Prehistoric Vertebrates
and
Prehistoric Invertebrates

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Acanthostega and Baphetidae

Acanthostega

Acanthostega
Temporal range: 365 Ma
Late Devonian
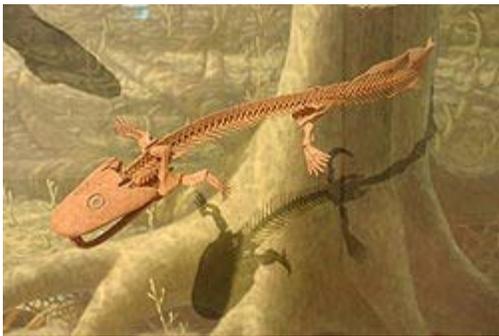
Acanthostega gunnari skeleton reconstruction

Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Amphibia
Order:	Ichthyostegalia
Family:	Acanthostegidae
Gemus:	**Acanthostega**
Binomial name	

Acanthostega gunnari
Jarvik, 1952

Acanthostega (meaning **Spiny Roof**) is an extinct labyrinthodont genus, among the first vertebrate animals to have recognizable limbs. It appeared in the Upper Devonian (Famennian) about 365 million years ago, and was anatomically intermediate between lobe-finned fishes and the first tetrapods fully capable of coming onto land.

Description

Skull of *Acanthostega gunnari*.

Restoration

It had eight digits on each hand (the number of digits on the feet is unclear) linked by webbing, it lacked wrists, and was generally poorly adapted to come onto land. *Acanthostega* also had a remarkably fish-like shoulder and forelimb. The front foot of *Acanthostega* could not bend forward at the elbow, and thus could not be brought into a weight bearing position, appearing to be more suitable for paddling or for holding on to aquatic plants. It had lungs, but its ribs were too short to give support to its chest cavity out of water, and it also had gills which were internal and covered like those of fish, not external and naked like those of some modern amphibians which are almost wholly aquatic. Acanthostega is the first tetrapod to show the shift in locomotory dominance from the pectoral to pelvic girdle. There are many morphological changes that allowed the pelvic girdle of Acanthostega to become a weight-bearing structure. In more ancestral

states the two sides of the girdle were not attached. In Acanthostega there in contact between the two dies and fusion of the girdle with the sacral rib of the vertebral column. These fusions would have made the pelvic region more powerful and equipped to counter the force of gravity when not supported by the buoyancy of and aquatic environment.

Therefore, paleontologists surmise that it probably lived in shallow, weed-choked swamps, the legs having evolved for some other purpose than walking on land. Jennifer A. Clack interprets this as showing that this was primarily an aquatic creature descended from fish that had never left the sea, and that tetrapods had evolved features which later proved useful for terrestrial life, rather than crawling onto land and then gaining legs and feet as had previously been surmised. At that period, for the first time, deciduous plants were flourishing and annually shedding leaves into the water, attracting small prey into warm oxygen-poor shallows that were difficult for larger fish to swim in. Clack remarks on how the lower jaw of *Acanthostega* shows a change from the jaws of fish which have two rows of teeth, with a large number of small teeth in the outer row, and two large fangs and some small teeth in the inner row. It differs, having a small number of larger teeth in the outer row and smaller teeth in the inner row, and she suggests that this change probably went with a shift in early tetrapods from feeding exclusively in water to feeding with the head above water or on land.

Research based on analysis of the suture morphology in its skull indicates that the species may have bitten directly on prey at or near the water's edge. Markey and Marshall compared the skull with the skulls of fish, which use suction feeding as the primary method of prey capture, and creatures known to have used the direct biting on prey typical of terrestrial animals. Their results indicate that *Acanthostega* was adapted for what they call terrestrial-style feeding, strongly supporting the hypothesis that the terrestrial mode of feeding first emerged in aquatic animals. If correct, this shows an animal specialized for hunting and living in shallow waters in the line between land and water.

Discovery

The fossilized remains are generally well preserved, with the famous fossil by which the significance of this species was discovered being found by Jennifer A. Clack in East Greenland in 1987, though fragments of the skull had been discovered in 1933 by Gunnar Säve-Söderbergh and Erik Jarvik.

Related species

Late Devonian lobe-finned fish and amphibious tetrapods.
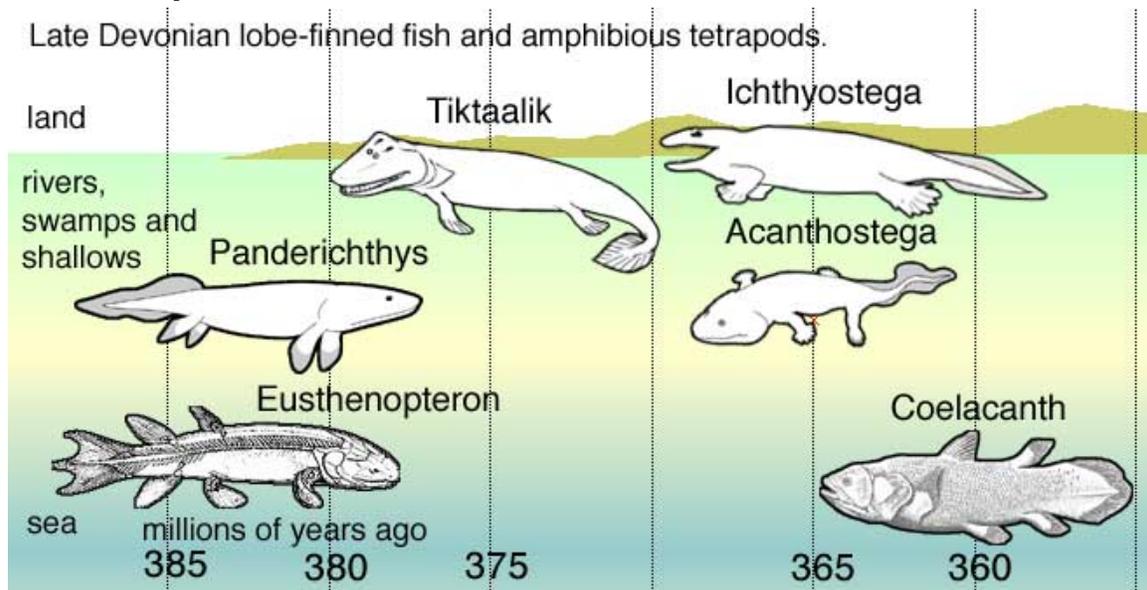
In Late Devonian vertebrate speciation, descendants of pelagic lobe-finned fish – like *Eusthenopteron* – exhibited a sequence of adaptations:

* *Panderichthys*, suited to muddy shallows;
* *Tiktaalik* with limb-like fins that could take it onto land;
* Early tetrapods in weed-filled swamps, such as:
    * *Acanthostega* which had feet with eight digits,
    * *Ichthyostega* with limbs.

Descendants also included pelagic lobe-finned fish such as coelacanth species.

Acanthostega is seen as part of widespread speciation in the late Devonian period, starting with purely aquatic lobe-finned fish, with their successors showing increased air breathing capability and related adaptions to the jaws and gills, as well as more muscular neck allowing freer movement of the head than fish have, and use of the fins to raise the body of the fish. These features are displayed by the earlier *Tiktaalik*, which like the *Ichthyostega* living around the same time as *Acanthostega* showed signs of greater abilities to move around on land, but is thought to have been primarily aquatic.

Baphetidae

Baphetidae is an extinct family of early tetrapods. Baphetids were large labyrinthodont predators of the Late Carboniferous period (Namurian through Westphalian) of Europe. Fragmentary remains from the Early Carboniferous of Canada have been tentatively assigned to the group. The phylogenetic relationships of baphetids is uncertain; while many studies have placed the group as a close relative of Amniota, other analyses have found Baphetidae to be a more basal clade of early stem tetrapods. Baphetids were among the first of the Carboniferous fossil tetrapods to be found and were originally described in 1850 by William Dawson. The baphetids have been referred to the family **Loxommatidae**, but this group was later shown to be a junior synonym of Baphetidae, which was named earlier in 1865. Baphetids are known mainly from skulls; very little skeletal material has been found.

Palaeobiology

The presence of lateral lines and the long rows of needle-like teeth show that most were fish-eaters. Their development were likely amphibian, though no larval fossils are known. Their best-known characteristic was a curious, keyhole-shaped orbit formed by excavation of the lacrimal and prefrontal bones in front of the eye. It has been suggested that this space accommodated a salt gland or some kind of electrosensory organ. Perhaps the better hypothesis is that the space allowed room for the contraction of an enlarged pterygoideus muscle. In that case, this skull modification would represent an early form of skull fenestration for jaw muscles.

The skull is shallow. Unlike the better-known embolomeres, the baphetid cheek and skull roof are sutured together. There is a strongly embayed spiracular ("otic") notch, but the stapes is distally broad, which seems to rule out a sensitive hearing apparatus. The palate is closed -- a primitive character, but very different from the temnospondyls. The coronoids bear no teeth or denticles, while the dentary has a double tooth row.

Since the taxon is based almost exclusively on skulls, the body is very poorly known. It is often said that the body was crocodile-like, but this appears to be largely supposition.

Megalocephalus

It is not clear whether all of the genera assigned to this group are really closely related. The traditional four genera of baphetids (*Loxomma*, *Baphetes*, *Megalocephalus*, and *Spathicephalus*) have recently been supplemented by *Eucritta*, a somewhat different form. It has also been suggested that *Crassigyrinus* may be closely related.

Taxonomy

Baphetids were first described by Edward Drinker Cope when he erected the family Baphetidae in 1865 for *Baphetes*. Richard Lydekker named Loxomatinae in 1889 for *Loxomma*, which later became known as Loxommatidae. D. M. S. Watson described the group as Loxommidae in 1917. Later studies have shown *Baphetes* and *Loxomma* to be close relatives within the same family, and because Baphetidae was named before Loxommatidae, it has seniority and is the valid name of the group.

Phylogeny

Baphetids have been previously considered primitive temnospondyls and more recently batrachosaurs (reptile-like amphibia). It is likely, however, that they represent one more of a number of early Carboniferous tetrapodomorph radiations. Computer-assisted phylogenetic analyses of a data matrix using characteristics of most of the major groups of terrestrial vertebrates place the Baphetids close to the ancestry of amniotes.

With the reinterpretation of *Ichthyostega* and its relatives as aquatic forms, baphetids are good candidates for the spot of first tetrapodomorph group to actually spend substantial time on land. If so, baphetids may be a rather important taxon.

Chapter 2

Casineria and Conodont

Casineria

Casineria kiddi from the Lower Carboniferous of Scotland, UK

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	Vertebrata
Class:	Amphibia/Reptilia (uncertain)
Order:	Cotylosauria?
Genus:	*Casineria*
Binomial name	

Casineria kiddi

Casineria was a tetrapod which lived 340 million years ago in the Mississippian epoch. *Casineria* was a very small animal, total length is estimated to have been a mere 15 centimeters. It lived in what was then a fairly dry environment in Scotland. It is noted for its mix of primitive (amphibian) and advanced (reptilian) characters, putting it at or very near the origin of the amniotes. The sole find lacking key elements (most of the skull and the whole lower body is missing), making exact analysis is difficult.

Its name, *Casineria*, is a latinization of *Cheese Bay*, the site near Edinburgh, where it was found.

Discovery

In 1992, an amateur fossil collector spotted the remnants of this four-legged creature on the shore of Cheese Bay, Scotland. For the next five years, the fossil languished at the National Museums of Scotland in Edinburgh while researchers focused on other projects. Around 1997, work began to expose the remainder of the fossil from the surrounding matrix. The work revealed that the animal probably lived in an environment much drier than previously understood. The findings were first reported in the April 8, 1999 edition of *Nature*.

Phylogenetic relationship

While retaining a general build like those found in the amphibian reptiliomorph groups like Seymouriamorpha and Diadectomorpha, *Casineria* also shows features that ties it in with early reptiles, notably a generally gracile build with light leg-bones, unfused ankles and toes terminating in claws. This would enable the animal to use their feet actively in traction, rather than as holdfasts, and indication of a primarily terrestrial lifestyle. These traits shows it was more closely related to amniotes than to other known reptiliomorph amphibians.

With its advanced features, *Casineria* may have been one of the very first true amniotes, and thus the first reptile under traditional classification. In phylogenetic parlance it would have been a stem amniote, close to, but outside the crown group Amniota (a group containing the last common ancestor of synapsids and sauropsids and all its descendants). *Casineria* pushes back the origin of amniote lineages much farther than was previously realized.

Casineria in life

Casineria was an insectivore. This earliest amniote had five fingers with claws on each hand, and marks the earliest clawed foot. Claws being an intimately bound to the formation of keratinous scales in reptiles, *Casineria* would in life in all likelihood bear scaly, reptilian type skin. In life, it would resemble a small lizzard.

Likely being among the first amniotes in the biological sense, it would have laid amnioic egg not dependent on on being laid in water to survive, possibly hiding them in damp vegetation or hollowed out tree stumps. This has been inferred from the fact that *Casineria* was found in rocks showing a rather dry environment. In the early Carboniferous period before the appearance of *Casineria*, vertebrates were primarily aquatic, only spending part of their time on land. *Casineria* and its relatives were the first vertebrates to live and reproduce on land.

Conodont

Conodonts
Temporal range: 495–199.6 Ma **Late Cambrian to Late Triassic**

Reconstruction of a Conodont

Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Chordata
(unranked):	Craniata
Subphylum:	Vertebrata
Class:	†**Conodonta** Eichenberg 1930

Groups

- **Protoconodonta**
- **Conodonta**
  - **Paraconodonta**
  - **Euconodonta**
    - Panderodontida
    - Prioniodontida
      - Prioniodinina
      - Ozarkodinina

Synonyms

- †Conodontophorida
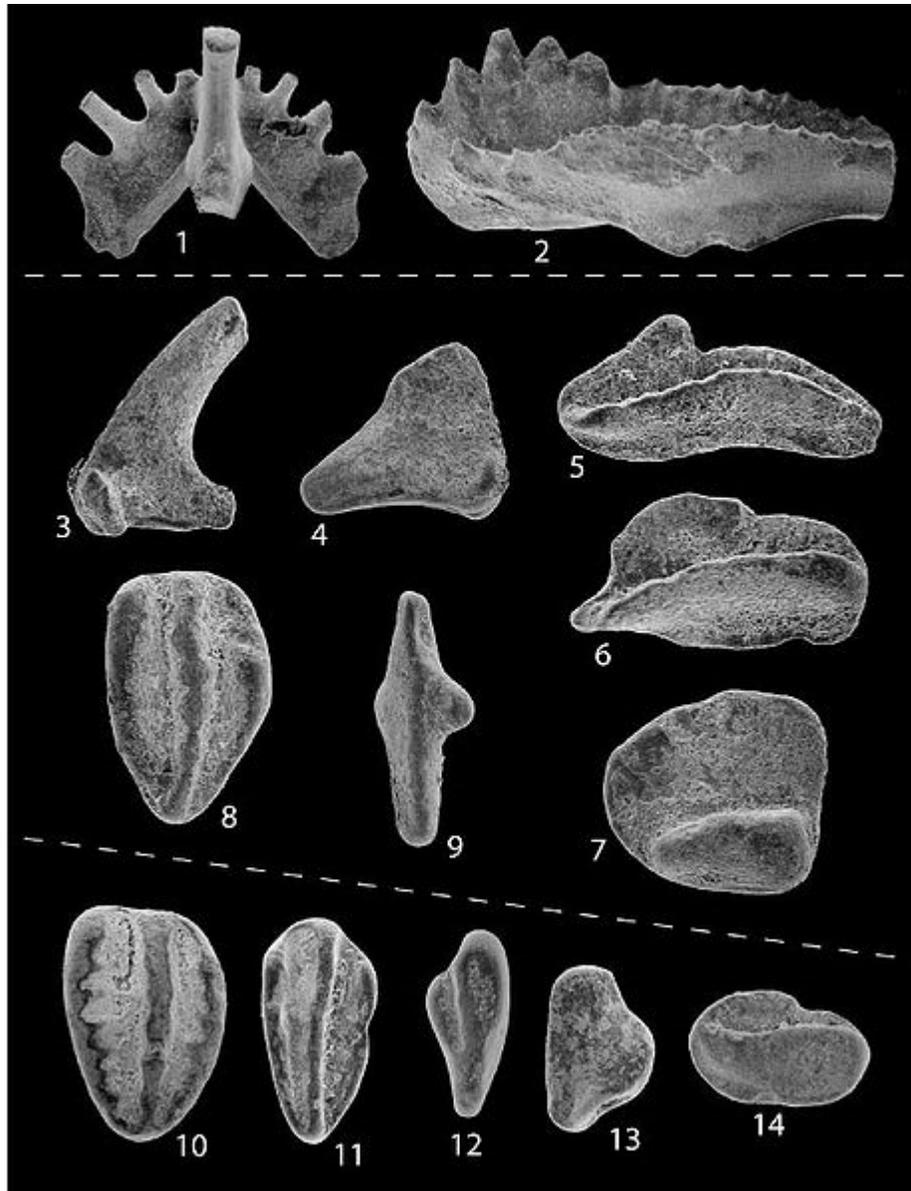
Conodont elements from the Deer Valley Member of the Mauch Chunk Formation

Conodonts are extinct chordates resembling eels, classified in the class **Conodonta**. For many years, they were known only from tooth-like microfossils now called **conodont elements**, found in isolation. Knowledge about soft tissues remains relatively sparse to this day. The animals are also called **Conodontophora** (conodont bearers) to avoid ambiguity.

Description

The eleven known fossil imprints of conodont animals depict an eel-like creature with 15 or, more rarely, 19 elements forming a bilaterally symmetrical array in the head. This array constituted a feeding apparatus radically different from the jaws of modern animals.

There are three forms of teeth, *coniform* cones, *ramiform* bars, and *pectiniform* platforms, which may have performed different roles.

The organisms range from a centimeter or so to the giant *Promissum*, 40 cm in length. It is now widely agreed that conodonts had large eyes, fins with fin rays, chevron-shaped muscles and a notochord.

The entire class of Conodonts, or at least what was left of them at the time, are postulated to have been wiped out by the Triassic–Jurassic extinction event, which occurred roughly 200 million years ago.

Ecology

The "teeth" of some conodonts have been interpreted as filter-feeding apparatuses, filtering out plankton from the water and passing it down the throat. Others have been interpreted as a "grasping and crushing array".

The lateral position of the eyes makes a predatory role unlikely.

The preserved musculature hints that some conodonts (*Promissum* at least) were efficient cruisers but incapable of bursts of speed.

Classification and Phylogeny

The conodonts are currently classified in the phylum Chordata because their fins with fin rays, chevron-shaped muscles and notochord are characteristic of Chordata.

They are considered by Milsom and Rigby to be vertebrates similar in appearance to modern hagfish and lampreys, and phylogenetic analysis suggests that they are more derived than either of these groups. This analysis, however, comes with one caveat: early forms of conodonts, the **protoconodonts**, appear to form a distinct clade from the later **paraconodonts** and **euconodonts**. It appears likely that the protoconodonts represent a stem group to the phylum containing chaetognath worms, indicating that they are not close relatives of true conodonts. Moreover, some analyses suggest that Conodonts were not Vertebrates nor Craniates, because they lack the main characteristics of these groups.

Elements

For many years, conodonts were known only from enigmatic tooth-like microfossils, which occur commonly but not always in isolation, and were not associated with any other fossil. These phosphatic microfossils are now termed "conodont elements" to avoid confusion. This confusion is apparent for the non-specialist in the book "Your Inner Fish", by Neil Shubin, who describes the origin of teeth in chapter 4. In this chapter, the author attaches the name "conodont" to both the "conodont bearer" (the animal) and the "conodont elements" (the teeth), and the reader may have a hard time to make sense of the concept of "animals living in the mouths of animals".

They are widely used in biostratigraphy.

Conodont elements are also used as paleothermometers, a proxy for thermal alteration in the host rock. This is because under higher temperatures the phosphate undergoes predictable and permanent color changes, measured with the conodont alteration index. This has made them useful for petroleum exploration where they are known, in rocks dating from the Cambrian to the Late Triassic.

It was not until early 1980s that the conodont teeth were found in association with fossils of the host organism, in a konservat lagerstätte. This is because most of the conodont animal was soft-bodied, thus everything but the teeth were not suited for preservation under normal circumstances.

The conodont apparatus may comprise a number of discrete elements, including the spathognathiform, ozarkodiniform, trichonodelliform, neoprioniodiform, and other forms.

Chapter 3

Heterostraci and Ichthyostega

Heterostraci

Heterostraci
Temporal range: 488–359 Ma **Ordovician - Devonian**

Drepanaspis gemuendenensis,
accompanied by the placoderm
Tiaraspis subtilis

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	**Heterostraci**
Orders	

- Cyathaspidiformes

- Pteraspidiformes

Heterostraci ("Different scales") is an extinct class of jawless vertebrate that lived primarily in marine and estuary environments. They arose during the Ordovician, and all, save for the Psammosteids, became extinct during the late Devonian. This last group of heterostracans died out in the extinction event at the end of the Devonian.

Description and anatomy

The Heterostracans differed from other Paleozoic agnathan classes both in the arrangement of their scales, as well as the histology of their scales.

Most heterostracans had two plates which form a large dorsal shield and a large ventral shield, and had series of scales arranged in various patterns on the sides of their bodies, the exact pattern differing from one group to another. In a few primitive forms, such as *Lepidaspis*, the dorsal and ventral shields are composed of a mosaic of tiny scales. In most other known forms, though, these tiny scales have fused together to form the shield-plates.

