil is found between two layers whose ages are known, the fossil's age must lie between the two known ages. Because rock sequences are not continuous, but may be broken up by faults or periods of erosion, it is very difficult to match up rock beds that are not directly next to one another. However, fossils of species that survived for a relatively short time can be used to link up isolated rocks: this technique is called *biostratigraphy*. For instance, the conodont

*Eoplacognathus pseudoplanus* has a short range in the Middle Ordovician period. If rocks of unknown age are found to have traces of *E. pseudoplanus*, they must have a mid-Ordovician age. Such index fossils must be distinctive, be globally distributed and have a short time range to be useful. However, misleading results are produced if the index fossils turn out to have longer fossil ranges than first thought. Stratigraphy and biostratigraphy can in general provide only relative dating (*A* was before *B*), which is often sufficient for studying evolution. However, this is difficult for some time periods, because of the problems involved in matching up rocks of the same age across different continents.

Family-tree relationships may also help to narrow down the date when lineages first appeared. For instance, if fossils of B or C date to X million years ago and the calculated "family tree" says A was an ancestor of B and C, then A must have evolved more than X million years ago.

It is also possible to estimate how long ago two living clades diverged – i.e. approximately how long ago their last common ancestor must have lived – by assuming that DNA mutations accumulate at a constant rate. These "molecular clocks", however, are fallible, and provide only a very approximate timing: for example, they are not sufficiently precise and reliable for estimating when the groups that feature in the Cambrian explosion first evolved, and estimates produced by different techniques may vary by a factor of two.

## ***Overview of the history of life***

The evolutionary history of life stretches back to over 3,000 million years ago, possibly as far as 3,800 million years ago. Earth formed about 4,570 million years ago and, after a collision that formed the Moon about 40 million years later, may have cooled quickly enough to have oceans and an atmosphere about 4,440 million years ago. However there is evidence on the Moon of a Late Heavy Bombardment from 4,000 to 3,800 million years ago. If, as seem likely, such a bombardment struck Earth at the same time, the first atmosphere and oceans may have been stripped away. The oldest clear evidence of life on Earth dates to 3,000 million years ago, although there have been reports, often disputed, of fossil bacteria from 3,400 million years ago and of geochemical evidence for the presence of life 3,800 million years ago. Even the simplest modern organisms are too complex to have emerged directly from non-living materials. Some scientists have proposed that life on Earth was "seeded" from elsewhere, but most research concentrates on various explanations of how life could have arisen independently on Earth.



This wrinkled "elephant skin" texture is a trace fossil of a non-stromatolite microbial mat. The image shows the location, in the Burgsvik beds of Sweden, where the texture was first identified as evidence of a microbial mat.

For about 2,000 million years microbial mats, multi-layered colonies of different types of bacteria, were the dominant life on Earth. The evolution of oxygenic photosynthesis enabled them to play the major role in the oxygenation of the atmosphere from about 2,400 million years ago. This change in the atmosphere increased their effectiveness as nurseries of evolution. While eukaryotes, cells with complex internal structures, may have been present earlier, their evolution speeded up when they acquired the ability to transform oxygen from a poison to a powerful source of energy in their metabolism. This innovation may have come from primitive eukaryotes capturing oxygen-powered bacteria as endosymbionts and transforming them into organelles called mitochondria. The earliest evidence of complex eukaryotes with organelles such as mitochondria, dates from 1,850 million years ago.

Multicellular life is composed only of eukaryotic cells, and the earliest evidence for it is the Francevillian Group Fossils from 2,100 million years ago, although specialization of cells for different functions first appears between 1,430 million years ago (a possible fungus) and 1,200 million years ago (a probable red alga). Sexual reproduction may be a prerequisite for specialization of cells, as an asexual multicellular organism might be at risk of being taken over by rogue cells that retain the ability to reproduce.

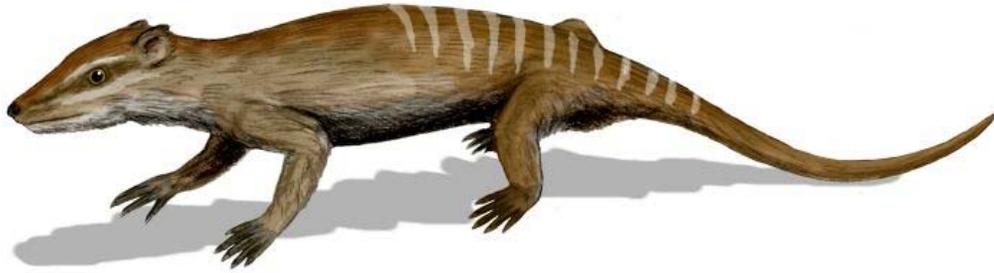


*Opabinia* made the largest single contribution to modern interest in the Cambrian explosion.

The earliest known animals are cnidarians from about 580 million years ago, but these are so modern-looking that the earliest animals must have appeared before then. Early fossils of animals are rare because they did not develop mineralized hard parts that fossilize easily until about 548 million years ago. The earliest modern-looking bilaterian animals appear in the Early Cambrian, along with several "weird wonders" that bear little obvious resemblance to any modern animals. There is a long-running debate about whether this Cambrian explosion was truly a very rapid period of evolutionary experimentation; alternative views are that modern-looking animals began evolving earlier but fossils of their precursors have not yet been found, or that the "weird wonders" are evolutionary "aunts" and "cousins" of modern groups. Vertebrates remained an obscure group until the first fish with jaws appeared in the Late Ordovician.

The spread of life from water to land required organisms to solve several problems, including protection against drying out and supporting themselves against gravity. The earliest evidence of land plants and land invertebrates date back to about 476 million years ago and 490 million years ago respectively. The lineage that produced land vertebrates evolved later but very rapidly between 370 million years ago and 360 million years ago; recent discoveries have overturned earlier ideas about the history and driving forces behind their evolution. Land plants were so successful that they caused an

ecological crisis in the Late Devonian, until the evolution and spread of fungi that could digest dead wood.



At about 13 centimetres (5.1 in) the Early Cretaceous *Yanoconodon* was longer than the average mammal of the time.



Birds are the last surviving dinosaurs.

During the Permian period synapsids, including the ancestors of mammals, may have dominated land environments, but the Permian–Triassic extinction event 251 million years ago came very close to wiping out complex life. During the slow recovery from this catastrophe a previously obscure group, archosaurs, became the most abundant and diverse terrestrial vertebrates. One archosaur group, the dinosaurs, were the dominant

land vertebrates for the rest of the Mesozoic, and birds evolved from one group of dinosaurs. During this time mammals' ancestors survived only as small, mainly nocturnal insectivores, but this apparent set-back may have accelerated the development of mammalian traits such as endothermy and hair. After the Cretaceous–Tertiary extinction event 65 million years ago killed off the non-avian dinosaurs – birds are the only surviving dinosaurs – mammals increased rapidly in size and diversity, and some took to the air and the sea.



A modern social insect collects pollen from a modern flowering plant.

Fossil evidence indicates that flowering plants appeared and rapidly diversified in the Early Cretaceous, between 130 million years ago and 90 million years ago. Their rapid rise to dominance of terrestrial ecosystems is thought to have been propelled by coevolution with pollinating insects. Social insects appeared around the same time and, although they account for only small parts of the insect "family tree", now form over 50% of the total mass of all insects.

Humans evolved from a lineage of upright-walking apes whose earliest fossils date from over 6 million years ago. Although early members of this lineage had chimp-sized brains, about 25% as big as modern humans', there are signs of a steady increase in brain size after about 3 million years ago. There is a long-running debate about whether *modern* humans are descendants of a single small population in Africa, which then migrated all

over the world less than 200,000 years ago and replaced previous hominine species, or arose worldwide at the same time as a result of interbreeding.

## ***Mass extinctions***

Life on earth has suffered occasional mass extinctions at least since 542 million years ago. Although they are disasters at the time, mass extinctions have sometimes accelerated the evolution of life on earth. When dominance of particular ecological niches passes from one group of organisms to another, it is rarely because the new dominant group is "superior" to the old and usually because an extinction event eliminates the old dominant group and makes way for the new one.

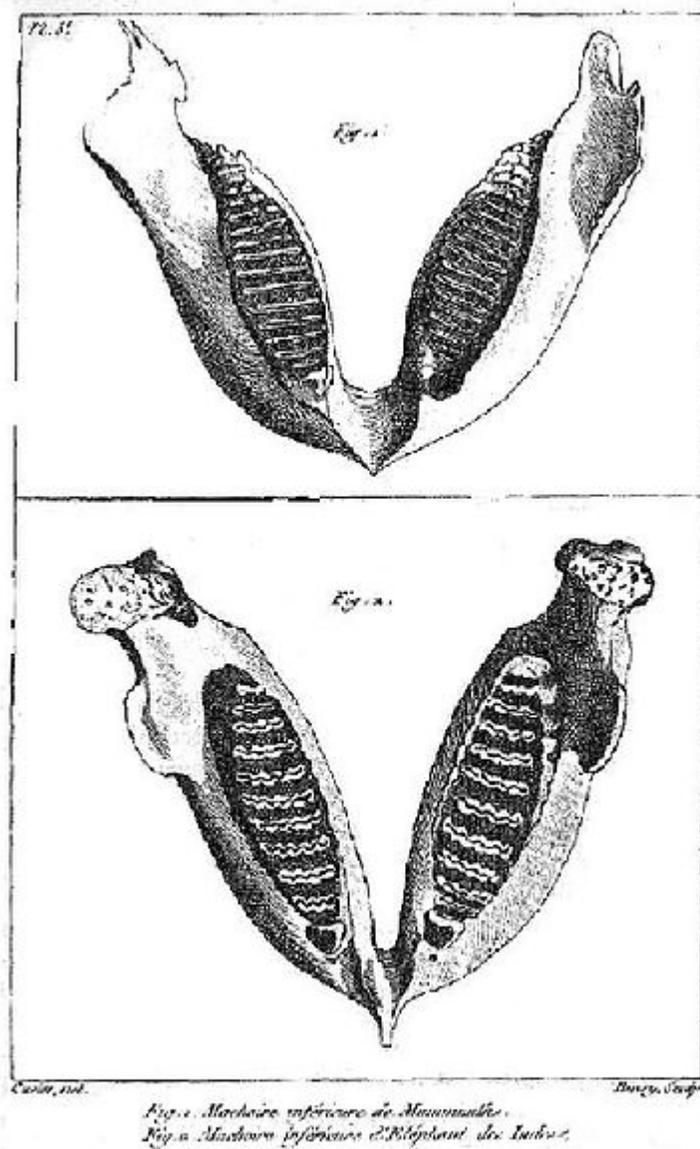
The fossil record appears to show that the rate of extinction is slowing down, with both the gaps between mass extinctions becoming longer and the average and background rates of extinction decreasing. However, it is not certain whether the actual rate of extinction has altered, since both of these observations could be explained in several ways:

- The oceans may have become more hospitable to life over the last 500 million years and less vulnerable to mass extinctions: dissolved oxygen became more widespread and penetrated to greater depths; the development of life on land reduced the run-off of nutrients and hence the risk of eutrophication and anoxic events; marine ecosystems became more diversified so that food chains were less likely to be disrupted.
- Reasonably complete fossils are very rare, most extinct organisms are represented only by partial fossils, and complete fossils are rarest in the oldest rocks. So paleontologists have mistakenly assigned parts of the same organism to different genera which were often defined solely to accommodate these finds – the story of *Anomalocaris* is an example of this. The risk of this mistake is higher for older fossils because these are often unlike parts of any living organism. Many of the "superfluous" genera are represented by fragments which are not found again and the "superfluous" genera appear to become extinct very quickly.

Biodiversity in the fossil record, which is

"the number of distinct genera alive at any given time; that is, those whose first occurrence predates and whose last occurrence postdates that time"

shows a different trend: a fairly swift rise from 542 to 400 million years ago, a slight decline from 400 to 200 million years ago, in which the devastating Permian–Triassic extinction event is an important factor, and a swift rise from 200 million years ago to the present.



This illustration of an Indian elephant jaw and a mammoth jaw (top) is from Cuvier's 1796 paper on living and fossil elephants.

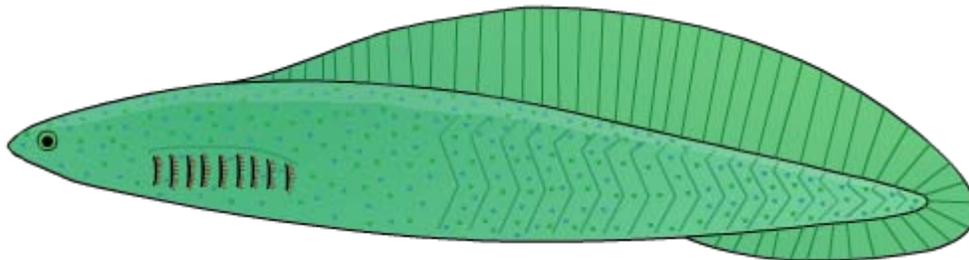
### ***History of paleontology***

Although paleontology became established around 1800, earlier thinkers had noticed aspects of the fossil record. The ancient Greek philosopher Xenophanes (570–480 BC) concluded from fossil sea shells that some areas of land were once under water. During the Middle Ages the Persian naturalist Ibn Sina, known as *Avicenna* in Europe, discussed fossils and proposed a theory of petrifying fluids on which Albert of Saxony elaborated in the 14th century. The Chinese naturalist Shen Kuo (1031–1095) proposed a theory of climate change based on the presence of petrified bamboo in regions that in his time were too dry for bamboo.

In early modern Europe, the systematic study of fossils emerged as an integral part of the changes in natural philosophy that occurred during the Age of Reason. At the end of the 18th century Georges Cuvier's work established comparative anatomy as a scientific discipline and, by proving that some fossil animals resembled no living ones, demonstrated that animals could become extinct, leading to the emergence of paleontology. The expanding knowledge of the fossil record also played an increasing role in the development of geology, particularly stratigraphy.

The first half of the 19th century saw geological and paleontological activity become increasingly well organized with the growth of geologic societies and museums and an increasing number of professional geologists and fossil specialists. Interest increased for reasons that were not purely scientific, as geology and paleontology helped industrialists to find and exploit natural resources such as coal.

This contributed to a rapid increase in knowledge about the history of life on Earth and to progress in the definition of the geologic time scale, largely based on fossil evidence. In 1822 Henri Marie Ducrotay de Blanville, editor of *Journal de Physique*, coined the word "paleontology" to refer to the study of ancient living organisms through fossils. As knowledge of life's history continued to improve, it became increasingly obvious that there had been some kind of successive order to the development of life. This encouraged early evolutionary theories on the transmutation of species. After Charles Darwin published *Origin of Species* in 1859, much of the focus of paleontology shifted to understanding evolutionary paths, including human evolution, and evolutionary theory.