The scales of heterostracans are histologically distinct from other vertebrates, having three layers composed of dentine and aspidine, an acellular bony tissue unique to this class. The middle layer was honeycombed with tiny spaces called "cancella."

As with many agnathan groups, heterostracans had no fins besides the tail or caudal fin. In some pteraspids, especially in the psammosteids, the ends of the branchial plates (the plates that covered the gills) is drawn out to form wing-like extensions.

Taxonomy

Heterostraca is divided into two main groups, the orders Cyathaspidiformes ("Cup Shields"), and Pteraspidiformes ("Wing Shields"). The Silurian heterostracan *Athenaegis* is regarded as being a sister group of both orders, while the Early Devonian *Lepidaspis* is regarded as being *incertae sedis*, possibly close to the original basal forms.

Cyathaspidiformes is divided into two main groups: the Amphiaspida of Early Devonian Siberia (grouped together with their relative *Ctenaspis* of Canada), and the Cyathaspidida (grouped together with their relative *Nahanbiaspis*.

The Pteraspidiformes is divided up into five families, Anchipteraspididae, Protopteraspididae, Pteraspididae, Protaspididae, and Psammosteidae.

Ichthyostega

Ichthyostega
Temporal range: Famennian (late Devonian)

Life restoration of *Ichthyostega* after Ahlberg, 2005.

Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Amphibia
Order:	Ichthyostegalia
Family:	Ichthyostegidae
Genus:	***Ichthyostega*** Säve-Söderbergh, 1932
Species	

I. stensioei
I. watsoni
I. eigili
I. kochi

Ichthyostega (Greek: "fish roof") is an early tetrapod genus that lived at the end of the Upper Devonian epoch (Famennian age, 374 – 359 million years ago). It was a labyrinthodont, one of the first fossil record of tetrapods. *Ichthyostega* possessed lungs and limbs that helped it navigate through shallow water in swamps. Though undoubtedly of amphibian build and habit, it is not considered a true member of the group in the narrow sense, as the first true amphibians appeared in the Carboniferous period.

Ichthyostega skull reconstruction at the Geological Museum, Copenhagen

Underside of skull

In 1932 Gunnar Säve-Söderbergh described four *Ichthyostega* species from the Upper Devonian of East Greenland and one species belonging to the genus *Ichthyostegopsis*, *I. wimani*. These species could be synonymous (in which case only *I. stensioei* would remain), because their morphological differences are not very pronounced. The species differ in skull proportions, skull punctuation and skull bone patterns. The comparisons were done on 14 specimens collected in 1931 by the Danish East Greenland Expedition. Additional specimens were collected between 1933 and 1955.

The genus is closely related to *Acanthostega gunnari*, also from East Greenland. *Ichthyostega'*s skull seems more fish-like than that of *Acanthostega*, but its girdle (shoulder and hip) morphology seems stronger and better adapted to land-life. *Ichthyostega* also had more supportive ribs and stronger vertebrae with more developed zygapophyses. The first tetrapods (who probably didn't walk on land) were *Elginerpeton* and *Obruchevichthys*.

Characteristics

Ichthyostega was about 1.5 m long and had seven digits on each hind limb. The exact number of digits on the forelimb is not yet known, since fossils with forelimbs have not been found. It had a fin containing fin rays on its tail.

Adaptations for land life

Early tetrapods like *Ichthyostega* and *Acanthostega* differed from animals like Crossopterygians (for instance *Eusthenopteron* or *Panderichthys*) in their increased adaptations for life on land. Though Crossopterygians possessed lungs, they used gills as their primary means of acquiring oxygen; *Ichthyostega* appears to have relied on its lungs as its primary apparatus for breathing. The skin of early tetrapods, unlike that of Crossopterygians, helped retain bodily fluids and deter desiccation. Crossopterygians used their body and tail for locomotion and their fins for balance; *Ichthyostega* used its limbs for locomotion and its tail for balance.
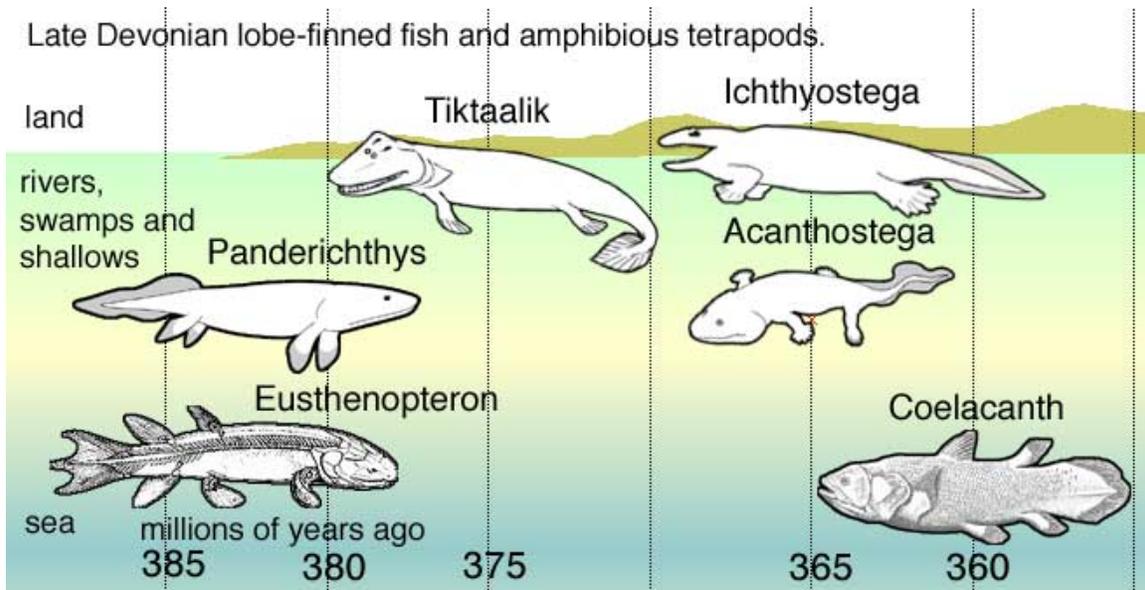
In Late Devonian vertebrate speciation, descendants of pelagic lobe-finned fish – like *Eusthenopteron* – exhibited a sequence of adaptations:

- *Panderichthys*, suited to muddy shallows;
- *Tiktaalik* with limb-like fins that could take it onto land;
- Early tetrapods in weed-filled swamps, such as:
    - *Acanthostega* which had feet with eight digits,
    - *Ichthyostega* with limbs.

Descendants also included pelagic lobe-finned fish such as coelacanth species.

The size of an adult *Ichthyostega* (1.5 m) precluded completely terrestrial locomotion. Juveniles, though, could have moved about on land much more easily. The massive ribcage was made up of overlapping ribs and the creatures possessed a stronger skeletal structure, a more rigid spine, and forelimbs apparently powerful enough to pull the body from the water. These anatomical modifications clearly evolved to handle the lack of buoyancy experienced on land. The hindlimbs were smaller than the forelimbs and unlikely to have born full weight in an adult. Jennifer A. Clack suggests that *Ichthyostega* and its relatives spent time basking in the sun to raise their body temperatures, much as some animals do today: the Marine Iguanas on the Galapagos Island or the Gharial. They would have returned to the water to cool themselves, hunt for food and reproduce. In that case, they would need strong forelimbs to pull at least their anterior part out of the water, and a stronger ribcage and spine to support them while sunbathing on their abdomen like modern crocodiles. The greater mobility of juveniles on land would have helped them avoid aquatic predators.

Water was also still a requirement, because the gel-like eggs of the earliest terrestrial tetrapods couldn't survive out of water, so reproduction could not occur without it. Water was also needed for their larvae and external fertilization. Most land-dwelling vertebrates have since developed two methods of internal fertilization; either direct as seen in all amniotes and a few amphibians, or indirect for many salamanders by placing a spermatophore on the ground which then is picked up by the female salamander.

The Ichthyostegalians (*Elginerpeton*, *Acanthostega*, *Ichthyostega*, etc.) were succeeded by temnospondyls and anthracosaurs, such as *Eryops*, amphibians that truly developed the ability to walk on land. Until 2002, there was a gap of 20 million years between the two groups (Romer's Gap). In 2002 a 350 million year old fossil from the lower Mississippian, *Pederpes finneyae* was described and helped to close the gap: it is the earliest-known tetrapod to show the beginnings of terrestrial locomotion.

Chapter 4

Pederpes and Westlothiana

Pederpes

Pederpes
Temporal range: Middle Mississippian

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Superclass:	Tetrapoda
Class:	Amphibia *sensu lato*
Family:	Whatcheeriidae
Genus:	***Pederpes*** Clack, 2002
Species	

P. finneyae Clack, 2002 (type)

Pederpes is an extinct genus of early Carboniferous tetrapod, dating from the Tournaisian age (lower Mississippian, 359 - 345 Ma). *Pederpes* contains one species, *P. finneyae*, 1 m long.

This most basal Carboniferous tetrapod had a large, somewhat triangular head, similar to that of later American sister-genus *Whatcheeria*, from which it is distinguished by various skeletal features, such as a spike-like latissimus dorsi (an arm muscle) attachment on the humerus and several minor skull features. The feet had characteristics that distinguished it from the paddle-like feet of the Devonian Ichthyostegalia and resembled the feet of later, more terrestrially adapted Carboniferous forms. *Pederpes* is the earliest-known tetrapod to show the beginnings of terrestrial locomotion and despite the probable presence of a sixth digit on the forelimbs it was at least functionally pentadactyl.

Discovery and Classification

Pederpes was discovered in 1971 in central Scotland and classified as a lobe-finned fish. Its fossils were found in the Ballagan Formation. The type specimen was a nearly complete, articulated skeleton. Only the tail and some bones of the skull and limbs were missing. It was not until 2002 that Jennifer Clack named and reclassified the fossil as a primitive tetrapod.

Pederpes is placed in the family Whatcheeriidae, of uncertain relationships to other tetrapod families. While undoubtedly amphibian in life and reproductive mode, under cladistic taxonomy, *Pederpes* is not considered an amphibian in the meaning of modern amphibians. As a very basal (primitive) tetrapod, it falls under the traditional class Amphibia in Linnaean taxonomy.

Pederpes is an important fossil because it comes from the period of time known as Romer's Gap and provides biologists with rare information about the development of tetrapods in a time where terrestrial life was rare.

Anatomy and Lifestyle.

Pederpes was 1 m long, making it average-sized for an early tetrapod.

The shape of the skull and the fact that the feet face forward rather than outward indicate that *Pederpes* was well adapted to land life. It is currently the earliest known fully terrestrial animal, although the structure of the ear shows that its hearing was still much more functional underwater than on land, and may have spent much of its time in the water and could have hunted there.

The narrow skull suggests that *Pederpes* breathed by inhaling with a muscular action like most modern tetrapods, rather than by pumping air into the lungs with a throat pouch the way many modern amphibians do.

Westlothiana

Westlothiana
Temporal range: Early Carboniferous

Westlothiana lizziae

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata

Class: Amphibia/Reptilia
Order: Cotylosauria?
Genus: ***Westlothiana***
Species: ***W. lizziae***

Binomial name

Westlothiana lizziae
Smithson and Rolfe, 1990

Westlothiana lizziae was a reptile-like amphibian or possibly early reptile that bore a superficial resemblance to modern-day lizards. It lived during the Carboniferous period, about 350 million years ago. The type specimen was discovered in East Kirkton Quarry, Bathgate, Scotland, in 1984, and was named after the West Lothian district where it was found. *Westlothiana*'s anatomy contained a mixtures of both labyrinthodont and reptilian features, and was originally regarded as the first reptile. Most scientists place them among the Reptilomorpha, as a sister group to the first amniotes.

Westlothiania *in life*

This species probably lived near a freshwater lake, probably hunting for other small creatures that lived in the same habitat. It was a slender animal, with rather small legs and a long tail. Together with *Casineria*, another transitional fossil found in Scotland, it is one of the smallest reptil-like amphibians known, being a mere 20 cm in adult length. The small size has made it a key fossil in the search for the earliest amniote, as amniote eggs are thought to have evolved in very small animals. Advanced features that ties it in with the reptilian rather than amphibian group is unfused ankle bones, lack of labyrinthodont infolding of the dentin, a lack of an otic notch and a generally small skull.

Ruta & al. (2003) interpreted the long body and small legs as a possible adaption to burrowing, similar to that seen in modern skinks.

Phylogeny

The phylogenetic placement of *Westlothiana* has varied from basal amniote (i.e. a primitive reptile) to an amphibian Lepospondyl only distantly related to the Reptiliomorpha. The actual phyllogenetic position of *Westlothiania* is uncertain, reflecting the uncertainty of labyrinthodont phylogeny in general.

Chapter 5

Pelycosaur

<table>
<tr><td colspan="2" align="center">Pelycosaurs
Temporal range:
Late Carboniferous–Late Permian, 320–251 Ma
Descendant taxon Mammalia survives to present.</td></tr>
<tr><td colspan="2" align="center">
<i>Dimetrodon grandis</i> skeleton at the
National Museum of Natural History</td></tr>
<tr><td colspan="2" align="center">Scientific classification [e l</td></tr>
<tr><td>Kingdom:</td><td>Animalia</td></tr>
<tr><td>Phylum:</td><td>Chordata</td></tr>
<tr><td>Class:</td><td>Synapsida</td></tr>
<tr><td><i>informal group</i>:</td><td>Pelycosauria
Cope, 1878</td></tr>
<tr><td colspan="2" align="center">Subgroups</td></tr>
<tr><td colspan="2">

†Caseasauria
Eupelycosauria

</td></tr>
</table>

The **pelycosaurs** were primitive Late Paleozoic synapsid amniotes. Some species were quite large and could grow up to 3 meters or more, although most species were much smaller.

Evolutionary history

The pelycosaurs appeared during the Late Carboniferous and reached their acme in the early part of the Permian Period, remaining the dominant land animals for some 40 million years. A few continued into the late Permian. They were succeeded by the therapsids.

Characteristics
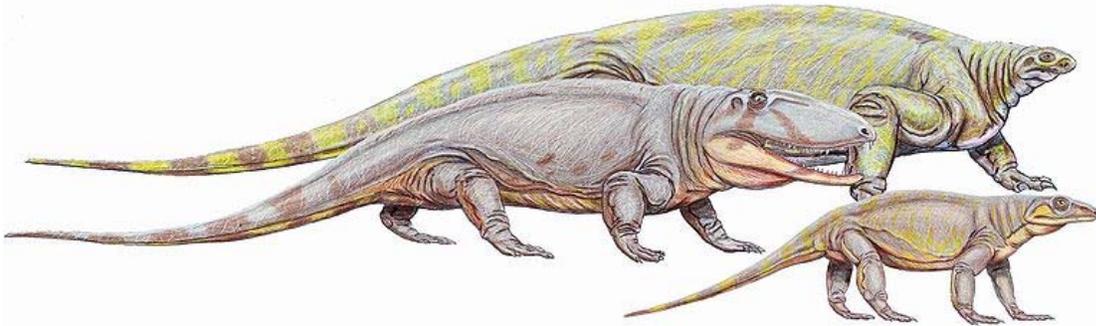
Cotylorhynchus (background), *Ophiacodon* and *Varanops*

At least two pelycosaur clades independently evolved a tall sail, consisting of elongated vertebral spines: the edaphosaurids and the sphenacodontids. In life, this would have been covered by skin, and possibly functioned as a thermoregulatory device and/or for mating display. Pelycosaur fossils have been found mainly in Europe and North America, although some small, late-surviving forms are known from Russia and South Africa.

Unlike lepidosaurian reptiles, pelycosaurs lacked epidermal scales. Fossil evidence from some ophiacodonts shows that parts of the skin was naked, but that the belly was covered in dermal scutes, looking like the scutes present in other reptile groups, which are of a different type of structure.

Dermal scutes are also found in a diverse number of extant mammals with conservative body types, such as in the tails of certain rodents, sengis, moonrats, the opossums and other marsupials, and as regular dermal armour with underlying bone in the armadillo.
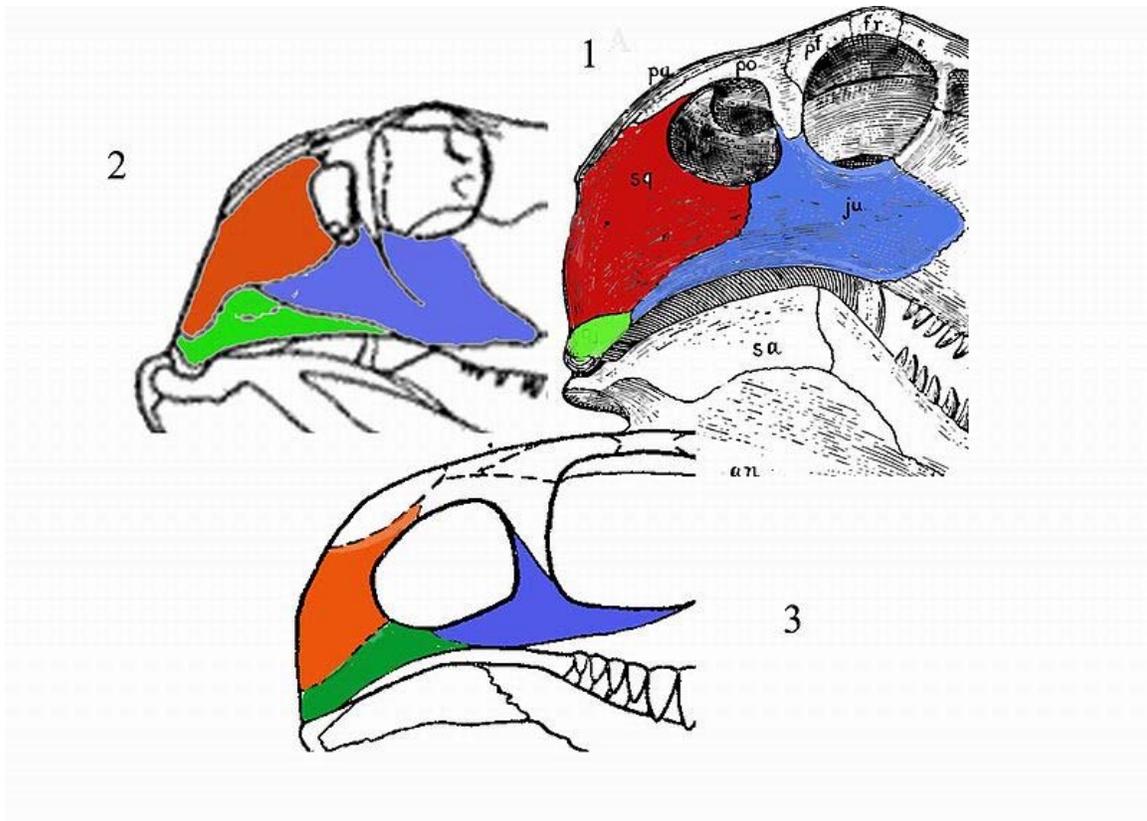
Comparison of "pelycosaurian" skulls: 1 - sphenacodont, 2 - ophiacodont, 3 - caseid. Quadratojugale is green, squamosale is red, jugale is blue.

In 1940 the group was reviewed in detail and every species known at the time described (and many illustrated) in an important monograph by Alfred Sherwood Romer and Llewellyn Price.

Pelycosauria is a paraphyletic taxon because it excludes the therapsids. For that reason the term is not used in some modern books. Eupelycosauria is used to designate the clade that includes most Pelycosaurs along with the Therapsida and the Mammals. In contrast to "Pelycosaurs", this is a monophyletic group. Caseasauria refers to a pelycosaur side-branch or clade that did not leave any descendants.
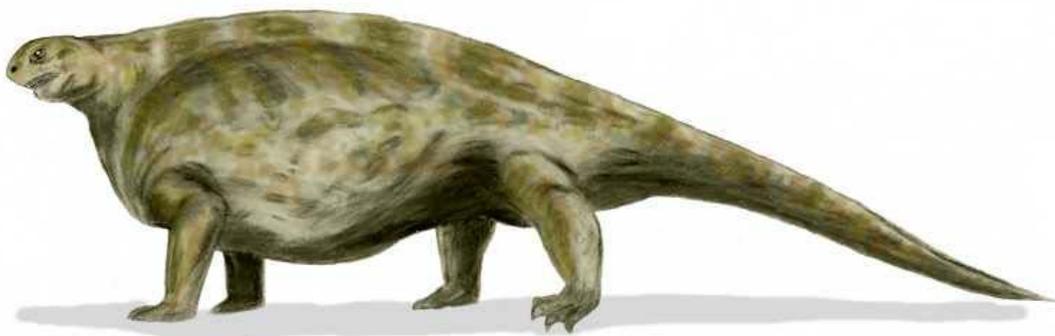
The pelycosaurs appear to have been a group of synapsids that had direct ancestral links with the mammalia, having differentiated teeth and a developing hard palate.

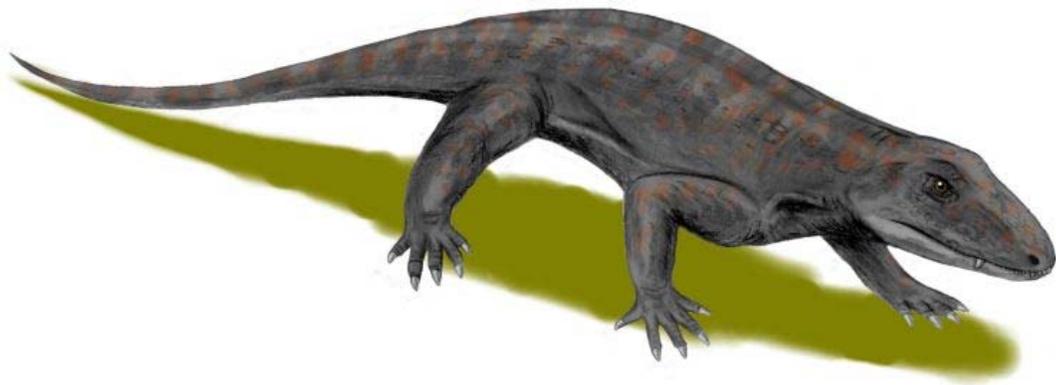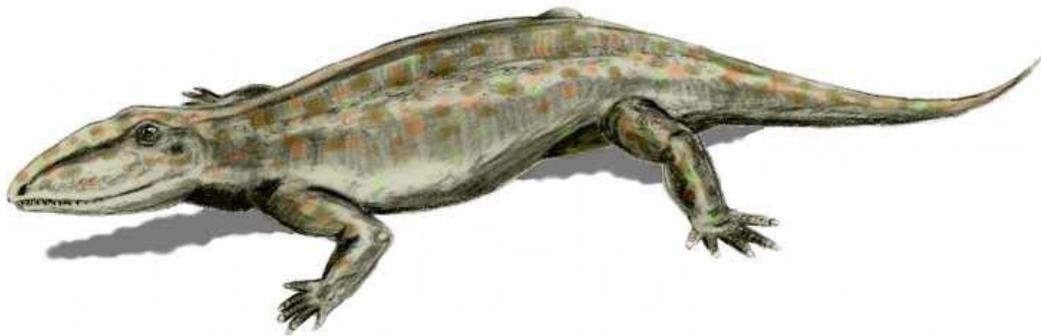Well-known pelycosaurs include the genera *Dimetrodon*, *Sphenacodon*, *Edaphosaurus*, and *Ophiacodon*.
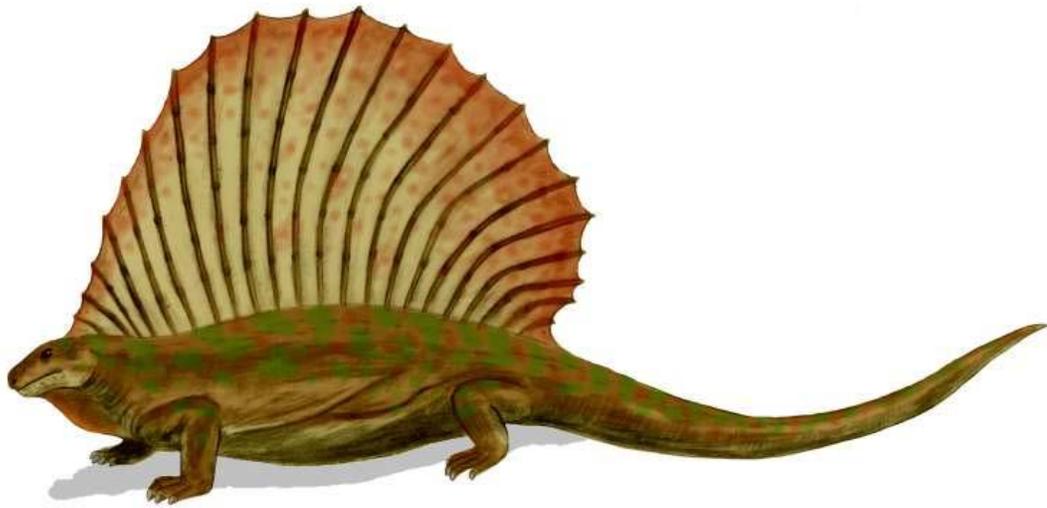
Systematics
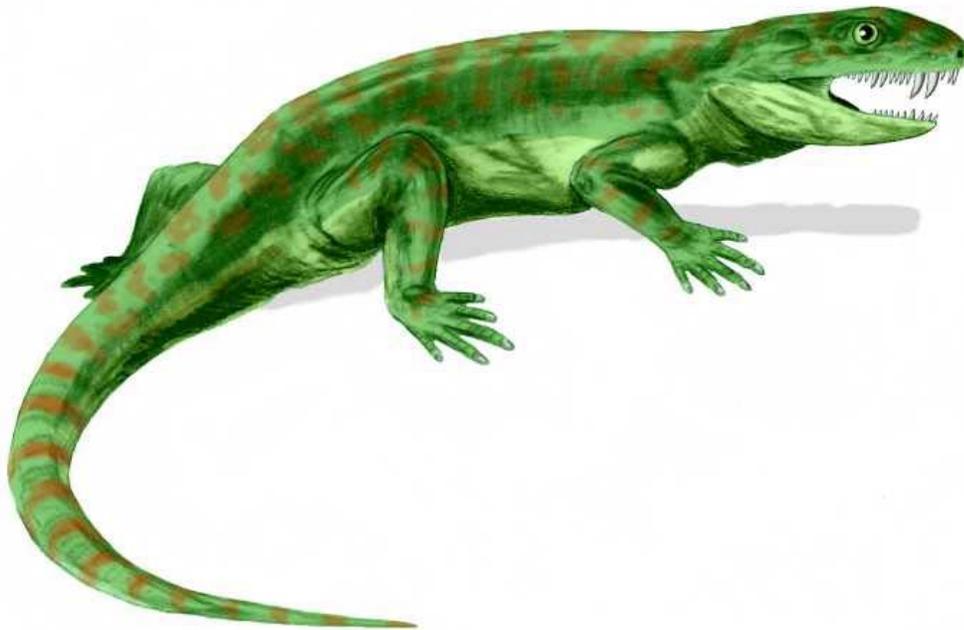
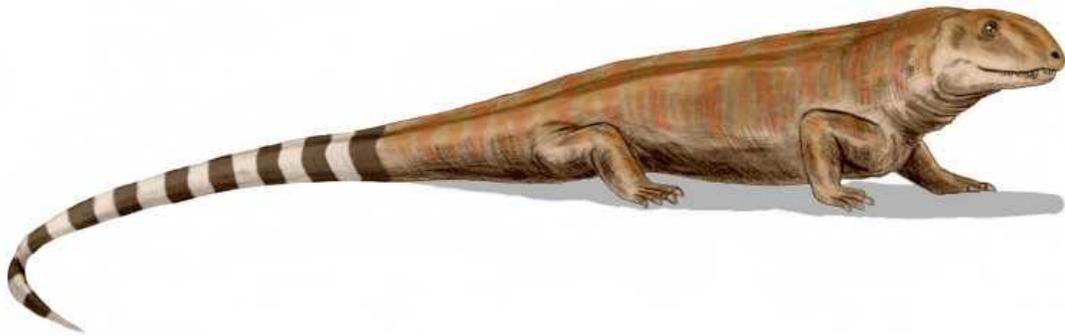*Eothyris*

Cotylorhynchus – a Caseid
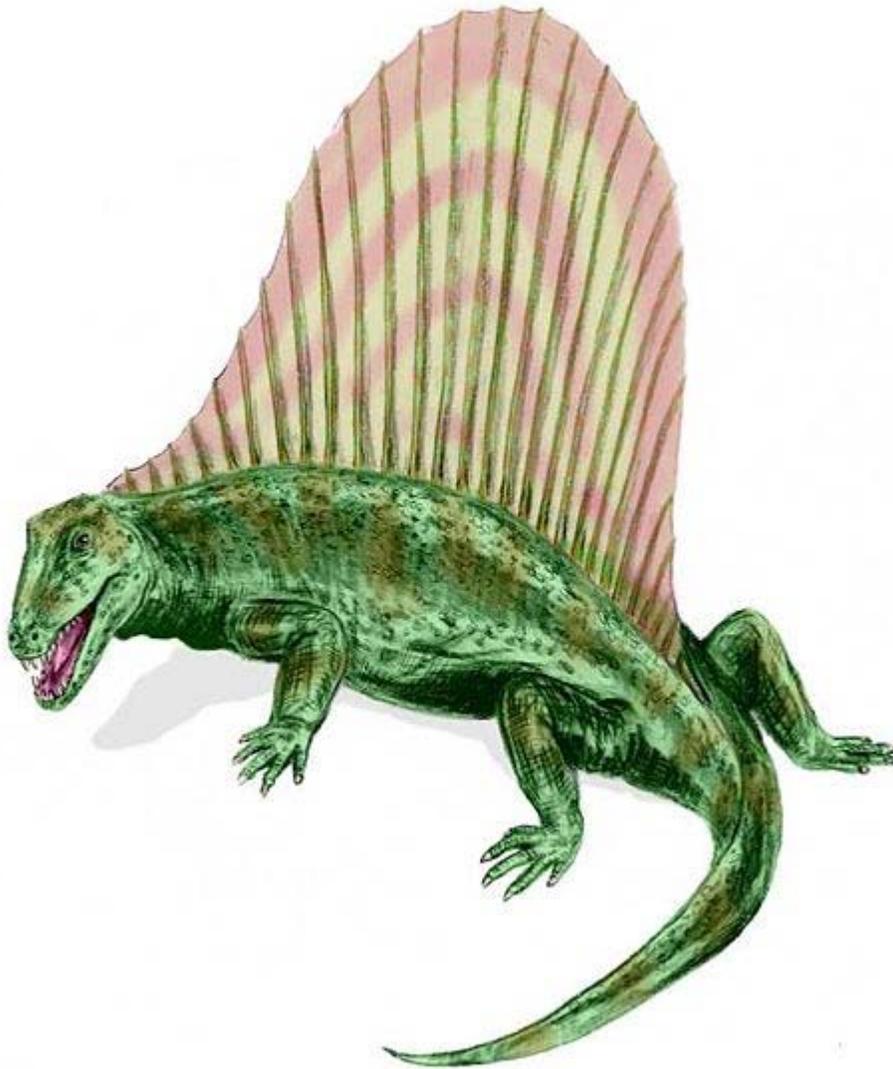
Varanops

Ophiacodon

Edaphosaurus

Haptodus

Dimetrodon

In traditional classification, the order Pelycosauria is paraphyletic--that is, it is a grouping of animals that does not contain all descendants of a common ancestor, as is often required by a different system of naming organisms, phylogenetic nomenclature. In the latter, Pelycosauria is treated as a clade rather than a taxon with the rank "order", and includes the clade Therapsida, which in turn contains the clade Mammalia. In traditional taxonomy, Therapsida is separated from Pelycosauria in its own biological order, and mammals are separated from both as their own class.

Taxonomy

- **Order Pelycosauria***
  - **Suborder †Caseasauria**
    - Family †Caseidae
    - Family †Eothyrididae
  - **Suborder Eupelycosauria**
    - Family †Edaphosauridae
    - Family †Haptodontidae*
      - †*Cutleria*
      - †*Haptodus*
      - †*Palaeohatteria*
      - †*Pantelosaurus*
    - Family †Lupeosauridae
      - †*Lupeosaurus*
      - †*Nitosaurus*
    - Family †Ophiacodontidae
    - Family †Sphenacodontidae
    - Family †Varanopseidae
- **Order Therapsida***

Phylogeny

In phylogenetic nomenclature, the "Pelycosauria" is not used, since it does not constitute a clade (a group of organisms descended from one common ancestor and including all the descendants of that ancestor) because the group excludes the therapsids. Instead, it represents a paraphyletic "grade" of basal synapsids leading up to the clade

Chapter 6

Therapsida

<table>
<tr><td colspan="2" align="center">Therapsids
Temporal range:
Early Permian–Early Cretaceous, 275–100 Ma
Descendant taxon Mammalia survives to present.</td></tr>
</table>

Illustration of *Pristerognathus*, a cat-sized therocephalian therapsid

Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Synapsida
(unranked):	Eupelycosauria
(unranked):	Sphenacodontia
(unranked):	Sphenacodontoidea
Order:	**Therapsida** Broom, 1905
Clades	

- Suborder †Biarmosuchia *
- (unranked) Eutherapsida
    - Suborder †Dinocephalia

- Infraorder †Anteosauria
- Infraorder †Tapinocephalia
- (unranked) Neotherapsida
  - Suborder †Anomodontia *
    - Infraorder †Dicynodontia
- (unranked) Theriodontia *
  - Suborder Cynodontia *
  - Suborder †Gorgonopsia
  - Suborder †Therocephalia

Therapsida is a group of synapsids that includes mammals and their immediate evolutionary ancestors. The earliest fossil attributed to Therapsida is believed to be *Tetraceratops insignis* (Lower Permian). Therapsids evolved from pelycosaurs (specifically sphenacodonts) 275 million years ago. They replaced the pelycosaurs as the dominant land animal. Mammals appeared 200 million years ago, and all therapsids other than mammals became extinct in the Early Cretaceous period (146 Ma to 100 Ma).

Characteristics

Therapsids' temporal fenestrae are larger than those of the pelycosaurs. The jaws of therapsids are more complex and powerful, and the teeth are differentiated into frontal incisors for nipping, large lateral canines for puncturing and tearing, and molars for shearing and chopping food. Their legs are positioned more vertically beneath their bodies than are the sprawling legs of reptiles and pelycosaurs.

Evolutionary history
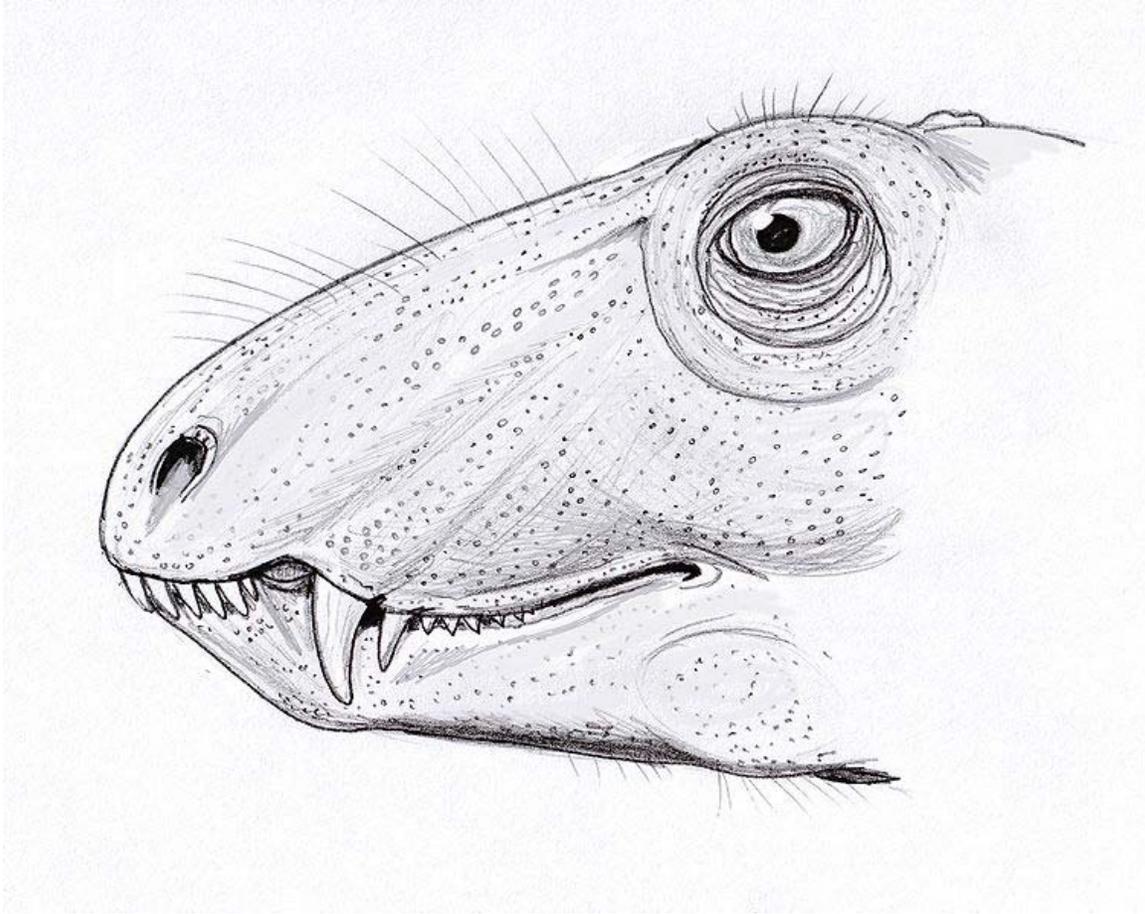
Raranimus, a primitive therapsid

Therapsids evolved from a group of pelycosaurs called sphenacodonts. Therapsids became the dominant land animals in the Middle Permian, displacing the pelycosaurs. Therapsida consists of three major clades, the dinocephalians, the herbivorous anomodonts and the mostly carnivorous theriodonts, with the carnivorous biarmosuchians as a paraphyletic assemblage of primitive forms. After a brief burst of evolutionary diversity, the dinocephalians died out in the later Middle Permian (Guadalupian) but the anomodont dicynodonts and the theriodont gorgonopsians and therocephalians flourished, being joined at the very end of the Permian by the first cynodonts

Like all land animals, the therapsids were seriously affected by the Permian–Triassic extinction event, with the very successful gorgonopsians dying out altogether and the remaining groups, dicynodonts, therocephalians and cynodonts of a few species, each surviving into the Triassic. The dicynodonts, now represented by a single family of large stocky herbivores, the Kannemeyeridae, and the medium-sized cynodonts (including both carnivorous and herbivorous forms), flourished worldwide, throughout the Early and Middle Triassic. They died out across much of Pangea at the end of the Carnian (Late

Triassic), although they continued for some time longer in the wet equatorial band and the south.
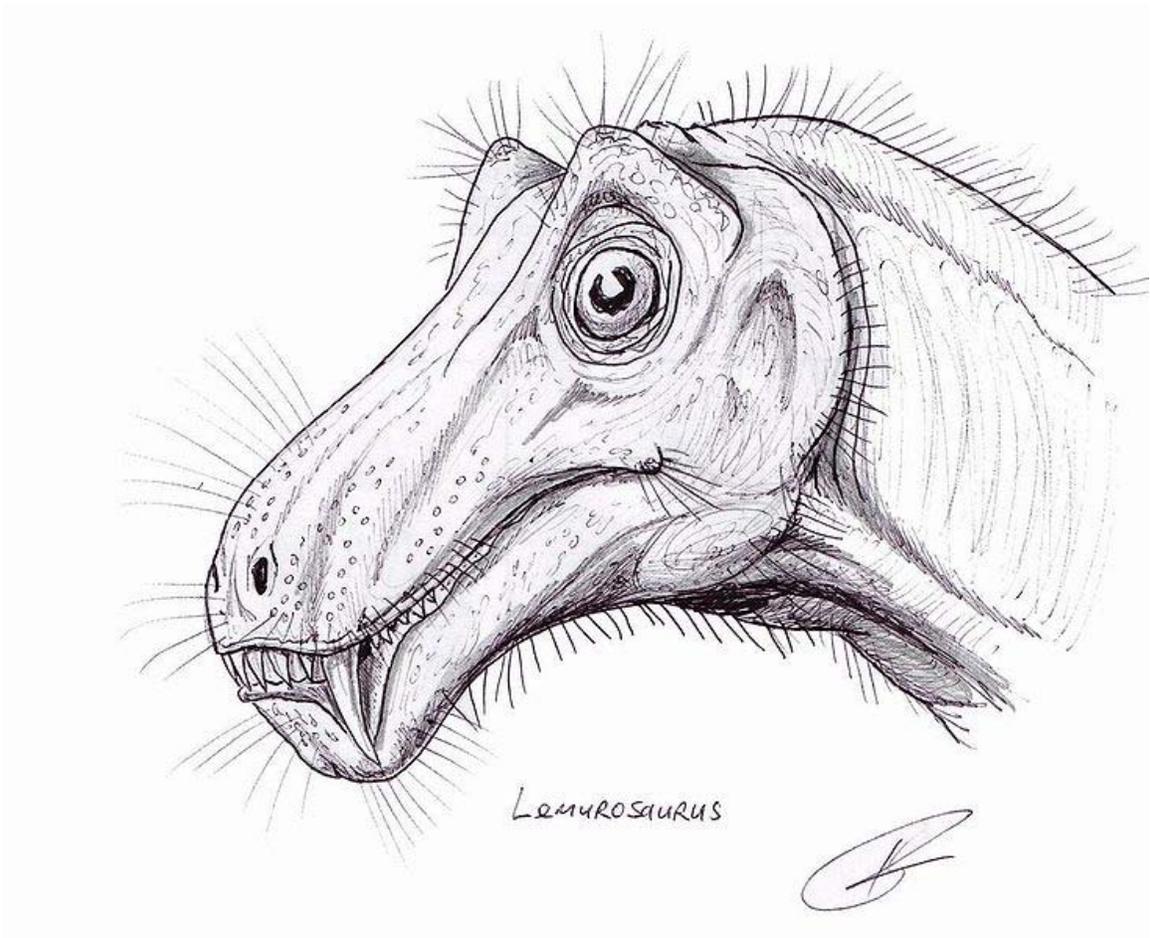
Lemurosaurus

Some exceptions were the still further derived eucynodonts. At least three groups of them survived. They all appeared in the Late Triassic period. The extremely mammal-like family, Tritylodontidae, survived into the Early Cretaceous. An extremely mammal-like family, Trithelodontidae, are unknown later than the Early Jurassic. The third group, *Morganucodon* and similar animals, were mammaliformes or the "stem-mammals".

Some non-eucynodont cynodonts survived the Permian-Triassic extinction, such as *Thrinaxodon* but only to become extinct by the Middle Triassic.

The therocephalians, relatives of the cynodonts, managed to survive the Permian-Triassic extinction and continued to diversify through the Early Triassic period. Approaching the end of the period, however, the therocephalians were declining to extinction and eventually became extinct, possibly due to climatic changes and competition from cynodonts and other animals struggling to survive.