*Haikouichthys*, from about 518 million years ago in China, may be the earliest known fish.

The last half of the 19th century saw a tremendous expansion in paleontological activity, especially in North America. The trend continued in the 20th century with additional regions of the Earth being opened to systematic fossil collection. Fossils found in China near the end of the 20th century have been particularly important as they have provided new information about the earliest evolution of animals, early fish, dinosaurs and the evolution of birds. The last few decades of the 20th century saw a renewed interest in mass extinctions and their role in the evolution of life on Earth. There was also a renewed interest in the Cambrian explosion that apparently saw the development of the body plans of most animal phyla. The discovery of fossils of the Ediacaran biota and developments

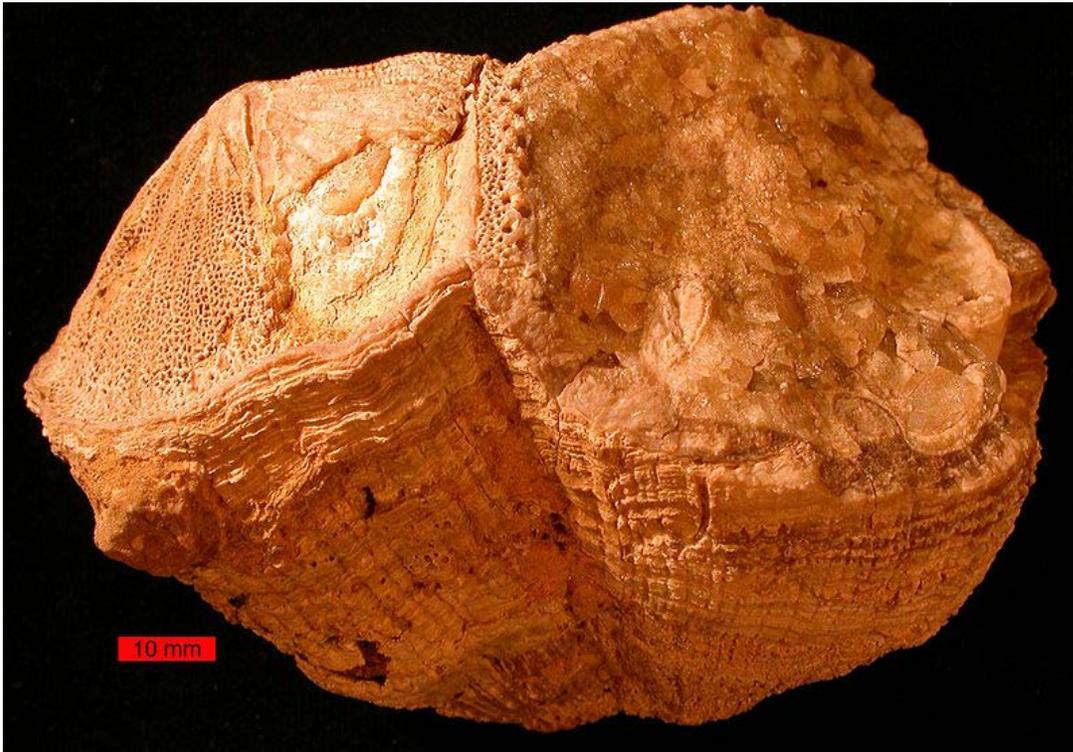
in paleobiology extended knowledge about the history of life back far before the Cambrian.

Increasing awareness of Gregor Mendel's pioneering work in genetics led first to the development of population genetics and then in the mid-20th century to the modern evolutionary synthesis, which explains evolution as the outcome of events such as mutations and horizontal gene transfer which provide genetic variation, with genetic drift and natural selection driving changes in this variation over time. Within the next few years the role and operation of DNA in genetic inheritance were discovered, leading to what is now known as the "Central Dogma" of molecular biology. In the 1960s molecular phylogenetics, the investigation of evolutionary "family trees" by techniques derived from biochemistry, began to make an impact, particularly when it was proposed that the human lineage had diverged from apes much more recently than was generally thought at the time. Although this early study compared proteins from apes and humans, most molecular phylogenetics research is now based on comparisons of RNA and DNA.

## Chapter 12

# Macrofossil and Trace Fossil

## Macrofossil



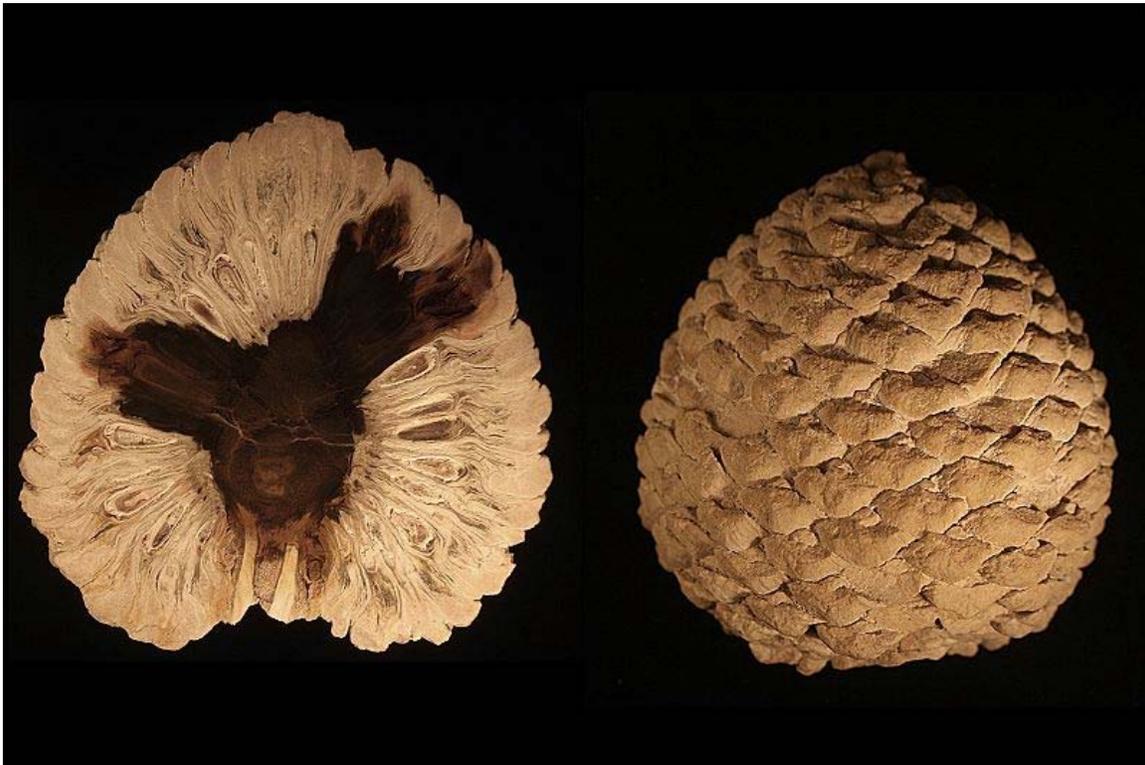
Rudist bivalves from the Cretaceous of the Omani Mountains, United Arab Emirates. Scale bar is 10 mm.

**Macrofossils** (occasionally spelled "**macro-fossil**") are preserved organic remains large enough to be visible without a microscope.