Dicynodonts have been thought to have become extinct before the end of the Triassic, but there is evidence that they survived the extinction. Their fossils have been found in Gondwana. Other animals that were common in the Triassic also took refuge here, such as the temnospondyls. This is an example of Lazarus taxon.

Mammals, the only living therapsids, evolved in the Early Jurassic period. They radiated from a group of Mammaliaformes that is related to the symmetrodonts. The Mammaliaformes themselves evolved from probainognathians, a lineage of the eucynodont suborder.
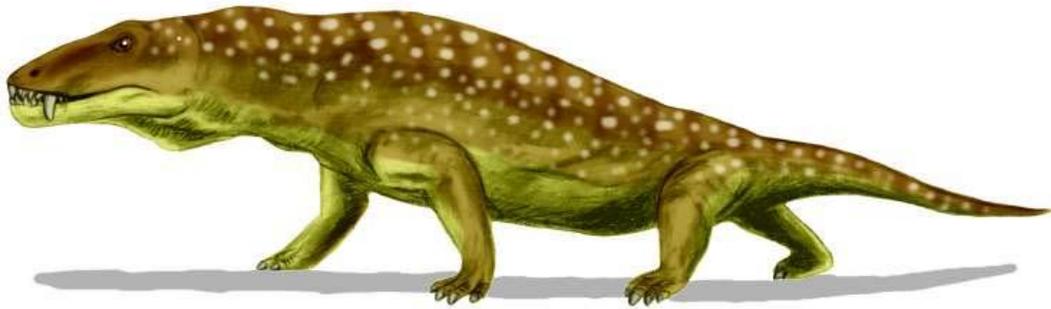
Taxonomy
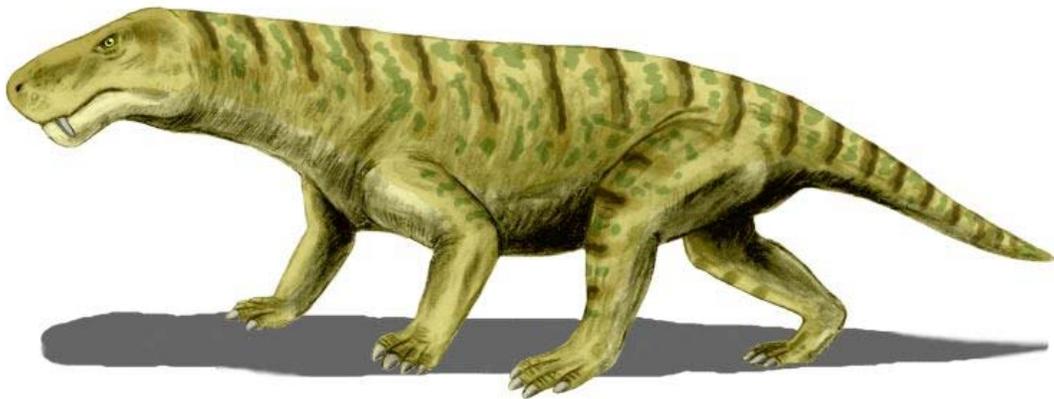
Classification
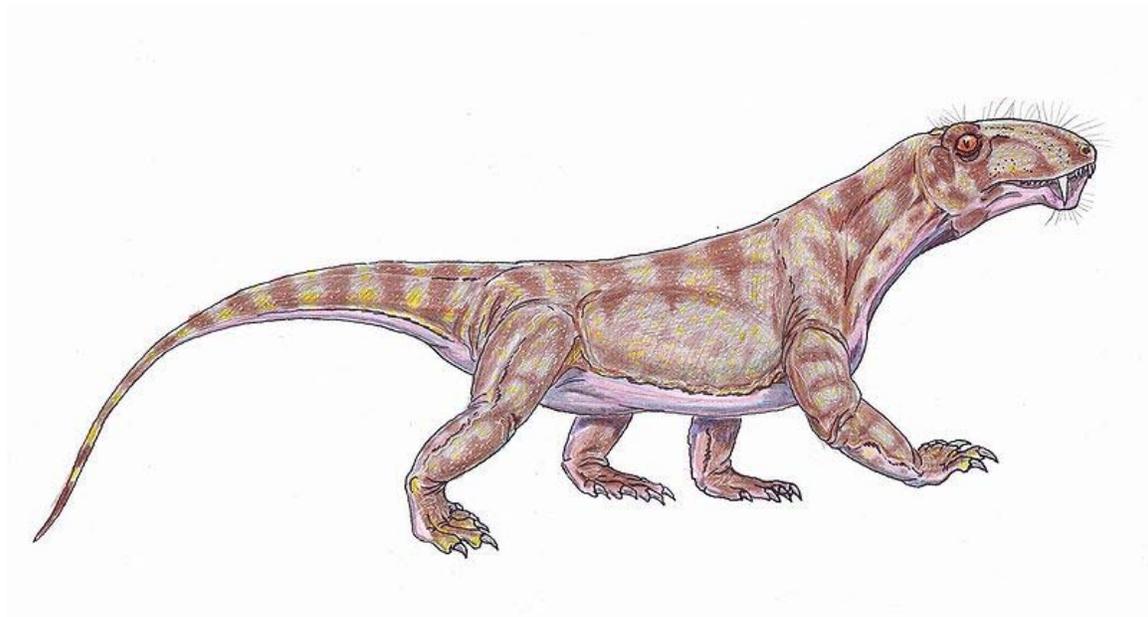
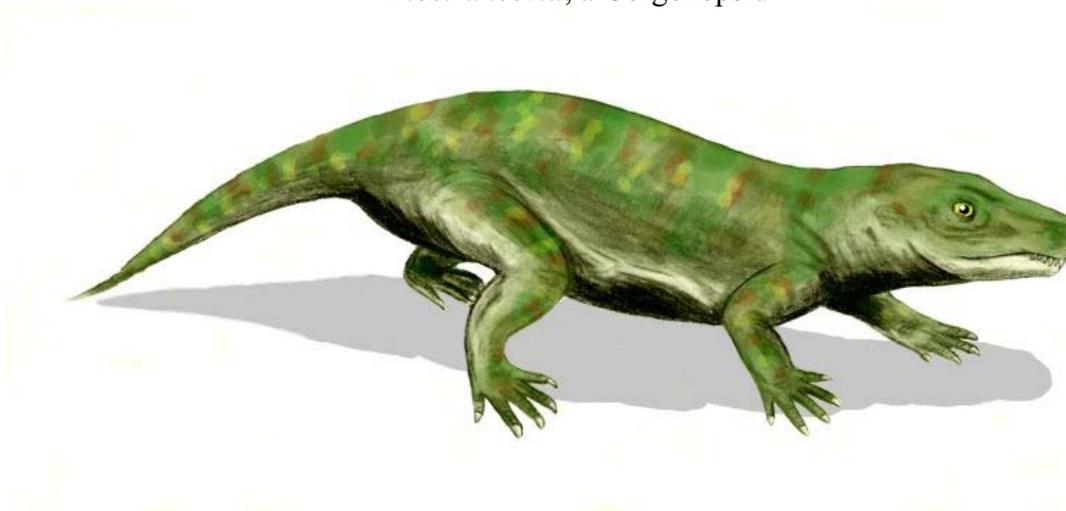*Biarmosuchus*, a Biarmosuchian

Estemmenosuchus, a Dinocephalian

Anteosaurus, an Anteosaur

Inostrancevia, a Gorgonopsid

Bauria, a Therocephalian

Oligokyphus, a Cynodont

- Class **Synapsida**
- ORDER **THERAPSIDA** *

  - ?Family †Tetraceratopsidae
  - Suborder †**Biarmosuchia** *
    - Family †Biarmosuchidae
    - Family †Eotitanosuchidae
  - **Eutherapsida**
    - Suborder †**Dinocephalia**
      - Family †Estemmenosuchidae
      - ?Infraorder †**Anteosauria**
        - Family †Anteosauridae
        - Family †Brithopodidae
        - Family †Deuterosauridae
        - Family †Syodontidae
        - ?Family †Stenocybidae
      - †**Tapinocephalia**
        - Family †Styracocephalidae
        - Family †Tapinocephalidae
        - Family †Titanosuchidae

Neotherapsida

  - Suborder †**Anomodontia** *
    - Superfamily †Venyukoviamorpha
      - Family †Otsheridae
      - Family †Venyukoviidae
    - Infraorder †**Dromasauria**
      - Family †Galeopidae
    - Infraorder †**Dicynodonta**
      - Family †Endothiodontidae
      - Family †Eodicynodontidae
      - Family †Kingoriidae
      - (unranked) †Diictodontia
        - Superfamily †Emydopoidea

- - Family †Cistecephalidae
    - Family †Emydopidae
  - Superfamily †Robertoidea
    - Family †Diictodontidae
    - Family †Robertiidae
- (unranked) †**Pristerodontia**
  - Family †Aulacocephalodontidae
  - Family †Dicynodontidae
  - Family †Kannemeyeriidae
  - Family †Lystrosauridae
  - Family †Oudenodontidae
  - Family †Pristerodontidae
  - Family †Shanisiodontidae
  - Family †Stahleckeriidae

Theriodontia *

- Suborder †**Gorgonopsia**
  - Family †Gorgonopsidae
- **Eutheriodontia**
  - Suborder †**Therocephalia**
    - Family †Lycosuchidae
  - (unranked) †**Scylacosauria**
    - Family †Scylacosauridae
  - Infraorder †**Eutherocephalia**
    - Family †Hofmeyriidae
    - Family †Moschorhinidae
    - Family †Whaitsiidae
    - Superfamily **Bauriodea**
      - Family †Bauriidae
      - Family †Ericiolacteridae
      - Family †Ictidosuchidae
      - Family †Ictidosuchopsidae
      - Family †Lycideopsidae

Suborder **Cynodontia ***

- Family †Dviniidae
- Family †Procynosuchidae
- (unranked) **Epicynodontia**
  - Family †Galesauridae
  - Family †Thrinaxodontidae
  - Infraorder **Eucynodontia**
    - (unranked) †**Cygnognathia**

    -

- Family †Cynognathidae
- Family †Diademodontidae
- Family †Traversodontidae
- Family †Trirachodontidae
- Family †Tritylodontidae

- (unranked) Probainognathia

  - Family †Chinquodontidae
  - Family †Probainognathidae
  - (unranked) †Ictidosauria
    - Family †Trithelodontidae
  - **(unranked) Mammaliformes**
    - Class **Mammalia**

Chapter 7

Synapsid

Dimetrodon grandis skeleton at the National Museum of Natural History of U.S.A.

Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Chordata
Superclass:	Tetrapoda
(unranked):	Reptiliomorpha
(unranked):	Amniota
Class:	**Synapsida** Osborn, 1903

Orders & Suborders

- Order **Pelycosauria** *
    - Suborder †**Caseasauria**
    - Suborder **Eupelycosauria** *
- Order **Therapsida** *
    - Suborder †**Biarmosuchia**
    - (unranked) **Eutherapsida**
        - Suborder †**Dinocephalia**

- o (unranked) **Neotherapsida**
  - ▪ Suborder †**Anomodontia**
- o (unranked) **Theriodontia**
  - ▪ Suborder †**Gorgonopsia**
- o (unranked) **Eutheriodontia**
- o Suborder **Cynodontia** *
- o Suborder †**Therocephalia**

Synapsids ('fused arch') are a group of animals that includes mammals and everything more closely related to mammals than to other living amniotes. They are easily separated from other amniotes by having an opening low in the skull roof behind each eye, leaving a bony arch beneath each, accounting for their name. Primitive synapsids are usually called pelycosaurs; more advanced mammal-like ones, therapsids. The non-mammalian members are described as **mammal-like reptiles** in classical systematics, but are referred to as **"stem-mammals"** or **"proto-mammals"** under cladistic terminology. Synapsids evolved from basal amniotes and are one of the two major groups of the later amniotes, the other major group being the sauropsids (reptiles and birds). They are distinguished from other amniotes by having a single opening (temporal fenestra) in their skull behind each eye, which developed in the ancestral synapsid about 324 million years ago (mya) during the late Carboniferous Period.

Synapsids were the dominant terrestrial animals in the middle to late Permian period. As with almost all groups then extant, their numbers and variety were severely reduced by the Permian extinction. Some species survived into the Triassic period, but archosaurs quickly became the dominant animals and few of the non-mammalian synapsids outlasted the Triassic, although survivors persisted into the Cretaceous. However, as a phylogenetic unit they included the mammal descendants, and in this sense synapsids are still very much a living group of vertebrates. In the form of mammals, Synapsids (most recently and notably humans) again became the dominant land animals after they outcompeted birds following the K-T extinction event.

Linnaean and cladistic classifications

Synapsids as a reptilian subclass

Synapsids were originally defined at the turn of the 20th century, as one of the four main subclasses of reptiles, on the basis of their distinctive temporal openings. These openings in the cheek bones allowed attachment of larger jaw muscles, hence a more efficient bite. Synapsids were considered to be the reptilian lineage that led to mammals via gradually evolved, increasingly mammalian features, hence the name "mammal-like reptiles" which became a broad, traditional description for all non-mammalian synapsids.

The "mammal-like reptiles"

The traditional classification of synapsids as reptiles is continued by a number of palaeontologists (e.g. Carroll 1988, Colbert & Morales 2001) and in general biology. In the 1990s this approach was complemented by a cladistic one, according to which the only valid groups are those that include common ancestors and all of their descendants: these are known as monophyletic groups, or clades. Because mammals are directly descended from the synapsids, mammals are included under Synapsida as a clade, though in formal classification mammals are treated as a separate class that has evolved from the (paraphyletically-defined) Synapsida.

Phylogenetically synapsids are the entire synapsid/mammal branch of the tree of life, though practically the term is used when referring to the reptile-grade synapsids. The term "mammal-like reptiles" is considered obsolete under the cladistic approach, but remains common in general use as a reference to all non-mammalian synapsids. The actual phylogeny of the synapsids are not in doubt though, and whether the term "synapsids contain the mammals" or "synapsids gave rise to the mammals" is used, remains a matter of individual preference, as they both express the same phylogeny.

Primitive and advanced synapsids

The mammal-like reptiles are traditionally divided into a primitive group and an advanced group, known respectively as 'pelycosaurs' and therapsids. 'Pelycosaurs' make up a paraphyletic grouping of the six most primitive families of synapsids. They were all rather lizard-like with sprawling gait and possibly horny scutes. The therapsids contain the more advanced synapsids, having a more erect pose and possibly hair, at least in some forms. The latter are the ancestors of mammals. Thus both of the two synapsid groups represent evolutionary grades: the pelycosaurs have given rise to the therapsids, who in their turn have given rise to the mammals. In traditional Linnaean systematics, the Pelycosauria and Therapsida are considered orders of the subclass Synapsida. In Bentons systematics, the two groups constitute a separate class.

Characteristics

Temporal openings
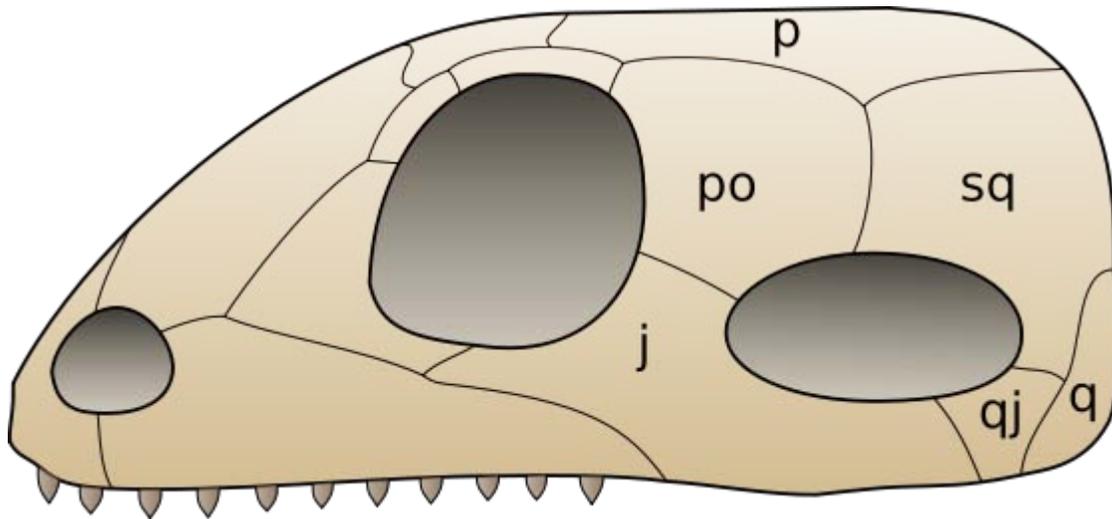
The synapsids are distinguished by a single hole behind each eye.

Synapsids evolved a temporal fenestra behind each eye orbit on the lateral surface of the skull. It may have evolved to provide new attachment sites for jaw muscles. A similar development took place in the Diapsids, who evolved two rather than one opening behind each eye. Originally, the opening in the skull left the inner cranium only covered by the jaw muscles, but in higher therapsids and mammals the sphenoid bone has expanded to close the opening. This has left the lower margin of the opening as an arch extending from the lower edges of the braincase.

Teeth
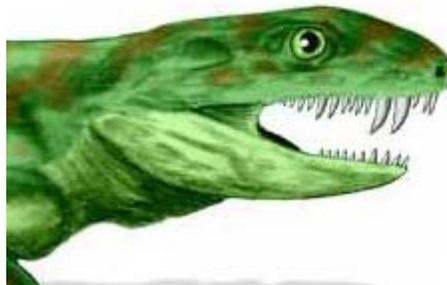
Eothyris, an early synapsid with multiple canines.

Synapsids are characterized by having differentiated teeth. These include the canines, molars, and incisors. The trend towards differentiation is found in some labyrinthodonts and early anapsid reptilians in the form of enlargement of the first teeth on the maxilla, forming a form of proto-canines. This trait was subsequently lost in the Sauropsid line,

but developed further in the synapsids. Early synapsids could have 2 or even 3 enlarged "canines", but in the therapsids, the pattern had settled to one canine in each upper jaw half. The lower canines developed later.

Jaw

Most paleontologists hold fossilized jaw remains to be the distinguishing feature used to classify synapsids and reptiles. The jaw transition is a good classification tool as most other fossilized features that make a chronological progression from a reptile-like to a mammalian condition follow the progression of the jaw transition. The mandible, or lower jaw, consists of a single, tooth-bearing bone in mammals (the dentary), whereas the lower jaw of modern and prehistoric reptiles consists of a conglomeration of smaller bones (including the dentary, articular, and others). As they evolved, these jaw bones were reduced in size and either lost or, in the case of the articular, gradually moved into the ear, forming one of the middle ear bones: while mammals possess the malleus, incus and stapes, mammal-like reptiles (like all other tetrapods) possess only a stapes. The malleus is derived from the articular (a lower jaw bone) while the incus is derived from the quadrate, (a skull bone).

Mammalian jaw structures are also set apart by the dentary-squamosal jaw joint. In this form of jaw joint, the dentary forms a connection with a depression in the squamosal known as the glenoid cavity. In contrast, all other jawed vertebrates, including reptiles and nonmammalian synapsids, possess a jaw joint in which one of the smaller bones of the lower jaw, the articular, makes a connection with a bone of the skull called the quadrate bone to form the articular-quadrate jaw joint. In forms transitional to mammals, the jaw joint is composed of a large, lower jaw bone (similar to the dentary found in mammals) that does not connect to the squamosal but connects to the quadrate with a receding articular bone.

Palate

Over time, as synapsids became more mammalian and less 'reptilian', they began to develop a secondary palate, separating the mouth and nasal cavity. In early synapsids, a secondary palate began to form on the sides of the maxilla, still leaving the mouth and nostril connected.

Eventually, the two sides of the palate began to curve together, forming a U-shape instead of a C-shape. The palate also began to extend back toward the throat, securing the entire mouth and creating a full palatine bone. The maxilla is also closed completely. In fossils of one of the first eutheriodonts, the beginnings of a palate are clearly visible. The later *Thrinaxodon* has a full and completely closed palate, forming a clear progression.

Skin

Synapsid combination of hair and scutes, detail of a rat's tail.

The actual skin of the synapsids has been subject to some discussion. Basal reptilian skin is rather thin, and lack the thick dermal layer that produces leather in mammals. Exposed parts of reptiles are protected by horny scales or scutes. Mammal hide has a thick, fibrous dermis and rarely exhibits scutes. A hallmark of mammals is the presence of copious glands and hair follicles.

When the change from reptilian to mammalian type skin took place is not known, though fossilized skin impressions indicate that at least the pelycosaurs retained the scutes of more primitive tetrapods on their undersides. The pelycosaur scutes probably were non-overlapping dermal structures with a horny overlay, like those found in modern crocodiles and turtles. These differed in structure from the scales of lizards and snakes, which are an epidermal feature (like mammalian hair or avian feathers). The upper surface of the pelycosaurs may have borne scutes too, or may have been glandular and leathery like that of a mammal. If so, they may perhaps be visualized as being "naked lizards", both furless and scaleless, as their overall anatomy was more like a modern lizard than a modern mammal.

It is currently unknown at what stage the synapsids acquired mammalian characteristics such as body hair and mammary glands, as the fossils only rarely provide direct evidence for soft tissues. An exceptionally well preserved skull of *Estemmenosuchus*, a therapsid from the Upper Permian show smooth hairless skin with what appears to be glandular depressions. The oldest known fossil showing unambiguous imprints of hair is the Callovian (late middle Jurassic) *Castorocauda*, an early mammal. Much, however, can be inferred from differences in skeletal structure. The more advanced therapsids could have had a combination of naked skin, scutes and hair, a combination still found in some modern mammals like rodents and the opossum.

Metabolism
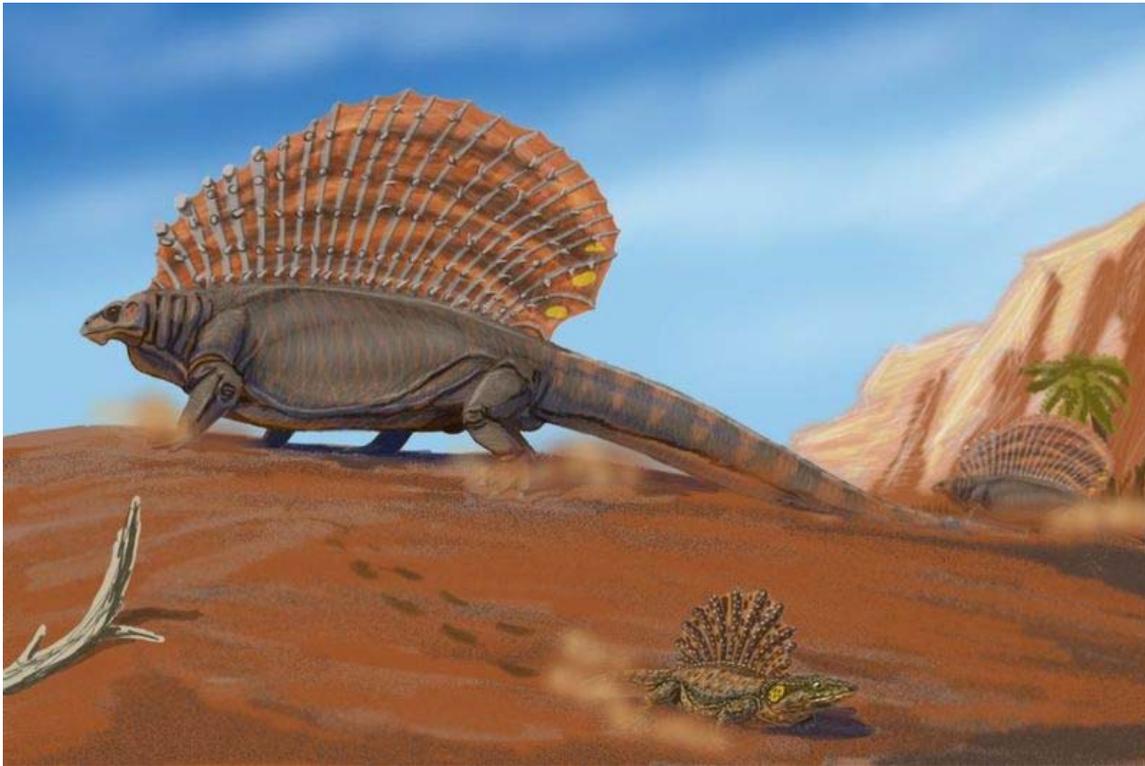
Sail-back pelycosaurs like *Edaphosaurus* indicate an early trend toward temperature regulation in synapsids.

The first pelycosaurs had the usual reptilian cold-blooded metabolism by all indications, including sprawling gait and a low slung body. However, there appears to have been an early trend towards a form of temperature regulation in several Pelycosaur lines, as indicated by the large "sails" in both edaphosaurids and sphenacodontids (e.g. *Dimetrodon*).

The sphenacodontids gave rise to the therapsids, who may have inherited the temperature regulation. The legs and feet of the early therapsid groups point to a more erect posture, traditionally interpreted as a sign of more efficient metabolism. None of them show any sign of a sail, indicating any temperature regulation would have relied on the creatures own metabolism rather than external heat. In the later cynodonts, the presence of a secondary palate, erect posture and other indicators of high metabolic rate suggests that many mammalian features, including an effective insulating layer of body hair, had evolved by this stage. This is now confirmed by impressions of fur in rocks directly underlying some fossil therapsids.

Evolutionary history
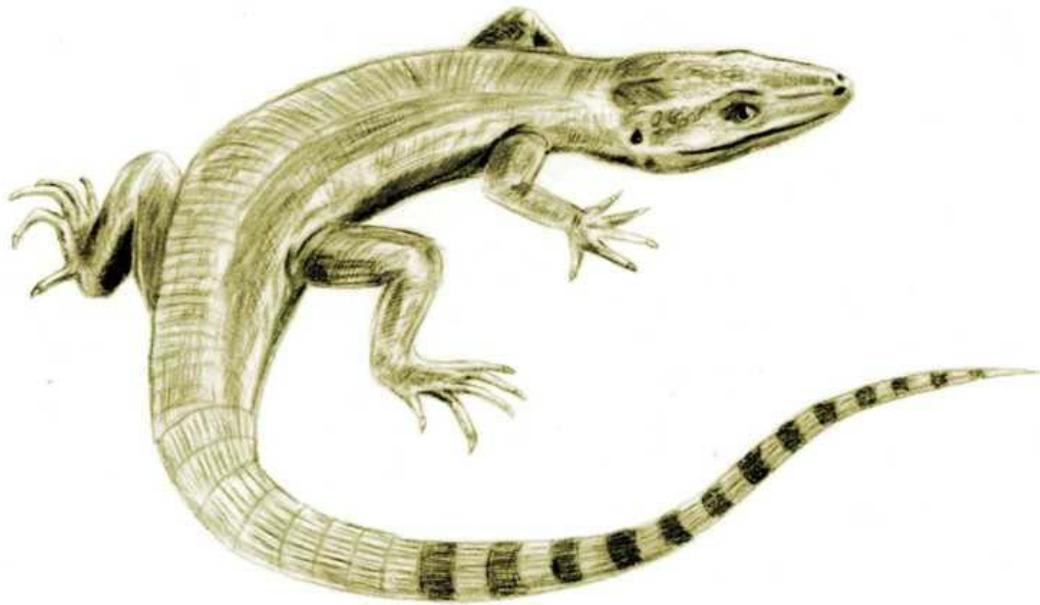
Archaeothyris, one of the oldest synapsids found.

Archaeothyris and *Clepsydrops* are the earliest known synapsids. They lived in the Pennsylvanian subperiod of the Carboniferous Period and belonged to the series of primitive synapsids which are conventionally grouped as pelycosaurs. The pelycosaurs were the first successful group of amniotes, spreading and diversifying until they became the dominant large terrestrial animals in the latest Carboniferous and Early Permian Periods. They were sprawling, bulky, cold-blooded and had small brains. They were the largest land animals of their time, ranging up to 3 m (10 ft) in length. Many, like *Dimetrodon*, had large sails that may have helped raise their body temperature. A few relict groups lasted into the later Permian, but most of the pelycosaurs became extinct before the end of Permian.
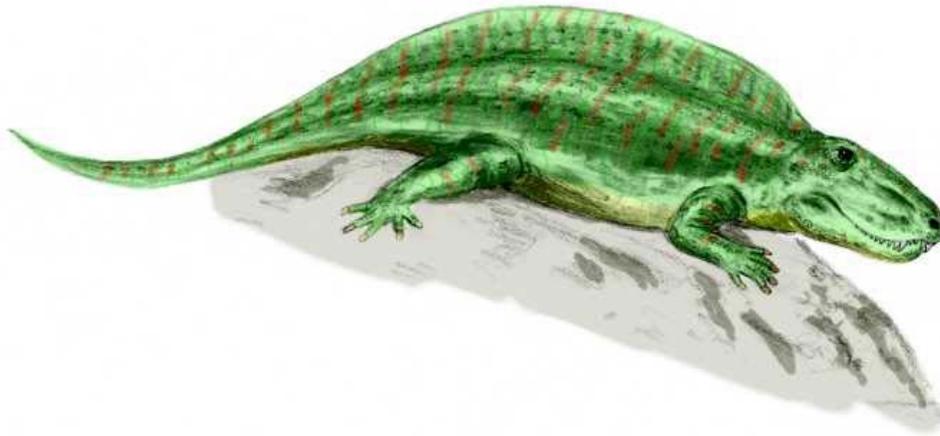
Sphenacodon was a carnivorous pelycosaur that was closely related to *Dimetrodon* and the therapsids.

The therapsids, a more advanced group of synapsids, appeared during the first half of the Permian and went on to become the dominant large terrestrial animals during the latter half. They have dominated the world twice: once in the Permian and once in the Cenozoic, the current era. They were by far the most diverse and abundant animals of the Middle and Late Permian and included herbivores and carnivores, ranging from small animals the size of a rat (e.g.: *Robertia*), to large bulky herbivores a ton or more in weight (e.g.: *Moschops*). After flourishing for many millions of years, these successful animals were all but wiped out by the Permian-Triassic mass extinction about 250 Mya, the largest extinction in Earth's history, which may have been related to the Siberian Traps volcanic event.
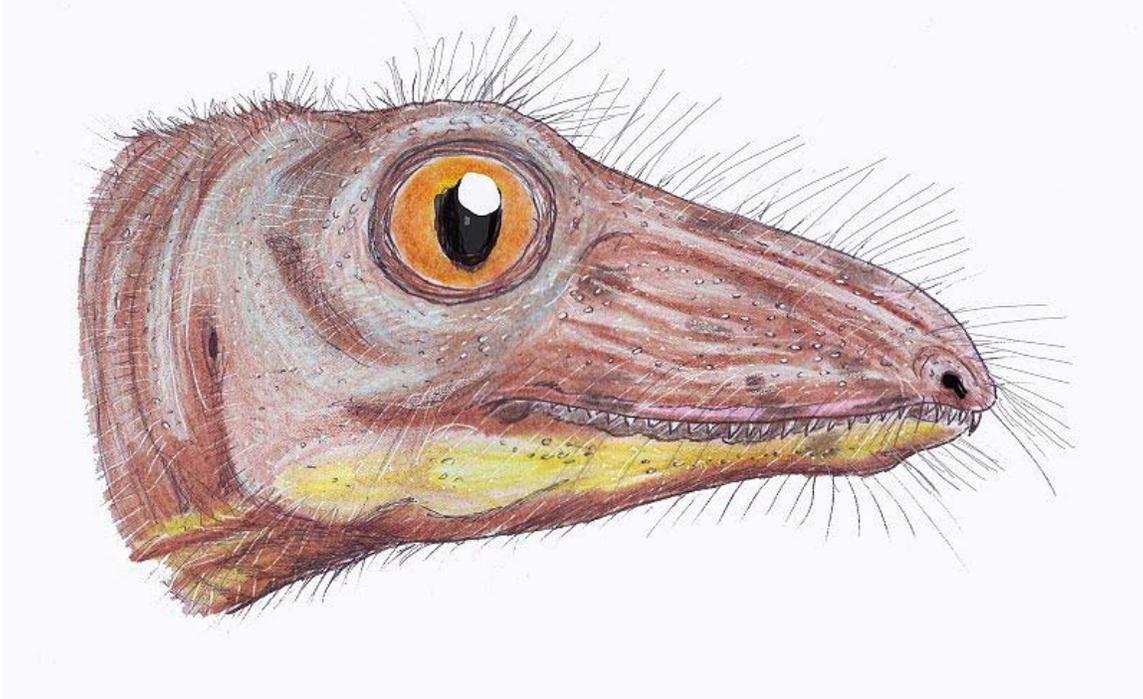
Nikkasaurus - an enigmatic synapsid from the Middle Permian of Russia.
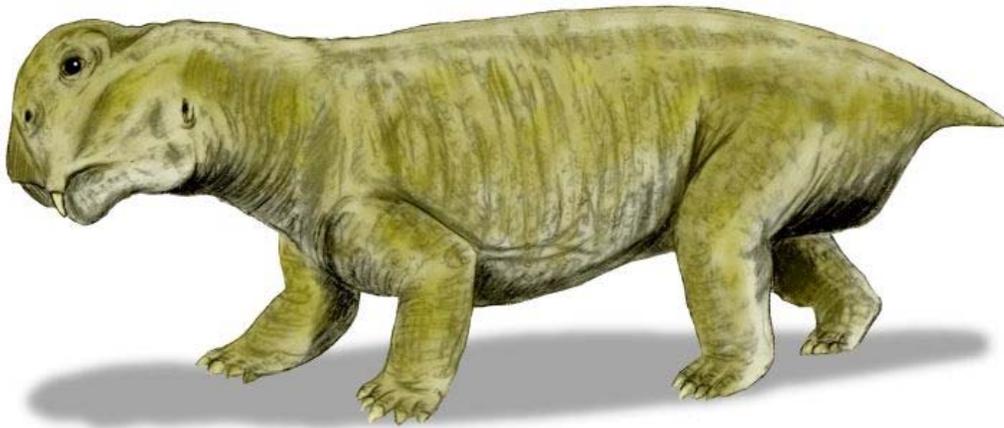
Lystrosaurus was the most common synapsid shortly after the Permian-Triassic extinction event.

Only a few therapsids (and some relict 'pelycosaur' taxa) survived the Permian extinction and went on to be successful in the new early Triassic landscape; they include *Lystrosaurus* and *Cynognathus*, the latter of which appeared later in the early Triassic. Now, however, they were accompanied by the early archosaurs (soon to give rise to the

dinosaurs). Some of these, like *Euparkeria*, were small and lightly built, while others, like *Erythrosuchus*, were as big as or bigger than the largest therapsids.

Triassic therapsids included three groups. Specialised, beaked herbivores known as dicynodonts (such as *Lystrosaurus* and its descendants, the Kannemeyeriidae), contained some members which reached large size (up to a tonne or more). The increasingly mammal-like carnivorous, herbivorous, and insectivorous cynodonts included the eucynodonts from the Olenekian age, an early representative of which was *Cynognathus*. Finally, there were the therocephalians, which only lasted into the early part of the Triassic.
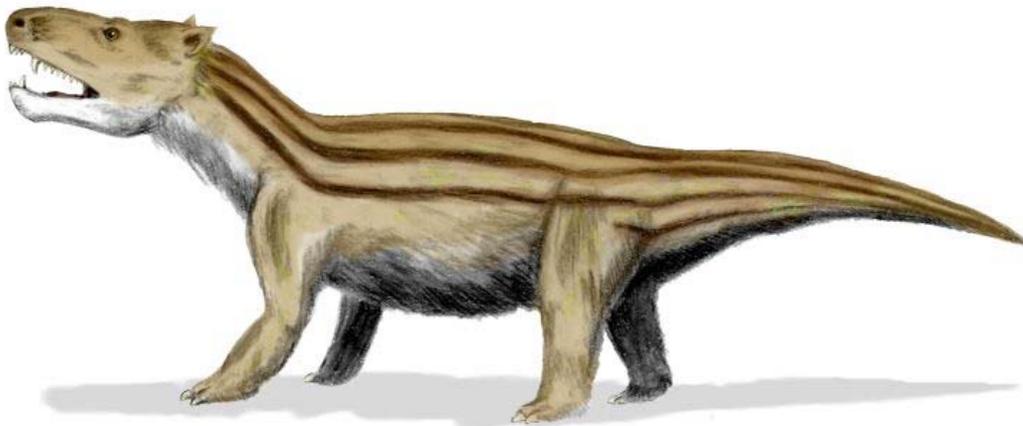
Cynognathus was the largest predatory cynodont of the Triassic.

Unlike the dicynodonts, which remained large, the cynodonts became progressively smaller and more mammal-like as the Triassic progressed. From the most advanced and tiny cynodonts, which were only the size of a shrew, came the first mammal precursors, during the Carnian age of the Late Triassic, about 220 Mya.

During the evolutionary succession from early therapsid to cynodont to eucynodont to mammal, the main lower jaw bone, the dentary, replaced the adjacent bones. Thus, the lower jaw gradually became just one large bone, with several of the smaller jaw bones migrating into the inner ear and allowing sophisticated hearing.

Whether through climate change, vegetation change, ecological competition, or a combination of factors, most of the remaining large cynodonts (belonging to the Traversodontidae) and dicynodonts (of the family Kannemeyeriidae) had disappeared by the Norian age, even before the Triassic-Jurassic extinction event that killed off most of the large non-dinosaurian archosaurs. The remaining Mesozoic synapsids were small, ranging from the size of a shrew to the badger-like mammal *Repenomamus*.

During the Jurassic and Cretaceous, the remaining non-mammalian cynodonts were small, such as *Tritylodon*. No cynodont grew larger than a cat. Most Jurassic and Cretaceous cynodonts were herbivorous, though some were carnivorous. The family Trithelodontidae first appeared near the end of the Triassic. They were carnivorous and persisted well into the Middle Jurassic. The other, Tritylodontidae, first appeared at the same time as the trithelodonts, but they were herbivorous. This group became extinct at the end of the Early Cretaceous epoch. Dicynodonts are thought to have become extinct near the end of the Triassic period, but there is evidence that this group survived. New fossil finds have been found in the Cretaceous rocks of Gondwana.

Today, there are 5,400 species of living synapsids known as the mammals, including both aquatic (whales) and flying (bats) species, and the largest animal ever known to have existed (the blue whale). Humans are synapsids as well. Uniquely among the synapsids, however, most mammals are viviparous and give birth to live young rather than laying eggs, the exception being the monotremes.

Synapsids' evolution into mammals is believed to have been triggered by moving to a nocturnal niche. Proto-mammals with higher metabolic rates were able to keep their bodies warm at night, and were more likely to survive. This meant consuming food (generally thought to be insects) in much greater quantity. To facilitate rapid digestion, proto-mammals evolved mastication (chewing) and specialized teeth that aided chewing. Limbs also evolved to move under the body instead of to the side, allowing proto-mammals to breathe more efficiently during locomotion and also to be able to change direction more quickly in order to catch small prey at a faster rate. This helped make it possible to support their higher metabolic demands. It is believed that, rather than out-running predators, proto-mammals adapted the strategy of outmaneuvering predators using their improved locomotor capabilities.

Taxonomy

Classification

Series **Amniota**

- CLASS **SYNAPSIDA** *
  - Order **Pelycosauria** *
    - Suborder **Caseasauria**
      - Family **Caseaidae**
      - Family **Eothyrididae**
    - Suborder **Eupelycosauria** *
      - Family **Edaphosauridae**
      - Family **Lupeosauridae**
      - Family **Ophiacodontidae**
      - Family **Sphenacodontidae**
      - Family **Varanopsidae**
- • Order **Therapsida** *
  - Suborder **Biarmosuchia**

- o (unranked) **Eutherapsida**
    - ▪ Suborder **Dinocephalia**
        - ▪ Infraorder **Anteosauria**
        - ▪ ?Infraorder **Tapinocephalia**
- o (unranked) **Neotherapsida**
    - ▪ Suborder **Anomodontia**
    - ▪ Superfamily **Venyukoviamorpha**
        - ▪ Family **Venyukoviidae**
    - ▪ ?Infraorder **Dicynodonta**
- o (unranked) **Theriodontia**
    - ▪ Suborder **Gorgonopsia**
- o (unranked) **Eutheriodontia**
- o Suborder **Therocephalia**
- o Suborder **Cynodontia** *

- CLASS MAMMALIA

Chapter 8

Prehistoric fish

Fish fossil of a *Priscacara*, an extinct genus of perch that lived in Wyoming during the Eocene, about 56 to 34 million years ago. It probably lived in freshwater streams and lakes, feeding on small creatures like snails, crabs, prawns, and tadpoles.

Prehistoric fish refers to early fish that are known only from fossil records. They are the earliest known vertebrates, and include the first and extinct fish that lived through the Cambrian to the Tertiary. The study of prehistoric fish is called *paleoichthyology*. A few living forms, such as the coelacanth are also referred to as prehistoric fish, or even living fossils, due to their current rarity and similarity to extinct forms. Fish which have become recently extinct are not usually referred to as prehistoric fish.

Overview

Late Devonian lobe-finned fish and amphibious tetrapods.
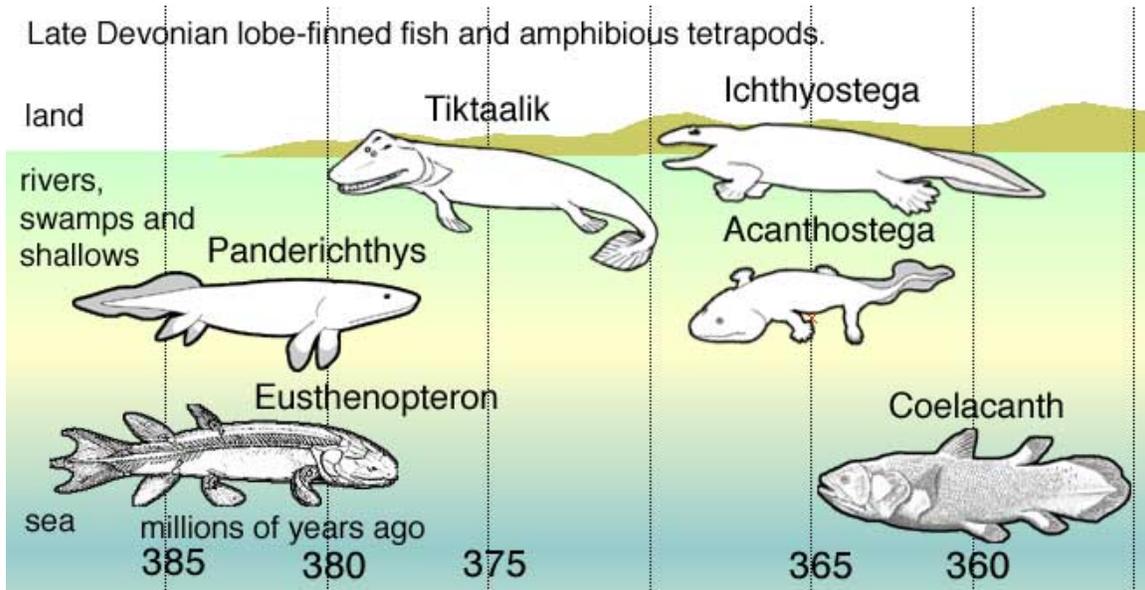
The Late Devonian was home to many species of lobe-finned fish like *Eusthenopteron*, *Panderichthys*, *Tiktaalik* and the first tetrapods, such as *Acanthostega* whose limbs had eight digits, and *Ichthyostega* which had seven. Other lobe-finned fishes common in the Paleozoic include the Coelacanths, which survive to this day.