## ***Macrofossil contrasted with Microfossil***

The term **macrofossil** stands in opposition to the term *microfossil* (a.k.a. "micro-fossil"). Microfossils, by contrast, require substantial magnification for evaluation by fossil-hunters or professional paleontologists. As a result, most fossils observed in the field and most "museum-quality" specimens are macrofossils.

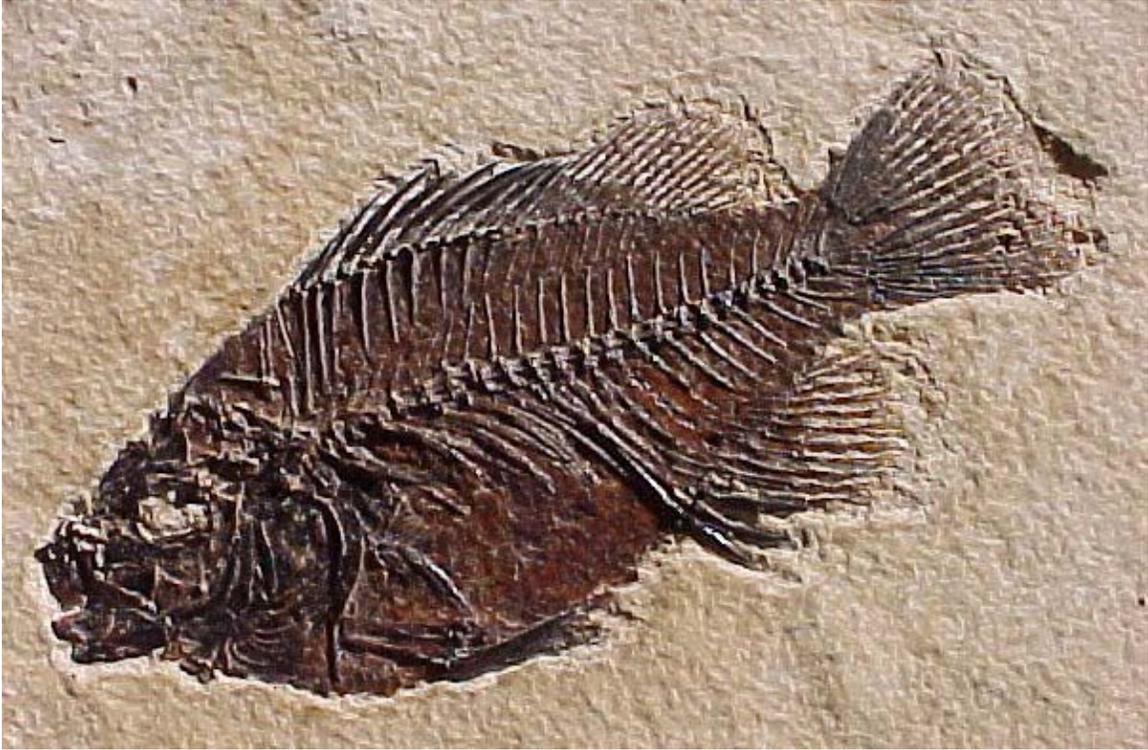
### ***Plant macrofossils***



Jurassic Petrified cone of *Araucaria* sp. from Patagonia, Argentina.

Plant macrofossils include leaf, needle, cone, and stem debris; and can be used to identify types of plants formerly growing in the area. Such botanical macrofossil data provide a valuable complement to pollen and faunal data that can be used to reconstruct the prehistoric terrestrial environment. Algal macrofossils (for instance, brown kelp, sea lettuce and large stromatolites) are increasingly used to analyze prehistoric marine and aquatic ecosystems.

## ***Animal macrofossils***



Eocene fossil fish *Priscacara liops* from the Green River Formation of Utah.

Animal macrofossils include the teeth, skulls, and bones of vertebrates, as well as such invertebrate remains as shells, tests, faunal armor, and exoskeletons. Fossilized dung (that is, coprolites) are also macrofossils.

## Trace fossil



*Chirotherium* footprints in a Triassic sandstone.



*Protichnites* tracks from the late Cambrian, central Wisconsin.

**Trace fossils**, also called **ichnofossils** are geological records of biological activity. Trace fossils may be impressions made on the substrate by an organism: for example, burrows, borings (bioerosion), urolites (erosion caused by evacuation of liquid wastes), footprints and feeding marks, and root cavities. The term in its broadest sense also includes the remains of other organic material produced by an organism — for example coprolites (fossilized droppings) or chemical markers — or sedimentological structures produced by biological means - for example, stromatolites. Trace fossils contrast with body fossils, which are the fossilized remains of parts of organisms' bodies, usually altered by later chemical activity or mineralization.

Sedimentary structures, for example those produced by empty shells rolling along the sea floor, are not produced through the behaviour of an organism and not considered trace fossils.

The study of traces is called ichnology, which is divided into *paleoichnology*, or the study of trace fossils, and *neoichnology*, the study of modern traces. This science is challenging, as most traces reflect the behaviour — not the biological affinity — of their makers. As such, trace fossils are categorised into form genera, based upon their appearance and the implied behaviour of their makers.

## **Occurrence**



Cross-section of mammoth footprints at The Mammoth Site, Hot Springs, South Dakota.

Traces are better known in their fossilised form than in modern sediments. This makes it difficult to interpret some fossils by comparing them with modern traces, even though they may be extant or even common. The main difficulties in accessing extant burrows stem from finding them in consolidated sediment, and being able to access those formed in deeper water.

Trace fossils are best preserved in sandstones; the grain size and depositional facies both contributing to the better preservation. They may also be found in shales and limestones.

## **Classification**

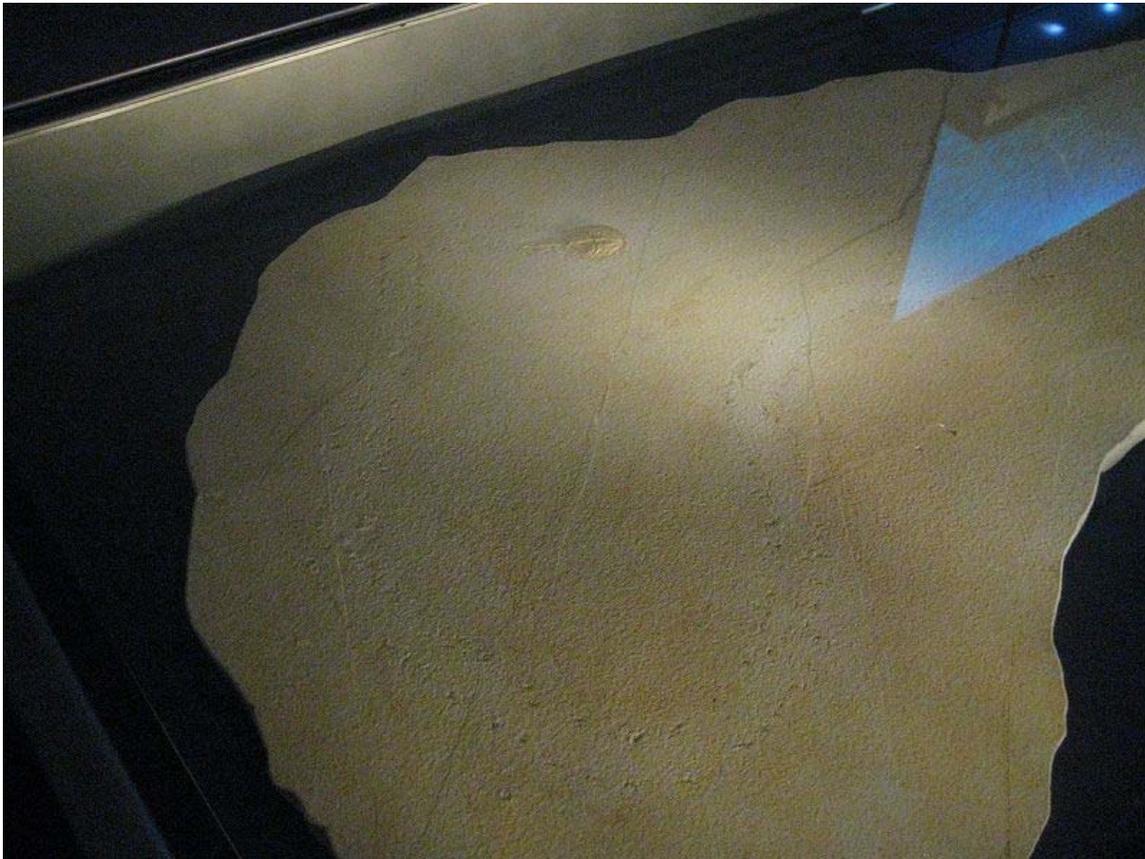
Trace fossils are generally difficult or impossible to assign to a specific maker. Only in very rare occasions are the makers found in association with their tracks. Further, entirely different organisms may produce identical tracks. Therefore conventional taxonomy is not applicable, and a comprehensive form taxonomy has been erected. At the highest level of the classification, five behavioral modes are recognized:

- **Domichnia**, dwelling structures reflecting the life position of the organism that created it.
- **Fodinichnia**, three-dimensional structures left by animals which eat their way through sediment, such as deposit feeders;

- **Pascichnia**, feeding traces left by grazers on the surface of a soft sediment or a mineral substrate;
- **Cubichnia**, resting traces, in the form of an impression left by an organism on a soft sediment;
- **Repichnia**, surface traces of creeping and crawling.

Fossils are further classified into form genera, a few of which are even subdivided to a "species" level. Classification is based on shape, form, and implied behavioural mode.

### ***Information provided by ichnofossils***



*Mesolimulus walchi* fossil and track, a rare example of tracks and the creature that made them fossilized together

Because identical fossils can be created by a range of different organisms, trace fossils can only reliably inform us of two things: the consistency of the sediment at the time of its deposition, and the energy level of the depositional environment. Attempts to deduce such traits as whether a deposit is marine or non-marine have been made, but shown to be unreliable.

## **Paleoecology**

Trace fossils provide us with indirect evidence of life in the past, such as the footprints, tracks, burrows, borings, and feces left behind by animals, rather than the preserved remains of the body of the actual animal itself. Unlike most other fossils, which are produced only after the death of the organism concerned, trace fossils provide us with a record of the activity of an organism during its lifetime.

Trace fossils are formed by organisms performing the functions of their everyday life, such as walking, crawling, burrowing, boring, or feeding. Tetrapod footprints, worm trails and the burrows made by clams and arthropods are all trace fossils.

Perhaps the most spectacular trace fossils are the huge, three-toed footprints produced by dinosaurs and related archosaurs. These imprints give scientists clues as to how these animals lived. Although the skeletons of dinosaurs can be reconstructed, only their fossilized footprints can determine exactly how they stood and walked. Such tracks can tell much about the gait of the animal which made them, what its stride was, and whether or not the front limbs touched the ground.

However, most trace fossils are rather less conspicuous, such as the trails made by segmented worms or nematodes. Some of these worm castings are the only fossil record we have of these soft-bodied creatures.

## Paleoenvironment



*Eubrontes*, a dinosaur footprint in the Lower Jurassic Moenave Formation at the St. George Dinosaur Discovery Site at Johnson Farm, southwestern Utah.

Fossil footprints made by tetrapod vertebrates are difficult to identify to a particular species of animal, but they can provide us with valuable information such as the speed, weight, and behavior of the organism that made them. Such trace fossils are formed when amphibians, reptiles, mammals or birds walked across soft (probably wet) mud or sand which later hardened sufficiently to retain the impressions before the next layer of sediment was deposited. Some fossils can even provide details of how wet the sand was when they were being produced, and hence allow estimation of paleo-wind directions.

Assemblages of trace fossils occur at certain water depths, and can also reflect the salinity and turbidity of the water column.

### **Stratigraphic correlation**

Some trace fossils can be used as local index fossils, to date the rocks in which they are found, such as the burrow *Arenicolites franconicus* which occurs only in a 4 cm (1.6") layer of the Triassic Muschelkalk epoch, throughout wide areas in southern Germany.

The base of the Cambrian period is defined by the first appearance of the trace fossil *Treptichnus pedum*.

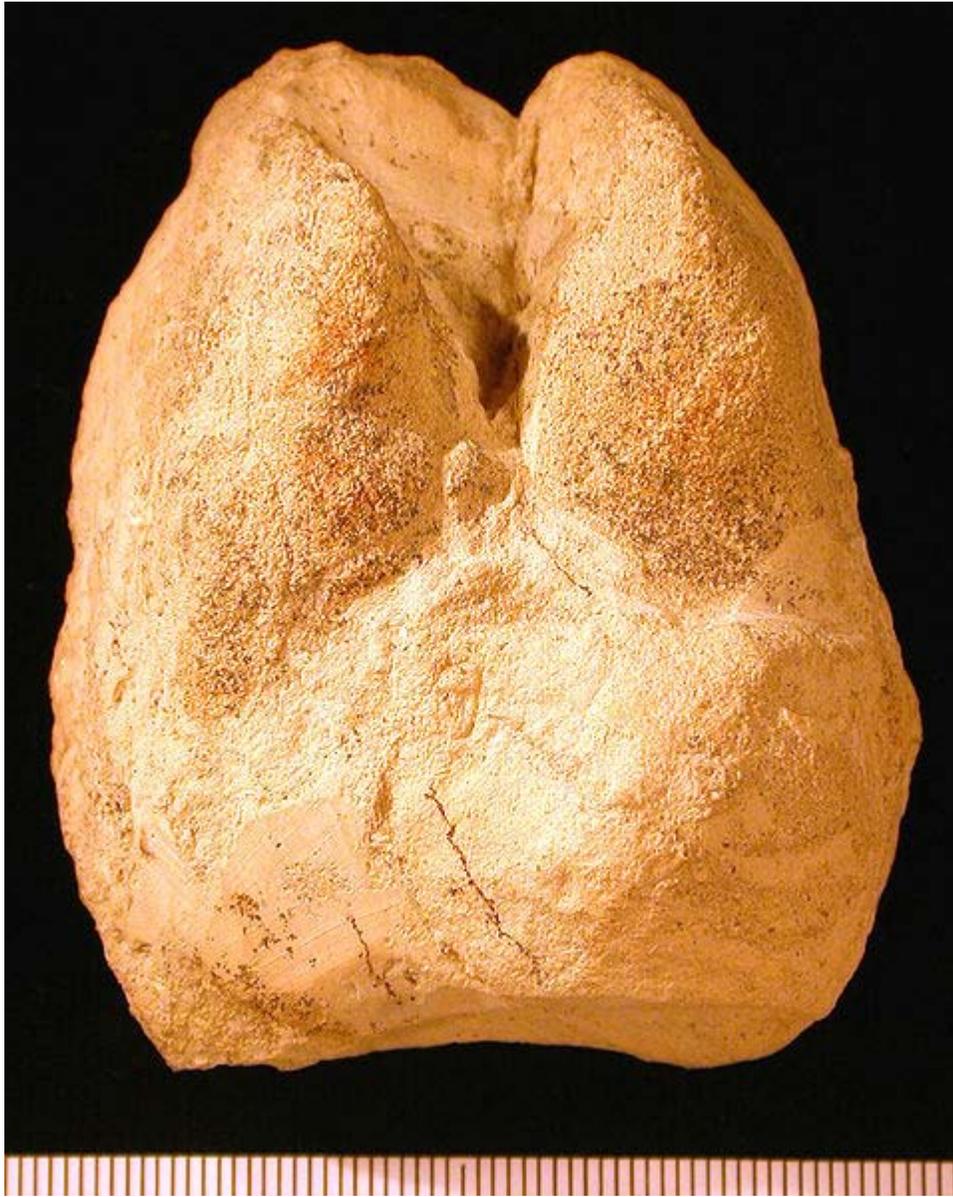
Trace fossils have a further utility as many appear before the organism thought to create them, extending their stratigraphic range.