The first fish and the first vertebrates, were the ostracoderms, which appeared in the Cambrian Period, about 510 million years ago, and became extinct near the end of the Devonian, about 377 million years ago. Ostracoderms were jawless fishes found mainly in fresh water. They were covered with a bony armor or scales and were often less than 30 cm (1 ft) long. The ostracoderms are placed in the class Agnatha along with the living jawless fishes, the lampreys and hagfishes, which are believed to be descended from the ostracoderms, as are all jawed fishes, or gnathostomes. Paired fins, or limbs, first evolved within this group.

The placoderms, a group of jawed fishes, appeared by the beginning of the Devonian, about 416 million years ago, and became extinct at the end of the Devonian or the beginning of the Mississippian (Carboniferous), about 360 million years ago. Recent studies suggest that the placoderms are a possibly paraphyletic group of basal gnathostomes, and the closest relatives of all living jawed vertebrates. Some Placoderms were small, flattened bottom-dwellers, such as antiarchs. However, many, particularly the arthrodires, were active midwater predators. *Dunkleosteus* was the largest and most famous of these. The upper jaw was firmly fused to the skull, but there was a hinge joint between the skull and the bony plating of the trunk region. This allowed the upper part of the head to be thrown back and, in arthrodires, this allowed them to take larger bites.
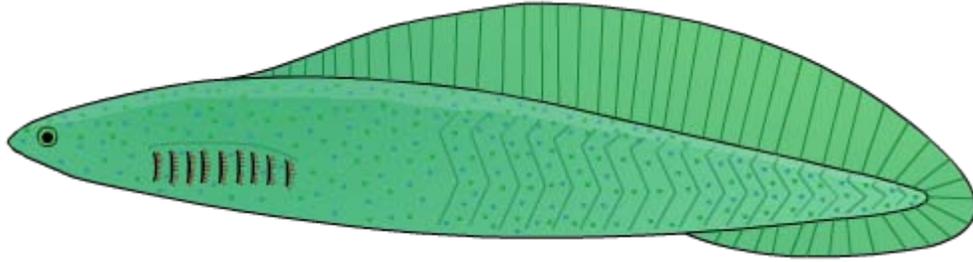
Haikouichthys, from about 518 million years ago in China, may be the earliest known fish.

The acanthodians, or spiny sharks, appeared by the late Silurian, about 420 million years ago, and became extinct before the end of the Permian, about 250 million years ago. However, scales and teeth attributed to this group, as well as more derived gnathostomes such as Chondrichthyes and Osteichthyes, date from the Ordovician (~460 million years ago). Acanthodians were generally small shark-like fishes varying from toothless filter-feeders to toothed predators. They were once often classified as an order of the class Placodermi, another group of primitive fishes, but recent authorities tend to place the acanthodians nearer to or within the living gnathostomes.

Cartilaginous fishes, class Chondrichthyes, consisting of sharks, rays and chimaeras, appeared by about 395 million years ago, in the middle Devonian. The modern bony fishes, class Osteichthyes, appeared in the late Silurian or early Devonian, about 416 million years ago. Both the Osteichthyes and Chondrichthyes may have arisen from either the acanthodians or placodermi. A subclass of the Osteichthyes, the ray-finned fishes (Actinopterygii), have become the dominant group of fishes in the post-Paleozoic and modern world, with some 30,000 living species. However, another subclass of Osteichthyes, the Sarcopterygii, including lobe-finned fishes including coelacanths and lungfish) and tetrapods, was the most diverse group of bony fishes in the Devonian. Sarcopterygians are basally characterized by internal nostrils, lobe fins containing a robust internal skeleton, and cosmoid scales.
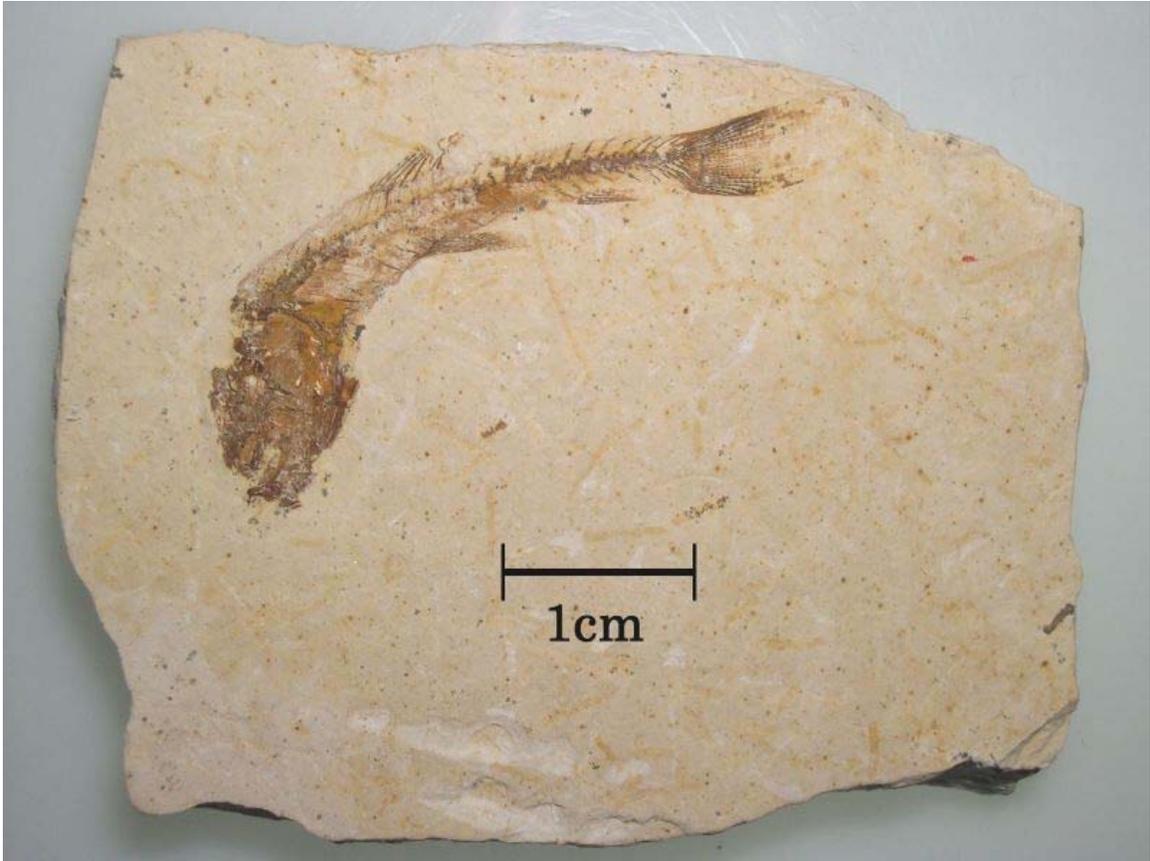
Dastilbe, an extinct genus of bony fish from Brazil that lived about 112 million years ago during the Aptian stage of the Early Cretaceous

Fish fossil from Cretaceous period
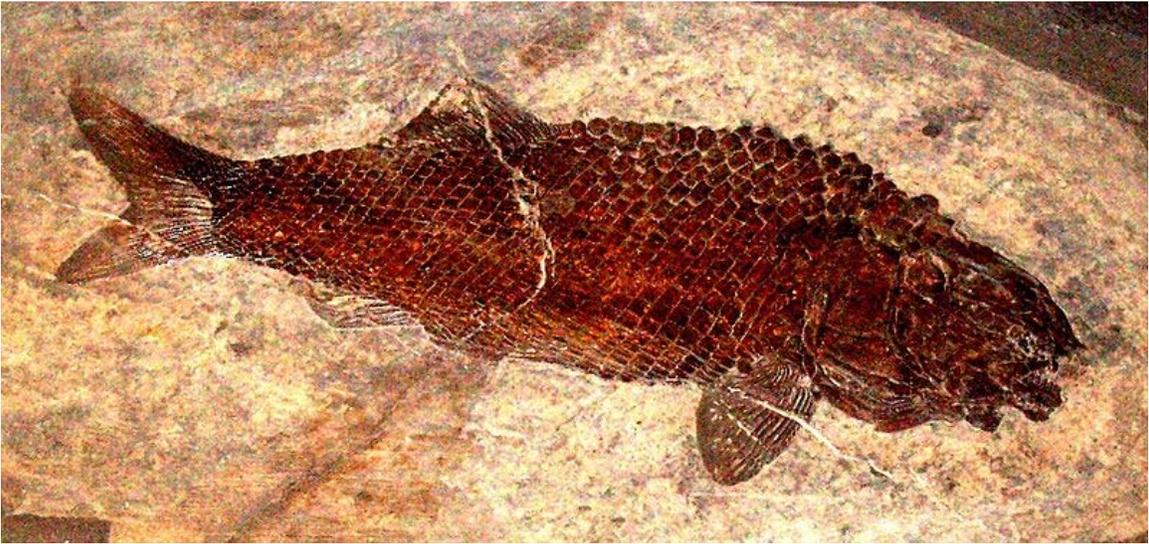
Heterolepidotus is an extinct Cyprinidae from the Lower Jurassic (208-146 million years)

Cimolichthys nepaholica, an extinct predatory salmonid fish from the Late Cretaceous of North America and Europe

Chapter 9

Graptolite

Graptolites
Temporal range: Mid Cambrian to Lower Carboniferous510–350 Ma

Amplexograptus from the Ordovician near Caney Springs, Tennessee.

Scientific classification [e]

Kingdom:	Animalia
Phylum:	Hemichordata
Class:	**†Graptolithina**

Orders

†Camaroidea
†Crustoidea
†Dendroidea
†Dithecoidea
†Graptoloidea
†Stolonoidea
†Tuboidea

Graptolites (Graptolithina) are fossil colonial animals known chiefly from the Upper Cambrian through the Lower Carboniferous (Mississippian). A possible early graptolite, *Chaunograptus*, is known from the Middle Cambrian.

The name graptolite comes from the Greek *graptos*, meaning "written", and *lithos*, meaning "rock", as many graptolite fossils resemble hieroglyphs written on the rock. Linnaeus originally regarded them as 'pictures resembling fossils rather than true fossils', though later workers, supposed them to be related to the hydrozoans. More recent work places them near the pterobranchs, possibly within.

Taxonomy

The name originates from the genus *Graptolithus*, which was used by Linnaeus in 1735 for inorganic mineralizations and crustations which resembled actual fossils. In 1768, in the 12th volume of Systema Naturae, he included *G. sagittarius* and *G. scalaris*, respectively a possible plant fossil and a possible graptolite. In his 1751 *Skånska Resa*, he included a figure of a "fossil or graptolite of a strange kind" currently thought to be a type of *Climacograptus* (a genus of biserial graptolites). Later workers used the name to refer to a specific group of organisms. *Graptolithus* was officially abandoned in 1954 by the ICZN, partly because of its original purpose as a grouping for inorganic mimicries of fossils. (Bulman, 1970: V 6)

Since the 1970s, as a result of advances in electron microscopy, graptolites have generally been thought to be most closely allied to the pterobranchs, a rare group of modern marine animals belonging to the phylum Hemichordata (hemichordates). Comparisons are drawn with the modern hemichordates *Cephalodiscus* and *Rhabdopleura*. *Cephalodiscus* numbers about 18 species, and was first discovered in 1882.

Graptolites as Index fossils

Graptolites are common fossils and have a worldwide distribution. The preservation, quantity and gradual change over a geologic time scale of graptolites allows the fossils to be used to date strata of rocks throughout the world. They are important index fossils for dating Palaeozoic rocks as they evolved rapidly with time and formed many different species. British geologists can divide the rocks of the Ordovician and Silurian periods into graptolite biozones; these are generally less than one million years in duration. A worldwide ice age at the end of the Ordovician eliminated the majority of the then-living graptolite; species present during the Silurian period were the result of diversification from only a one or two species that survived the Ordovician glaciation.

Graptolites are also used to estimate water depth and temperature during the graptolites lifetimes.
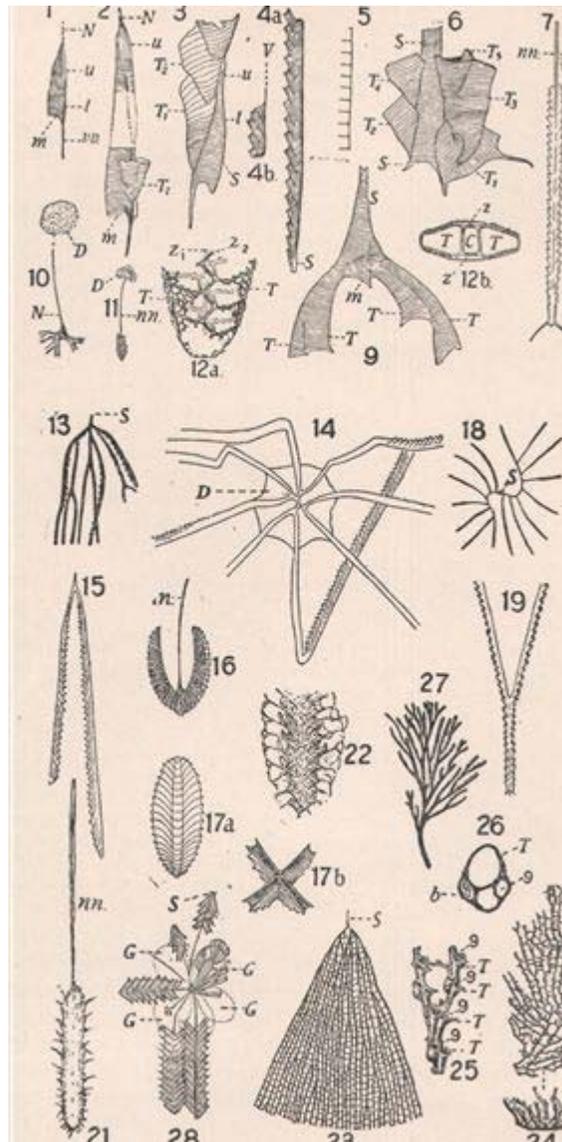
Graptolite morphology illustrated

Thallograptus sphaericola, a dendroid graptolite, attached to the cystoid *Echinosphaerites aurantium*; Ordovician of northeastern Estonia.

Each graptolite colony is known as a **rhabdosome** and has a variable number of branches (called stipes) originating from an initial individual (called a sicula). Each subsequent individual (zooid) is housed within a tubular or cup-like structure (called a theca). In some colonies, there are two sizes of theca, and it has been suggested that this difference is due to sexual dimorphism. The number of branches and the arrangement of the thecae are important features in the identification of graptolite fossils. Their general shape has been compared with that of a hacksaw blade.

Most of the dendritic or many-branched types are classified as dendroid graptolites (order Dendroidea). They appear earlier in the fossil record (in the Cambrian period), and were generally benthic animals (attached to the sea-floor by a root-like base). Graptolites with relatively few branches were derived from the dendroid graptolites at the beginning of the Ordovician period. This latter type (order Graptoloidea) were pelagic, drifting freely on the surface of ancient seas or attached to floating seaweed by means of a slender thread. They were a successful and prolific group, being the most important animal members of the plankton until they died out in the early part of the Devonian period. The dendroid graptolites survived until the Carboniferous period.

Preservation

Graptolite fossils are often found in shales and mud rocks where sea-bed fossils are rare, this type of rock having formed from sediment deposited in relatively deep water that had poor bottom circulation, was deficient in oxygen, and had no scavengers. The dead planktonic graptolites, having sunk to the sea-floor, would eventually become entombed in the sediment and are thus well preserved.

Graptolites are also found in limestones and cherts, but generally these rocks were deposited in conditions which were more favorable for bottom-dwelling life, including scavengers, and undoubtedly most graptolite remains deposited here were generally eaten by other animals.

Graptolite fossils are often found flattened along the bedding plane of the rocks in which they occur, though may be found in three dimensions when they are infilled by iron pyrite. They vary in shape, but are most commonly dendritic or branching (such as *Dictyonema*), saw-blade like, or "tuning fork" shaped (such as *Didymograptus murchisoni*). Their remains may be mistaken for fossil plants by the casual observer.

Graptolites are normally preserved as a black carbonized film on the rock's surface or as light grey clay films in tectonically distorted rocks. They may be sometimes difficult to see, but by slanting the specimen to the light they reveal themselves as a shiny marking. Pyritized graptolite fossils are also found.

A well known locality for graptolite fossils in Britain is Abereiddy Bay, Dyfed, Wales where they occur in rocks from the Ordovician period.
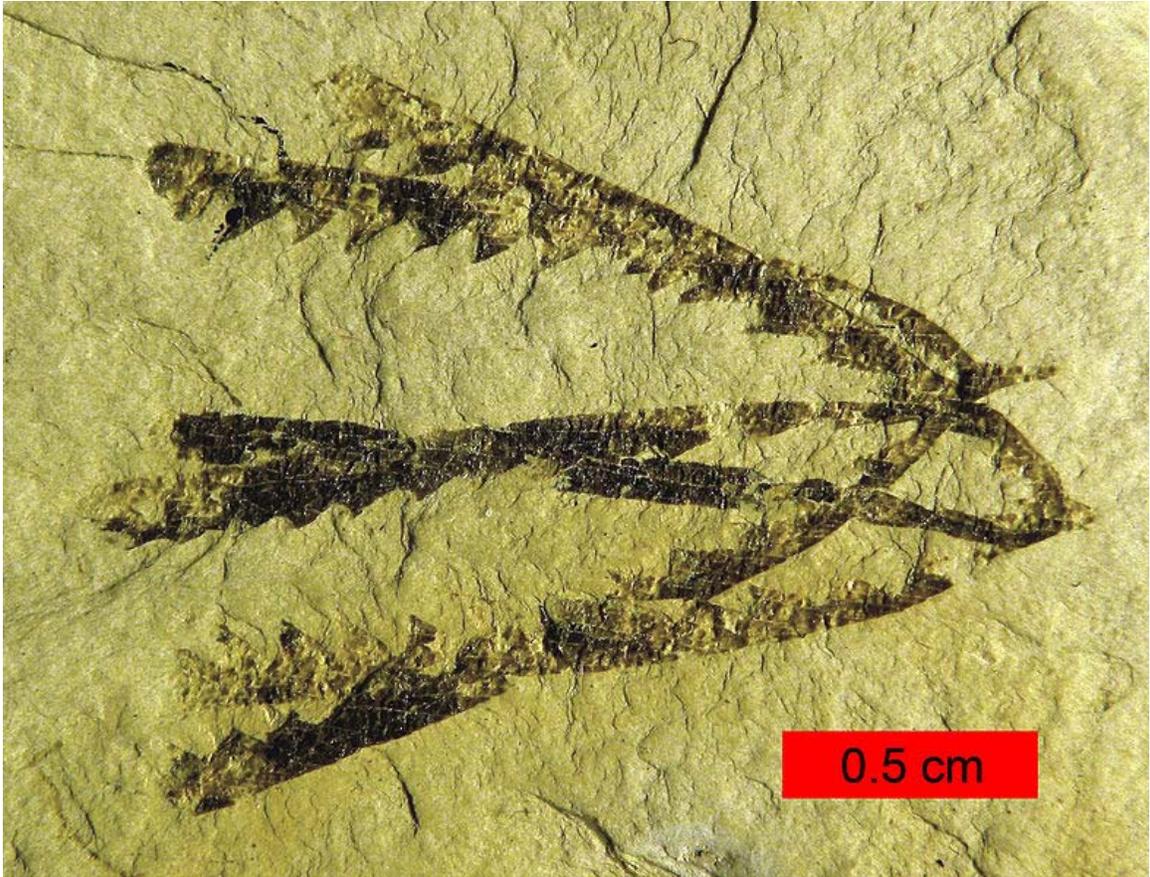
Pendeograptus fruticosus from the Bendigonian Australian Stage (Lower Ordovician; 477-474 mya) near Bendigo, Victoria, Australia. Two overlapping, three-stiped rhabdosomes.

Chapter 10

Odontogriphus

Odontogriphus
Temporal range: Burgess Shale ↓
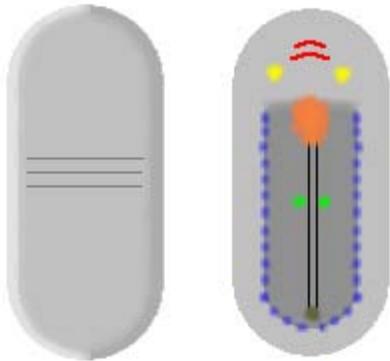
Top (left) and underside (right)

Scientific classification [e]	
Kingdom:	Animalia
Superphylum:	Lophotrochozoa
Phylum:	Mollusca (?)
Family:	**Odontogriphidae** Conway Morris, 1976
Genus:	***Odontogriphus*** Conway Morris, 1976
Species	

O. omalus Conway Morris, 1976

Odontogriphus (literally "toothed riddle") is a genus of soft-bodied animals known from middle Cambrian Lagerstätte. Reaching as much as 12.5 centimetres (4.9 in) in length, *Odontogriphus* is a flat, oval bilaterian which apparently had a single muscular foot, and a "shell" on its back that was moderately rigid but of a material unsuited to fossilization.