### ***Ichnofacies***

Trace fossil assemblages are far from random; the range of fossils recorded in association is constrained by the environment in which the trace-making organisms dwelt.

Palaeontologist Adolf Seilacher pioneered the concept of ichnofacies, whereby the state of a sedimentary system at its time of deposition could be implied by noting the fossils in association with one another.

## ***Inherent bias***



Cameloid footprint (convex hyporelief) from the Barstow Formation (Miocene) of Rainbow Basin, California.

Most trace fossils are known from marine deposits. Essentially, there are two types of traces, either exogenic ones, which are made on the surface of the sediment (such as tracks) or endogenic ones, which are made within the layers of sediment (such as burrows).

Surface trails on sediment in shallow marine environments stand less chance of fossilization because they are subjected to wave and current action. Conditions in quiet, deep-water environments tend to be more favorable for preserving fine trace structures.

Most trace fossils are usually readily identified by reference to similar phenomena in modern environments. However, the structures made by organisms in recent sediment have only been studied in a limited range of environments, mostly in coastal areas, including tidal flats.

## ***Evolution***



*Climactichnites*, probably trackways from a slug-like animal, from the late Cambrian, central Wisconsin. Ruler in background is 45cm (18") long.

The earliest complex trace fossils, not including microbial traces such as stromatolites, date to 2,000 to 1,800 million years ago. This is far too early for them to have an animal origin, and they are thought to have been formed by amoebae. Putative "burrows" dating as far back as 1,100 million years may have been made by animals which fed on the undersides of microbial mats, which would have shielded them from a chemically unpleasant ocean; however their uneven width and tapering ends make a biological origin so difficult to defend that even the original author no longer believes they are authentic.

The first evidence of burrowing which is widely accepted dates to the Ediacaran (Vendian) period, around 560 million years ago. During this period the traces and burrows basically are horizontal on or just below the seafloor surface. Such traces must have been made by motile organisms with heads, which would probably have been bilateran animals. The trace observed imply simple behaviour, and point to organisms

feeding above the surface and burrowing for protection from predators. Contrary to widely circulated opinion that Ediacaran burrows are only horizontal the vertical burrows *Skolithos* are also known. The producers of burrows *Skolithos declinatus* from the Vendian (Ediacaran) beds in Russia with date 555.3 million years ago have not been found, they might have been filter feeders subsisting on the nutrients from the suspension. The density of these burrows is up to 245 burrows/dm<sup>2</sup>. Some Ediacaran trace fossils have been found directly associated with an body fossils. *Yorgia* and *Dickinsonia* are often found at the end of long pathways of trace fossils matching their shape. The feeding was performed in a mechanical way, supposedly the ventral side of body these organisms was covered with cilia. The potential mollusc related *Kimberella* is associated with scratch marks, perhaps formed by a radula, further traces from 555 million years ago appear to imply active crawling or burrowing activity.

As the Cambrian got underway, new forms of trace fossil appeared, including vertical burrows (e.g. *Diplocraterion*) and traces normally attributed to arthropods. These represent a “widening of the behavioural repertoire”, both in terms of abundance and complexity.

Trace fossils are a particularly significant source of data from this period because they represent a data source that is not directly connected to the presence of easily-fossilized hard parts, which are rare during the Cambrian. Whilst exact assignment of trace fossils to their makers is difficult, the trace fossil record seems to indicate that at the very least, large, bottom-dwelling, bilaterally symmetrical organisms were rapidly diversifying during the early Cambrian.

Further, less rapid diversification occurred since, and many traces have been converged upon independently by unrelated groups of organisms.

Trace fossils also provide our earliest evidence of animal life on land. The earliest arthropod trackways date to the Cambro-Ordovician, and trackways from the Ordovician Tumblagooda sandstone allow the behaviour of these organisms to be determined. The enigmatic trace fossil *Climactichnites* may represent an earlier still terrestrial trace, perhaps made by a slug-like organism.

***Common ichnogenera***



*Petroxestes* borings in a hardground from the Upper Ordovician of southern Ohio.



*Rusophycus* trace fossil from the Ordovician of southern Ohio. Scale bar is 10 mm.



*Skolithos* trace fossil. Scale bar is 10 mm.



*Thalassinoides*, burrows produced by crustaceans, from the Middle Jurassic, Makhtesh Qatan, southern Israel.



*Trypanites* borings in an Upper Ordovician hardground from northern Kentucky. The borings are filled with diagenetic dolomite (yellowish). Note that the boring on the far right cuts through a shell in the matrix.

- *Asteriacites* is the name given to the five-rayed fossils found in rocks and they record the resting place of starfish on the sea floor. *Asteriacites* are found in European and American rocks, from the Ordovician period onwards, and are numerous in rocks from the Jurassic period of Germany.
- *Chondrites* (not to be confused with stony meteorites of the same name) are small branching burrows of the same diameter, which superficially resemble the roots of a plant. The most likely candidate for having constructed these burrows is a nematode (roundworm). *Chondrites* are found in marine sediments from the Cambrian period of the Paleozoic onwards. They are especially common in sediments which were deposited in reduced-oxygen environments.
- *Climactichnites* is the name given to trackways that usually consist of two parallel ridges separated by chevron-shaped raised cross bars. They somewhat resemble tire tracks, and are larger (typically about four inches wide) than most of the other trace fossils made by invertebrates. The tracks were produced on sandy tidal flats during late Cambrian time. While the identity of the animal is still conjectural, it may have been a large slug-like animal - its trackways produced as it crawled over and processed the wet sand to obtain food.
- *Cruziana* are excavation trace marks made on the sea floor which have a two-lobed structure with a central groove. The lobes are covered with scratch marks made by the legs of the excavating organism, usually a trilobite or allied arthropod. *Cruziana* are most common in marine sediments formed during the Paleozoic era, particularly in rocks from the Cambrian and Ordovician periods. Over 30 ichnospecies of *Cruziana* have been identified.
- *Entobia* is a boring produced by endolithic elionaid sponges consisting of galleries excavated in a carbonate substrate; often has swollen chambers with connecting canals.
- *Gastrochaenolites* are clavate (club-shaped) borings also produced in calcareous hard substrates, usually by bivalves.
- *Petroxestes* is a shallow groove boring produced by mytilacean bivalves in carbonate hard substrates.
- *Protichnites* consists of two rows of tracks and a linear depression between the two rows. The tracks are believed to have been made by the walking appendages of arthropods. The linear depression is thought to be the result of a dragging tail. The structures bearing this name were typically made on the tidal flats of Paleozoic seas, but similar ones extend into the Cenozoic.
- *Rhizocorallium* is a type of burrow, the inclination of which is typically within 10° of the bedding planes of the sediment. These burrows can be very large, over a meter long in sediments that show good preservation, e.g. Jurassic rocks of the Yorkshire Coast (eastern United Kingdom), but the width is usually only up to 2 cm, restricted by the size of the organisms producing it. It is thought that they represent fodinichnia as the animal (probably a nematode) scoured the sediment for food.
- *Rogerella* is a small pouch-shaped boring with a slit-like aperture currently produced by acrothoracican barnacles.
- *Rusophycus* are bilobed "resting traces" associated with trilobites and other arthropods such as horseshoe crabs.