Originally it was known from only one specimen, but 189 new finds in the years immediately preceding 2006 made a detailed description possible. (221 specimens of *Odontogriphus* are known from the Greater Phyllopod bed, where they comprise 0.42% of the community.) As a result *Odontogriphus* has become prominent in the debate that has gone on since 1990 about the evolutionary origins of molluscs, annelid worms and brachiopods. A group of scientists think that *Odontogriphus*'s feeding apparatus, which is "nearly identical" to Wiwaxia's, is an early version of the molluscan radula, a chitinous "tongue" that bears multiple rows of rasping teeth. Hence they classify *Odontogriphus* and *Wiwaxia* as close to the ancestors of the first true molluscs. One scientist has presented a different analysis, arguing since 1990 that *Wiwaxia* is not closely related to molluscs but is much more like a polychaete worm. He argues that the supposed "radula" is nothing of the sort; he classifies *Odontogriphus* as a basal lophotrochozoan, in other words close to the last common ancestor of molluscs, annelid worms and brachiopods.

History of discovery

Charles Doolittle Walcott found one specimen during one of his field trips to the Burgess Shale between 1910 and 1917. In the 1970s Simon Conway Morris re-examined the specimen and tentatively concluded that it was a swimming lophophorate, in other words related to the ancestors of molluscs, annelid worms and brachiopods. In 2006 Caron, Scheltema *et al.* published a new analysis based on 189 recently collected specimens, all from the Burgess Shale.

Description

Odontogriphus was apparently a very rare species, accounting for less than 0.5% of the individual organisms found in the same fossil beds. Most of the fossils consist of two parts of a split block of rock, the upper part giving a "casting" of the animal's upper surface and the lower giving one of its underside.

Odontogriphus was a flat-bodied animal ranging from 3.3 millimetres (0.13 in) to 125 millimetres (4.9 in) in length, with parallel sides and semi-circular ends. The specimens examined by Caron, Scheltema *et al.* (2006) had the same ratio of length to width irrespective of size. The body outlines are bilaterally symmetrical in all fairly complete specimens, even those in which internal features were preserved asymmetrically. Caron, Scheltema *et al.* (2006) interpreted this as evidence that the animals had on their backs "shells" that were rigid enough to resist whatever stresses distorted the internal features, but were not tough enough to be preserved by fossilization – similar, for example, to finger nails. Relatively broad wrinkles, parallel to each other and usually straight, run across the central region of the body in some specimens.
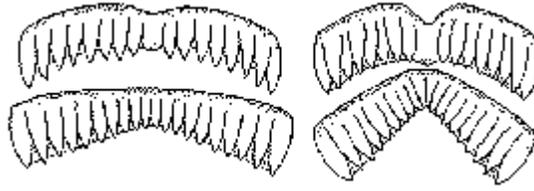
Wiwaxia usually had two tooth-rows: opened for feeding (left); folded (right). In both cases the front of the animal is at the top. Caron, Scheltema *et al.* (2006) regarded this as "nearly identical" to structures they found in *Odontogriphus*.

Caron, Scheltema *et al.* (2006) found evidence of a circular mouth on the underside, with two and occasionally three tooth-bearing structures that they interpreted as a feeding apparatus and very similar to that of *Wiwaxia*. *Odontogriphus*'s feeding apparatus was located on the midline, about 15% of the total body length from the front edge of the fossils. Where a third tooth-row was found, it was less distinct, which they thought indicated that it was still growing at the time of the animal's death. Since they occasionally found pairs of tooth-rows that were not associated with body fossils but were spaced like the tooth-rows in "complete" fossils, they concluded that the tooth-rows were mounted on a material that was tough enough to keep them in the same relative positions but not suitable for fossilization.

On either side of the feeding apparatus there is a circular structure that Caron, Scheltema *et al.* (2006) interpreted as salivary glands. They also found evidence of other parts of the digestive tract: a gullet connecting to the rear of the mouth; a relatively short stomach; and a straight much longer intestine, ending at an anus near the rear of the underside. A pair of structures on either side of the intestine and a little behind the stomach may have been gonads or digestive organs.

The fossils showed signs of a thickened central structure that Caron, Scheltema *et al.* (2006) thought was on the underside and probably represents a muscular sole that was a little over half as wide as the whole animal. It was U-shaped, with the "open" end behind the mouth and the rounded end a little forward of the animal's rear edge. The anus apparently was slightly ahead of the rounded end. All the edges of the "foot" except the front were surrounded by darker patches, which are sometimes separated from the rest of the body by a thin layer of sediment.

Phylogeny

Odontogriphus has become prominent in the debate that has gone on since 1990 about the evolutionary origins of molluscs, annelid worms and brachiopods. Caron, Scheltema *et al.* (2006) interpreted *Odontogriphus*'s feeding apparatus as a forerunner of the molluscan radula, on the grounds that: the occasional and less distinct third tooth-row looked like evidence that the animals grew replacement tooth-rows at the rear of their mouths and shed worn-out ones from the front, as happens with molluscan radulae; the isolated pairs of tooth-rows they found, not associated with body fossils but in the same relative positions as in the more complete fossils, suggested they were mounted on a

fairly tough surface, like the chitinous "belt" of a modern radula; they even found signs that discarded tooth-rows were sometimes eaten by the animals. Hence they classified both *Odontogriphus*, and *Wiwaxia* with its "nearly identical" feeding apparatus, as primitive relatives of molluscs.

In line with this classification they interpreted the dark patches round the foot as gill-like ctenidia, another feature of some molluscs; and the sediment that sometimes appeared in the fossils between the foot and supposed ctenidia suggested the presence of a mantle cavity. They also concluded that *Odontogriphus* was closely related to the Ediacaran animal *Kimberella*, whose fossils also show signs of a fairly rigid upper "shell" made of a material that did not fossilize, and which has been interpreted as a very mollusc-like organism.

They went on to classify the halkieriids as nearly-modern molluscs, since in their opinion halkieriids' "chain mail" coats of mineralized sclerites were an advance on the unmineralized sclerites of *Wiwaxia* and also resembled the armor of some living shell-less aplacophoran molluscs, the Neomeniomorpha. As a result they concluded that the whole *Kimberella-Odontogriphus-Wiwaxia*-mollusc lineage must have diverged from that of the annelid worms some time before the appearance of *Kimberella* in the Ediacaran period.

This brought *Odontogriphus* into the center of a debate that had been going on since 1990, when Butterfield denied that *Wiwaxia* was a forerunner of molluscs and argued that it was an evolutionary "aunt" of annelids. In particular he had argued that: *Wiwaxia*'s sclerites were internally much more like the bristles of polychaete annelids such as *Canadia* than like any forerunner of molluscan shell plates; and in his opinion *Wiwaxia*'s feeding apparatus was more similar to that of some polychaetes than to a molluscan radula. Caron, Scheltema, *et al.* (2006) thought Wiwaxia bore little resemblance to polychaetes as it showed no signs of segmentation, appendages in front of the mouth, or "legs" – all of which are typical polychaete features.

A few months later in 2006 Butterfield returned to the fray. As in 1990, he argued that *Wiwaxia*'s sclerites were internally much more like the bristles of polychaete annelids such as *Canadia* than like any forerunner of molluscan shell plates; since a 2005 paper had downplayed this argument with the comment that similar bristles also appear in molluscs and brachiopods,, he pointed out that modified bristles appear as a covering over the back only in polychaetes and hence *Wiwaxia*'s sclerites should indeed be regarded as like polychaetes' bristles.

In addition he argued that *Odontogriphus*' shedding and replacement of tooth-rows, the rows' staying in the same relative positions when isolated and the evidence that *Odontogriphus* sometimes swallowed discarded tooth-rows did not prove that *Odontogriphus* was an evolutionary "aunt" of molluscs, since eunicid polychaetes also molt and replace their feeding apparatus, and sometimes eat the discarded material. He also doubted whether the two tooth-rows of *Odontogriphus* and *Wiwaxia* could perform all the functions of the multi-row radula – rasping, capturing scraped food, sorting it and

transporting it to the gullet. In his opinion the differences between the narrower first tooth-row and slightly wider second one in both *Odontogriphus* and *Wiwaxia* were unlike those of a molluscan radula, in which the much more numerous tooth-rows are identical; instead he argued that these two rows resembled the permanent lower jaw and moltable upper jaw of modern dorvilleid polychaetes.

While Butterfield agreed that the dark patches round the foot served as gills, he denied that they were similar in structure and mode of development to molluscan ctenidia. In his opinion the flattened remains of *Odontogriphus* were formed by relatively tough extracellular secretions, such as jaws, bristles and toughened skin, and do not include purely or primarily cellular tissues, such as muscles or gonads. He therefore thought the respiratory organs round the edge of *Odontogriphus'* foot could not be molluscan ctenidia, since these are covered by purely cellular tissue. Instead he suggested that they might be brachiopod lophophores, which are feeding organs that contain a lot of extracellular material, or polychaete branchiae, which are respiratory organs composed largely of non-cellular cuticle – both of these types of structure have been found in the Burgess Shale, in which all the known specimens of *Odontogriphus* have been discovered.

Caron, Scheltema, *et al.* (2006) had suggested that the wrinkles on the top surfaces of *Odontogriphus* specimens were caused by the rippling contractions of a mollusc-like muscular foot. Butterfield disputed this on the grounds that: a molluscan foot is also mainly composed of cellular material, which he thought unlikely to be fossilized in Burgess Shale conditions; the wrinkles were too straight and ran too precisely across the animals' bodies; the gaps between them were the same size as the gaps between the gill-like structures round the foot. Instead he argued that they were evidence of externally visible segmentation, which is found in polychaetes but not in molluscs. He concluded that *Wiwaxia* was an evolutionary "aunt" of polychaetes, while *Odontogriphus* could be an evolutionary "aunt" of polychaetes or of molluscs or of brachiopods – or even a "great aunt" of all three, as it could have been an early member of the lophotrochozoa, a "super-phylum" that includes the polychaetes, molluscs and brachiopods.

In January 2007 Caron, Scheltema, *et al.* published a vigorous reply to Butterfield's arguments – near the end they wrote, "Many of Butterfield's misconceptions might well have been avoided had he taken the opportunity to examine all the new material that formed the basis of our study. …" They said they had found in body fossils of *Odontogriphus* visible traces of the membrane on which its tooth-rows were mounted; in their opinion this was clear evidence of a basic belt-like radula assembly with regularly-spaced tooth-rows, a feature unique to molluscs. On the other hand, they wrote, eunicid polychaetes' jaws have only the vaguest similarity to radulae, and other annelids' jaws grow continuously without replacement; and they supported this with a point-by-point comparison of *Odontogriphus'* feeding apparatus with that of the dorvilleid polychaetes which Butterfield claimed it resembled. In answer to Butterfield's claim that the respiratory organs round the foot could not be molluscan ctenidia because these mainly cellular structures would not have fossilized in the Burgess Shale conditions, they wrote that: fairly soft cellular tissue belonging to the stomach is fossilized in many

Odontogriphus specimens; some molluscan gills are stiffened by non-cellular material, for example in polyplacophorans. They pointed out that the wrinkles that appear across the body in views from the top occur only in the mid-section, and there is no sign that the tough "shell" plate on the animal's back was segmented; hence in their opinion *Odontogriphus* could not have been an annelid. On the other hand wrinkles are seen in the feet of dead chitons. *Wiwaxia*, they argued, was clearly not segmented, as the numbers of sclerites in its three concentric groups did not match at all. They criticized Butterfield's main argument for "shoehorning" *Wiwaxia* into the polychaetes, that its sclerites were secreted by microvillae; such structures, they wrote, were also found in several groups of molluscs. Finally, in their opinion the absence of "legs" in *Wiwaxia* ruled out a close relationship with polychaetes.

In 2008 Butterfield described a set of micro-fossils dated to between 515 million years ago and 510 million years ago, found in the Mahto Formation in Alberta's Jasper National Park – this fossil bed is 5 – 10 M years older than the Burgess Shale in which the only known specimens of *Odontogriphus* and *Wiwaxia* were found. Some groupings of these micro-fossils showed a consistent arrangement that he interpreted as an "articulated apparatus" with tens of closely-spaced tooth rows, apparently mounted on an organic base, and with noticeable signs of wear in the rows at one end. The rows were not quite identical, but he noted that some modern aplacophoran molluscs show similar variations. He concluded that the "articulated apparatus" was a genuine molluscan radula, most similar to those of modern aplacophorans or gastropods. He then commented on the contrast between this apparatus and the two or rarely three widely-spaced and more heteregeneous tooth-rows found in fossils of *Odontogriphus* and *Wiwaxia*, and concluded that *Odontogriphus* and *Wiwaxia* were unlikely to be molluscs.

Chapter 11

Opabinia

Opabinia
Temporal range: Middle Cambrian

Fossil specimen on display at the
Smithsonian in Washington, D.C.

Scientific classification [e]	
Kingdom:	Animalia
Stem-group:	Arthropoda
Class:	†Dinocaridida
Order:	†Radiodonta
Family:	†**Opabiniidae**
Genus:	†*Opabinia* Walcott, 1912

Binomial name
Opabinia regalis   Walcott, 1912

Opabinia is an animal genus found in Cambrian fossil deposits. Its sole species, *Opabinia regalis*, is known from the Middle Cambrian Burgess Shale of British Columbia, Canada. Fewer than twenty good specimens have been described; 3 specimens of *Opabinia* are known from the Greater Phyllopod bed, where they comprise less than 0.1% of the community. *Opabinia* was a soft-bodied animal of modest size, and its segmented body had lobes along the sides and a fan-shaped tail. The head shows unusual

features: five eyes, a mouth under the head and facing backwards, and a proboscis that probably passed food to the mouth. *Opabinia* probably lived on the seafloor, using the proboscis to seek out small, soft food.

When the first thorough examination of *Opabinia* in 1975 revealed its unusual features, it was thought to be unrelated to any known phylum, although possibly related to a hypothetical ancestor of arthropods and of annelid worms. However other finds, most notably *Anomalocaris*, suggested that it belonged to a group of animals that were closely related to the ancestors of arthropods and of which the living animals onychophorans and tardigrades may also be members.

In the 1970s there was an ongoing debate about whether multi-celled animals appeared suddenly during the Early Cambrian, in an event called the Cambrian explosion, or had arisen earlier but without leaving fossils. At first *Opabinia* was regarded as strong evidence for the "explosive" hypothesis. Later the discovery of a whole series of similar lobopod animals, some with closer resemblances to arthropods, and the development of the idea of stem groups suggested that the Early Cambrian was a time of relatively fast evolution but one that could be understood without assuming any unique evolutionary processes.

History of discovery
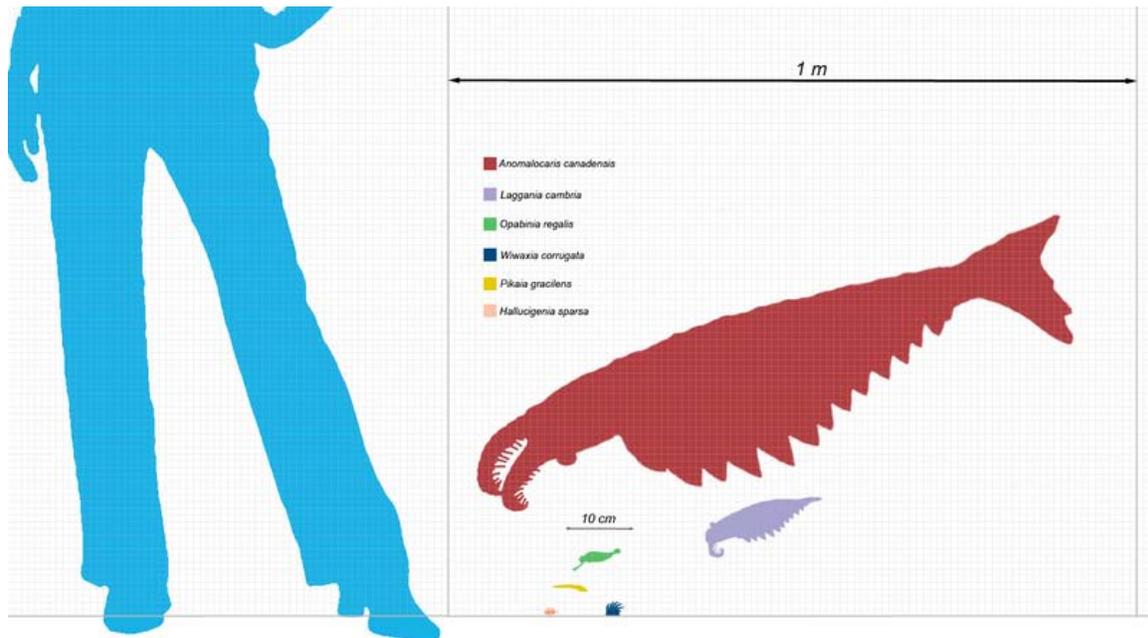
Scale diagram of various Burgess Shale invertebrates, *Opabinia* in green

Charles Doolittle Walcott found in the Burgess Shale nine almost complete fossils of *Opabinia regalis* and a few of what he classified as *Opabinia media*, and published a description of all of these in 1912. The generic name is derived from Opabin pass between Mount Hungabee and Mount Biddle, southeast of Lake O'Hara, British

Columbia, Canada. In 1966-1967 Harry B. Whittington found another good specimen, and in 1975 he published a detailed description based on very thorough dissection of some specimens and photographs of these specimens lit from a variety of angles. Whittington's analysis did not cover *Opabinia media*: Walcott's specimens of this species could not be identified in his collection. In 1960 Russian paleontologists described specimens which they found in the Norilsky region of Siberia and labelled *Opabinia norilica*, but these fossils were poorly preserved, and Whittington did not feel they provided enough information to be classified as members of the genus *Opabinia*.

Occurrence

Artist's impression of *Opabinia* at the sea floor

All the recognized *Opabinia* specimens found so far come from the "Phyllopod bed" of the Burgess Shale, in the Canadian Rockies of British Columbia.

In 1997 Briggs and Nedin reported from South Australia a new specimen of *Myoscolex* which was much better preserved than previous specimens, leading them to conclude that it was a close relative of *Opabinia* - although this interpretation was later questioned by Dzik, who instead concluded that *Myoscolex* was an annelid worm.

Description

Opabinia looks so strange that the audience at the first presentation of Whittington's analysis laughed. The length of *Opabinia regalis* from head to tail ranged between 4 centimetres (1.6 in) and 7 centimetres (2.8 in). The animal also had a hollow proboscis, whose total length was about one third of the body's and which projected down from under the head and then curved forwards and upwards. The proboscis was striated like a vacuum cleaner's hose and probably flexible, and it ended with a claw-like structure whose inner edges bore spines that projected inwards and forwards. The head bore *five* eyes: two on stalks near the front and fairly close to the middle of the head, pointing upwards and forwards; two larger eyes, also stalked, near the rear and outer edges of the head, pointing upwards and sideways; and a single eye with a shorter stalk between the larger pair of stalked eyes, pointing upwards. It has been assumed that the eyes were all compound, like arthropods' lateral eyes, but this reconstruction, which is not backed up by any evidence, is "somewhat fanciful". The mouth was under the head, behind the proboscis, and pointed *backwards*, so that the digestive tract formed a U-bend on its way towards the rear of the animal. The proboscis appeared sufficiently long and flexible to reach the mouth.

The main part of the body was typically about 5 millimetres (0.20 in) wide and had 15 segments, on each of which there was a pair of lobes (flaps) pointing downwards and outwards. The lobes overlapped so that the front of each was covered by the rear edge of the one ahead of it. The body ended with what looked like a single conical segment bearing three pairs of overlapping lobes that pointed up and out, forming a tail like a V-shaped double fan.

Interpretations of other features of *Opabinia* fossils differ. Since the animals did not have mineralized armor nor even tough organic exoskeletons like those of insects, their bodies were flattened as they were buried and fossilized, and smaller or internal features appear as markings within the outlines of the fossils.

Whittington interpreted as gills some markings on the upper surfaces of all lobes except the first on each side, and thought that these gills were flat underneath, had overlapping layers on top, and attached to the bases of the lobes. Budd (1996, 2011) thought they consisted of separate "blades" attached along the front edges on the undersides of the lobes. He also found marks inside the lobes' front edges that he interpreted as internal channels connecting the gills to the interior of the body, much as Whittington interpreted the mark along the proboscis as an internal channel. On the other hand Bergström (1986) interpreted both the "gills" and the lobes as part of a covering over the upper surface of the body.

Whittington found evidence of near-triangular features along the body, and concluded that they were internal structures, most likely sideways extensions of the gut. Chen *et al.* (1994) interpreted them as contained within the lobes along the sides. Budd thought the "triangles" were too wide to fit within *Opabinia*'s slender body, and that cross-section views showed they were attached separately from and lower than the lobes, and extended

below the body. He later found specimens that appeared to preserve the legs' exterior cuticle. He therefore interpreted the "triangles" as short, fleshy, conical legs. He also found small mineralized patches at the tips of some, and interpreted these as claws. Zhang and Briggs (2007) analyzed the chemical composition of the "triangles", and concluded that they had the same composition as the gut, and therefore agreed with Whittington that they were part of the digestive system. Instead they regarded *Opabinia*'s lobe+gill arrangement as an early form of the biramous limbs which are seen in trilobites and crustaceans and which may be the original form in all arthropods. However, this similar chemical composition is not only associated with the digestive tract; Budd and Daley suggest that it represents mineralization forming within fluid-filled cavities within the body (consistent with hollow lobopod legs).