- *Skolithos*: One well-known occurrence of Cambrian trace fossils from this period is the famous 'Pipe Rock' of northwest Scotland. The 'pipes' that give the rock its name are closely packed straight tubes- which were presumably made by some kind of worm-like organism. The name given to this type of tube or burrow is *Skolithos*, which may be 30 cm (12") in length and between 2 to 4 cm (0.8 to 1.6") in diameter. Such traces are known worldwide from sands and sandstones deposited in shallow water environments, from the Cambrian period (542–488 Ma) onwards.
- *Thalassinoides* are burrows which occur parallel to the bedding plane of the rock and are extremely abundant in rocks, worldwide, from the Jurassic period onwards. They are repeatedly branched, with a slight swelling present at the junctions of the tubes. The burrows are cylindrical and vary from 2 to 5 cm (0.8" to 2") in diameter. *Thalassinoides* sometimes contain scratch marks, droppings or the bodily remains of the crustaceans which made them.
- *Teichichnus* has a distinctive form produced by the stacking of thin 'tongues' of sediment, atop one another. They are again believed to be fodinichnia, with the organism adopting the habit of retracing the same route through varying heights of the sediment, which would allow it to avoid going over the same area. These 'tongues' are often quite sinuous, reflecting perhaps a more nutrient-poor environment in which the feeding animals had to cover a greater area of sediment, in order to acquire sufficient nourishment.
- *Trypanites* are elongated cylindrical borings in calcareous substrates such as shells, carbonate hardgrounds and limestones. Usually produced by worms of various types and sipunculids.

### **Other notable trace fossils**

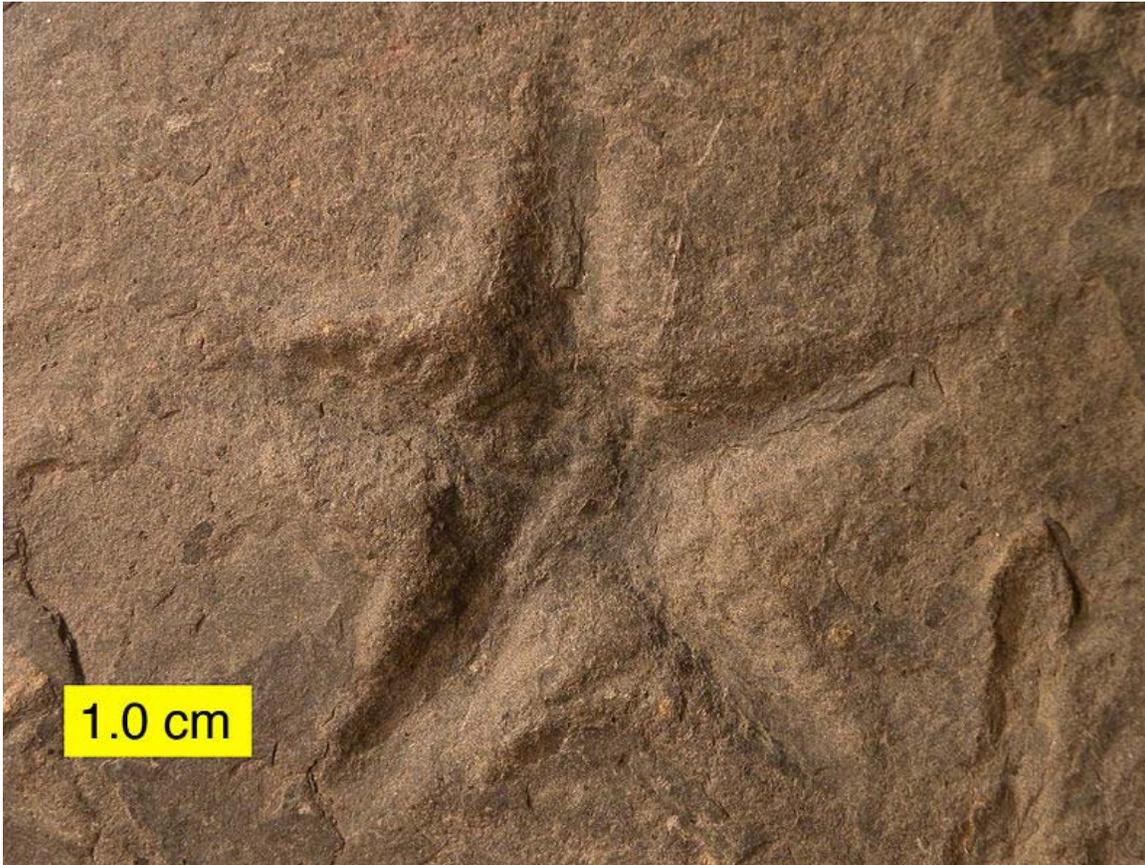
Less ambiguous than the above ichnogenera, are the traces left behind by invertebrates such as *Hibbertopterus*, a giant "sea scorpion" or eurypterid of the early Paleozoic era. This marine arthropod produced a spectacular hibbertopteroid track preserved in Scotland.

Bioerosion through time has produced a magnificent record of borings, gnawings, scratchings and scrapings on hard substrates. These trace fossils are usually divided into macroborings and microborings. Bioerosion intensity and diversity is punctuated by two events. One is called the Ordovician Bioerosion Revolution and the other was in the Jurassic.

The oldest types of tetrapod tail-and-foot prints date back to the latter Devonian period. These vertebrate impressions have been found in Ireland, Scotland, Pennsylvania, and Australia.

Important human trace fossils are the Laetoli (Tanzania) footprints, imprinted in volcanic ash 3.7 Ma (million years ago) -- probably by an early *Australopithecus*.

## ***Confusion with other types of fossils***

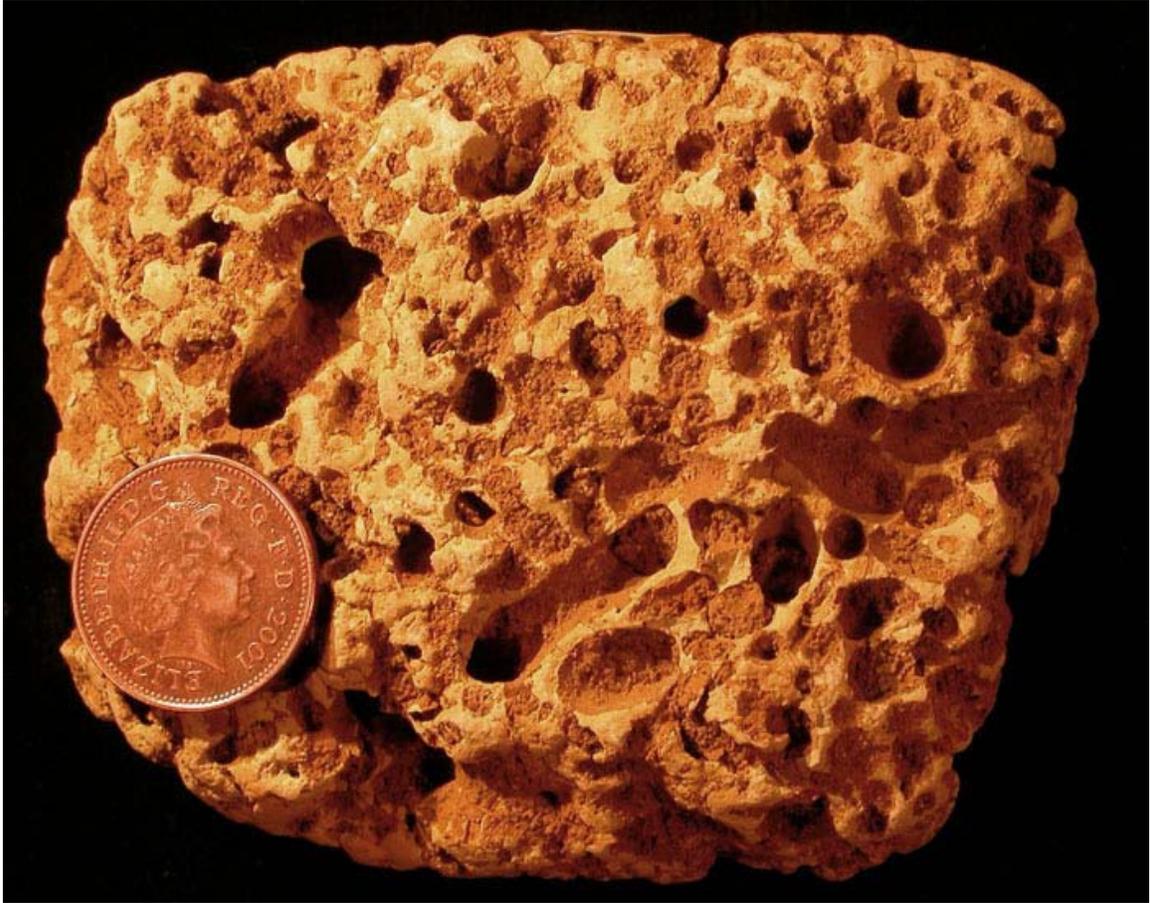


*Asteriacites* (sea star trace fossil) from the Devonian of northeastern Ohio. It appears at first to be an external mold of the body, but the sediment piled between the rays shows that it is a burrow.

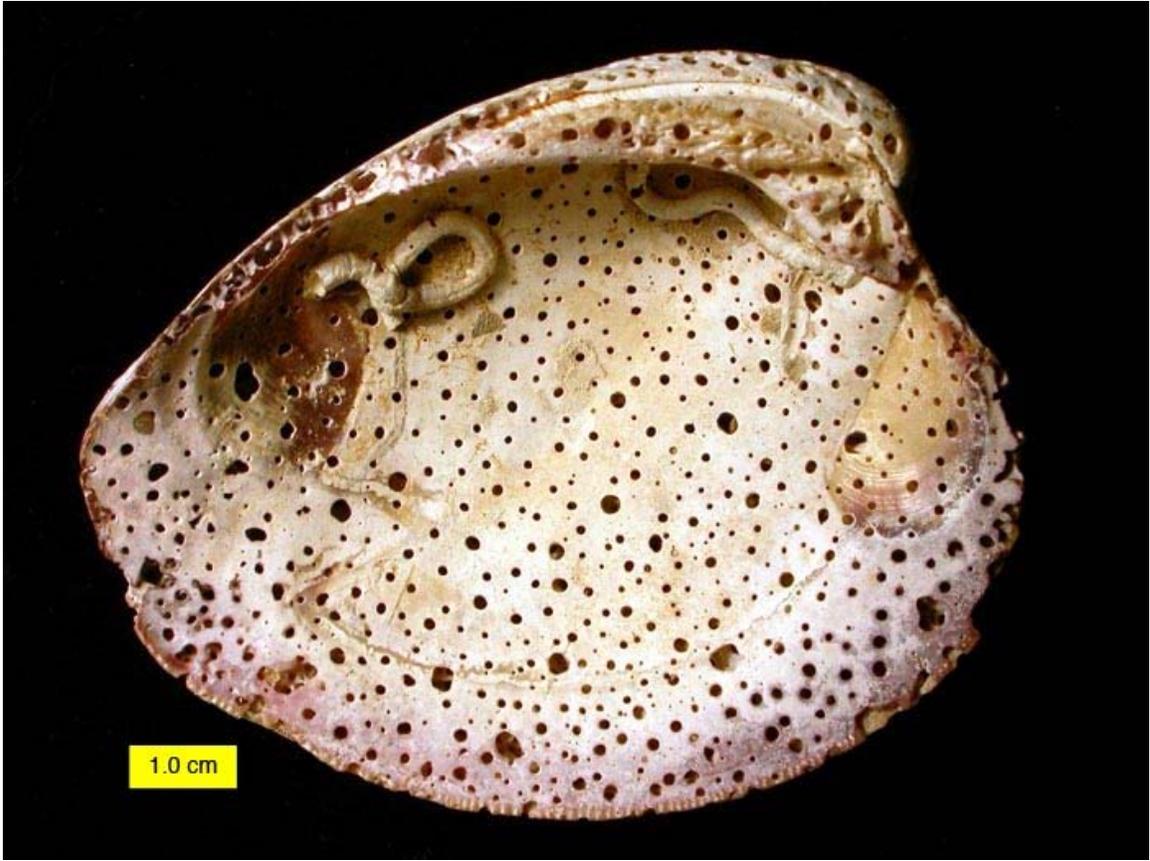
Trace fossils are not body casts. The Ediacara biota, for instance, primarily comprises the casts of organisms in sediment. Similarly, a footprint is not a simple replica of the sole of the foot, and the resting trace of a seastar has different details than an impression of a seastar.

Early paleobotanists misidentified a wide variety of structures they found on the bedding planes of sedimentary rocks as fucoids (Fucales, a kind of brown algae or seaweed). However, even during the earliest decades of the study of ichnology, some fossils were recognized as animal footprints and burrows. Studies in the 1880s by A. G. Nathorst and Joseph F. James comparing 'fucoids' to modern traces made it increasingly clear that most of the specimens identified as fossil fucoids were animal trails and burrows. True fossil fucoids are quite rare.

Pseudofossils, which are *not* true fossils, should also not be confused with ichnofossils, which are true indications of prehistoric life.



Numerous borings in a Cretaceous cobble, Faringdon, England.



Sponge borings (*Entobia*) and encrusters on a modern bivalve shell, North Carolina.



*Helminthopsis* ichnosp.; a trace fossil from the Logan Formation (Lower Carboniferous) of Wooster, Ohio.



*Gigandipus*, a dinosaur footprint in the Lower Jurassic Moenave Formation at the St. George Dinosaur Discovery Site at Johnson Farm, southwestern Utah.