Lifestyle

The way in which the Burgess Shale animals were buried, by a mudslide or a sediment-laden current that acted as a sandstorm, suggests they lived on the surface of the seafloor. *Opabinia* probably used its proboscis to search the sediment for food particles and pass them to its mouth. Since there is no sign of anything that might function as jaws, its food was presumably small and soft. Whittington, believing that *Opabinia* had no legs, thought that it crawled on its lobes and that it could also have swum slowly by flapping the lobes, especially if it timed the movements to create "Mexican waves". On the other hand he thought the body was not flexible enough to allow fish-like undulations of the whole body.

Classification
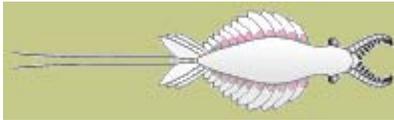
Reconstruction of *Anomalocaris saron*, viewed from the top with the head to the right. The shaded patches at the bases of the flaps are thought to have acted as gills.

Considering how paleontologists' reconstructions of *Opabinia* differ, it is not surprising that the animal's classification is still debated. Walcott, the original describer, considered it to be an anostracan crustacean, while Leif Størmer, following earlier work by Percy Raymond, thought that it belonged to the so-called "trilobitoids". After his thorough analysis Whittington concluded that *Opabinia* was no arthropod, as he found no evidence for arthropodan jointed limbs, and nothing like the flexible, probably fluid-filled proboscis was known in arthropods. Although he left *Opabinia*'s classification above the family level open, the annulated but not articulated body and the unusual lateral lobes with gills persuaded him that it may have been a representative of the ancestral stock from which both the annelids and arthropods arose.

In 1985, Derek Briggs and Whittington published a description of *Anomalocaris*, also from the Burgess Shale. Swedish palaeontologist Jan Bergström suggested that the two animals were related, as they shared lateral flaps with gills, stalked eyes and other

features; and he classified them as primitive arthropods, although he considered that arthropods are not a single phylum.

Modern tardigrades may be *Opabinia*'s closest living evolutionary relatives.

In 1996 Graham Budd found what he considered evidence of short, un-jointed legs in *Opabinia*, His examination of the anomalocarid *Kerygmachela* from the Sirius Passet lagerstätte, about 518 million years ago and over 10M years older than the Burgess Shale, convinced him that this had similar legs. He considered the legs of these two genera very similar to those of the Burgess Shale *Aysheaia* and the modern onychophorans, which are regarded as closely related to the ancestors of arthropods. After examining several sets of features shared by these and similar lobopods he drew up a "broad-scale reconstruction of the arthropod stem-group", in other words of arthropods and what he considered to be their evolutionary "aunts" and "cousins". One striking feature of this family tree is that modern tardigrades may be *Opabinia*'s closest living evolutionary relatives.

Although Zhang and Briggs (2007) disagreed with Budd's diagnosis that *Opabinia*'s "triangles" were legs, the resemblance they saw between *Opabinia*'s lobe+gill arrangement and arthropods' biramous limbs led them to conclude that *Opabinia* was very closely related to arthropods. In fact they presented a family tree very similar to Budd's except that theirs did not mention tardigrades.

Theoretical significance

Opabinia made it clear how little was known about soft-bodied animals, which do not usually leave fossils. When Whittington described it in the mid-1970s, there was already a vigorous debate about the early evolution of animals. Preston Cloud argued in 1948 and 1968 that the process was "explosive", and in the early 1970s Niles Eldredge and Stephen Jay Gould developed their theory of punctuated equilibrium, which views evolution as long intervals of near-stasis "punctuated" by short periods of rapid change. On the other hand around the same time Wyatt Durham and Martin Glaessner both argued that the animal kingdom had a long Proterozoic history that was hidden by the lack of fossils.

Whittington (1975) concluded that *Opabinia*, and other taxa such as *Marrella* and *Yohoia*, cannot be accommodated in modern groups. This was one of the primary reasons why Gould in his book on the Burgess Shale, *Wonderful Life*, considered that Early Cambrian life was much more diverse and "experimental" than any later set of animals and that the Cambrian explosion was a truly dramatic event, possibly driven by unusual evolutionary mechanisms. He regarded *Opabinia* as so important to understanding this phenomenon that he wanted to call his book *Homage to Opabinia*.

However, other discoveries and analyses soon followed, revealing similar-looking animals such as *Anomalocaris* from the Burgess Shale and *Kerygmachela* from Sirius Passet. Another Burgess Shale animal, *Aysheaia*, was considered very similar to modern Onychophora, which are regarded as close relatives of arthropods. Paleontologists defined a group called lobopods to include animals that are thought to be close relatives of arthropods but which lack jointed limbs. There is still debate about whether lobopods are monophyletic, i.e. whether they include all and only the descendants of a single common ancestor, and about whether arthropods are a sub-group of lobopods or a sister-group.

While this discussion about specific fossils such as *Opabinia* and *Anomalocaris* was going on, the concept of stem groups was introduced to cover evolutionary "aunts" and "cousins". A crown group is a group of closely-related living animals plus their last common ancestor plus all its descendants. A stem group contains offshoots from members of the lineage earlier than the last common ancestor of the crown group; it is a *relative* concept, for example tardigrades are living animals which form a crown group in their own right, but Budd (1996) regarded them also as being a stem group relative to the arthropods. Viewing strange-looking organisms like *Opabinia* in this way makes it possible to see that, while the Cambrian explosion was unusual, it can be understood in terms of normal evolutionary processes.

Chapter 12

Spriggina and Tabulate Coral

Spriggina

Spriggina
Temporal range: Ediacaran
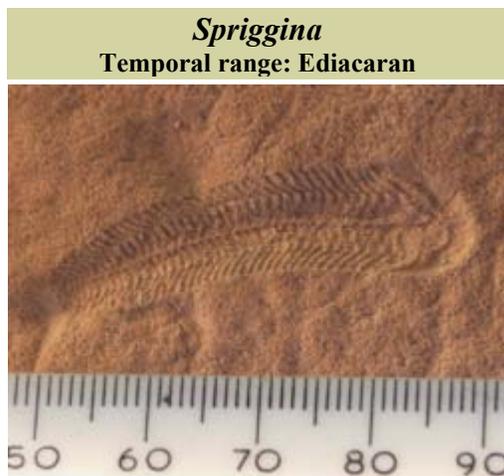
Fossil of *S. floundersi*. Scale in millimetres.

Scientific classification	
Kingdom:	Animalia
(unranked):	Bilateria
Phylum:	?Proarticulata
Family:	Sprigginidae
Genus:	***Spriggina*** Glaessner, 1958
Species:	***S. floundersi***
Binomial name	
Spriggina floundersi Glaessner, 1958	

Fossils of **Spriggina** are known from the Ediacaran period, around 550 million years ago. The segmented organism reached about 3 cm in length and may have been predatory. Its bottom is covered with two rows of tough interlocking plates, while one row covered its

top; its front few segments fused to form a head, which may have borne eyes and antennae.

*Spriggina'*s affinity is currently unknown; it has been classified as an annelid worm, a rangeomorph-like frond, Proarticulata, and an arthropod, perhaps related to the trilobites. Lack of known segmented legs or limbs may make an arthropod classification premature.

Morphology

Spriggina grew to around three centimetres in length, and was approximately oblong. The organism was segmented, with no fused segments, with the segments sometimes being curved. The upper surface of the organism was covered by one row of overlapping cuticular plates; the underside, paired plates.

The first two segments formed a "head". The front segment was the shape of a horseshoe, with a pair of depressions on its upper surface which may represent eyes. The second segment may have borne antennae. Subsequent segments bore annulations.

Some fossils have what may be a circular mouth at the centre of the semicircular head – although interpretation is hampered by the small size of the creature relative to the large grains of sandstones in which it is preserved. Legs are not preserved.

The symmetry observed is not exactly bilaterian, but appears to be a glide reflection, where opposite segments are shifted by half an interval. In some specimens the body segments tilt backwards, making roughly chevron patterns; while in others they are more or less straight. There appear to be fairly complex variations between these two end members.

Fossil occurrences

Spriggina is known only from beds of Ediacaran age. Fossils from the Vindyhan, reliably dated to around 1,200 million years old, have been classified as *Spriggina*, but in all likelihood represent microbial artifacts. *Spriggina* possessed a tough, though uncalcified, body, evident from the fossils' preservation: always as a mould in the lower surface of the fossiliferous bed.

Affinity

Digitally enhanced image of a *Spriggina* fossil

Like many of the Ediacara biota, the relationship of *Spriggina* to other groups is unclear. It bears some similarity to the living polychaete worm *Tomopteris*, but its lack of chaetae, along with other lines of evidence, suggests that it cannot be placed in this phylum. It was also compared to the rangeomorphs, frondose members of the Ediacara biota that may represent a separate kingdom. While its glide symmetry may suggest otherwise, *Spriggina* is currently considered to be an arthropod; its resemblance to the trilobites may suggest a close relationship to this class. *Spriggina* may have been predatory, and played a role in initiating the Cambrian transition.

History

The genus was named after Reg Sprigg who discovered the fossils of the Ediacara Hills—part of the Flinders Ranges in South Australia—and was a proponent of their recognition as multicellular organisms. *Spriggina floundersi* is at present the only generally accepted species in this genus. *Spriggina ovata* has now been moved into its own genus, *Marywadea*. *Spriggia wadea* is probably a junior synonym of *Aspidella* preserved under specific conditions.
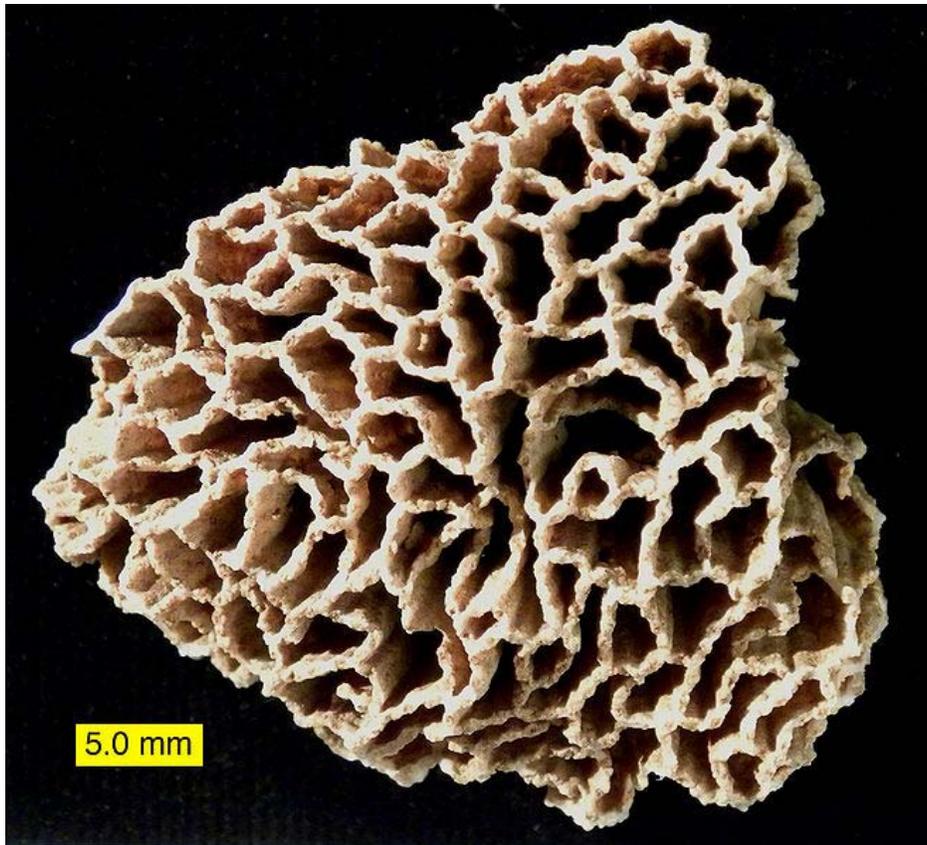
Tabulate coral

Tabulata
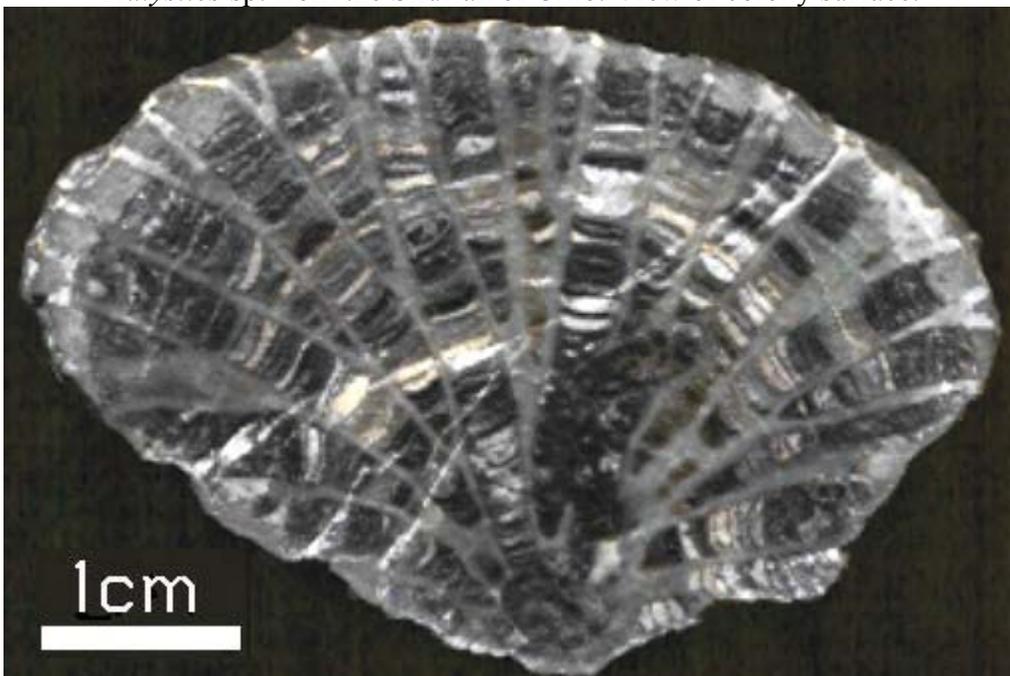**Temporal range: 488–251.4 Ma**
Ordovician–Permian

Tabulate coral (a syringoporid); Boone Limestone (Lower Carboniferous) near Hiwasse, Arkansas. Scale bar is 2.0 cm.

Scientific classification

Kingdom:	Animalia
Phylum:	Cnidaria
Class:	Anthozoa
Subclass:	Zoantharia
Order:	**Tabulata**

Halysites sp. from the Silurian of Ohio. View of colony surface.

Etched section of an Ordovician tabulate coral

Aulopora from the Silica Shale (Middle Devonian) of northwestern Ohio. Image shows colony origin encrusting a brachiopod.

The **tabulate corals**, forming the order **Tabulata**, are an extinct form of coral. They are almost always colonial, forming colonies of individual hexagonal cells known as corallites defined by a skeleton of calcite, similar in appearance to a honeycomb. Adjacent cells are joined by small pores. Their distinguishing feature is their well-developed horizontal internal partitions (*tabulae*) within each cell, but reduced or absent vertical internal partitions (*septae*). They are usually smaller than rugose corals, but vary considerably in shape, from flat to conical to spherical.

Around 300 species have been described. Among the most common tabulate corals in the fossil record are *Aulopora*, *Favosites*, *Halysites*, *Heliolites*, *Pleurodictyum*, *Sarcinula* and *Syringopora*.

Like rugose corals, they lived entirely during the Paleozoic, being found from the Ordovician to the Permian. With Stromatoporoidea and rugose corals, the tabulate corals are characteristic of the shallow waters of the Silurian and Devonian. Sea levels rose in the Devonian, and tabulate corals became much less common. They finally became extinct in the Permian-Triassic extinction event.

Chapter 13

Dinocaridida and Gogia

Dinocaridida

Dinocaridida	
Temporal range: Cambrian– Lower Devonian	
Scientific classification [e]	
Kingdom:	Animalia
Stem-group:	Arthropoda
(unranked):	†Lobopodia
Class:	**†Dinocaridida** Collins, 1996

Dinocaridida is a proposed extinct taxon of fossil arthropod-like marine animals found in the early and middle Cambrian. It is subdivided into the anomalocarids and the opabinids. The name of this group comes from Greek, "deinos" and "caris," meaning "terror shrimp" or "terror crab," due to their crustacean-like appearance and the hypotheses suggesting that members of this class were the apex predators of their time.

Dinocaridids are bilaterally symmetrical, with a non-mineralized cuticle and a body divided into two major tagmata, or body-sections. The frontal section should have one or more claws found just in front of the mouth, which is located on these creatures' underside. The body will possess thirteen or more segments, each with its own gill branch and swimming lobe. It is thought that these lobes moved in an up-and-down motion to propel the animal forward in a fashion similar to the cuttlefish.

The placement of Dinocaridida is uncertain: they appear to be stem group arthropods. In some recent works they are grouped with other enigmatic forms in the phylum Lobopodia.
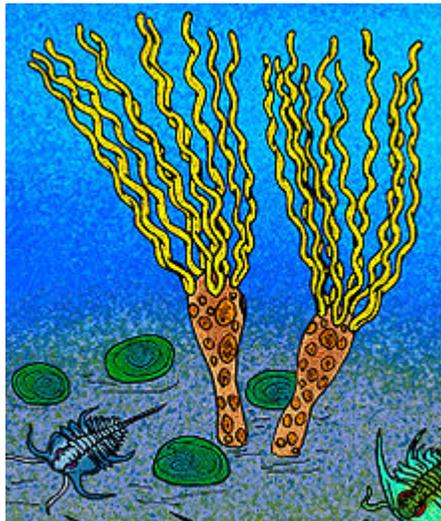
The group is geographically widespread, and has been reported from Cambrian strata in Canada, China and Russia, as well as the Devonian of Germany.

Gogia

G. kitchnerensis specimen from Utah

A colourful reconstruction of *G. ojenai*

Scientific classification	
Kingdom:	Animalia
Phylum:	Echinodermata
Subphylum:	†Blastozoa
Class:	Eocrinoidea Miller, 1821
Order:	Gogiida
Family:	Eocrinidae
Genus:	*Gogia* Walcott 1917

Type species
G. prolifica

Species

- *G. prolifica* WALCOTT 1917
- *G. (Eocrinus) longidactylus* (Walcott 1886) ROBINSON 1965
- *G. granulosa* ROBINSON 1965
- *G. multibrachiata* (Kirk 1945) ROBINSON 1965
- *G. spiralis* ROBINSON 1965
- *G. ojenai* DURHAM 1978

Synonyms

- *Eocrinus*

Gogia is a primitive genus of the Class Eocrinoidea, belonging to the early echinoderm Subphylum Blastozoa (Sprinkle 1973), dated from the Cambrian.

G. ojenai dates to the late Early Cambrian; other species come from various Middle Cambrian strata throughout North America, but the genus has yet to be described outside this continent.

The species of *Gogia*, like other eocrinoids, were not closely related to the true crinoids, instead, being more closely related to the blastoids.

Gogia radiata

Gogia is distinguished from sea lilies, and most other blastoids, in that the plate-covered body was shaped like a vase, or a bowling pin (with the pin part stuck into the substrate), and that the five ambulacra were split into pairs of coiled or straight, ribbon-like strands. Six specimens of *Gogia* are known from the Greater Phyllopod bed, where they comprise < 0.1% of the community.

As a whole, the Eocrinoids are regarded as basal blastozoans very close to the ancestry of the entire subphylum.

Chapter 14

Helicoplacus, Homalozoa and Blastoid

Helicoplacus

Helicoplacus guthi

Helicoplacus guthi

Scientific classification	
Kingdom:	Animalia
Phylum:	Echinodermata
Class:	†Helicoplacoidea
Genus:	*Helicoplacus*

Species
• *Helicoplacus curtisi*
• *Helicoplacus guthi*

Helicoplacus (often misspelled ***Helioplacus***) is the earliest well-studied fossil echinoderm. Fossil plates are known from several regions. Complete specimens were found in Lower Cambrian strata of the White Mountains of California.

The animal was a cigar-shaped creature up to 7 centimetres (2.8 in) long that stood upright on one end. Unlike more typical echinoderms such as sea stars, *Helicoplacus* does not have fivefold symmetry. Instead, there is a spiral food groove on the outside along which food was moved to a mouth that is thought to be located on the side. The respiratory system appears to be primitive. Although the animal does not look like a typical echinoderm, the plates are composed of the characteristic calcareous plates known as *stereom* that are common to all echinoderms. The ambulacrum is similar to that of the Edrioasteroidea; as a result, Helicoplacoidea may belong to Pelmatozoa.
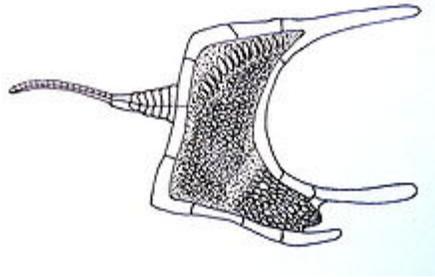
Other contemporaneous echinoderms are known to have existed from their dissociated plates, but other than a few possible edrioasteroids, *Helicoplacus* is the earliest echinoderm that is well enough preserved to analyze its characteristics. One much earlier form called *Arkarua* has been hypothesized to be an ancestral echinoderm because of its fivefold symmetry. But *Arkarua* appears to lack both stereoms and a mouth.

Helicoplacoids seem to have existed for about 15 million years in the Lower Cambrian, around 525 million years ago.

Helicoplacoids are thought to have been suspension feeders living at moderate depths in highly-oxygenated water with strong enough currents to ensure a steady food supply. They are typically found in greenish shales and are rarely found in shallow water sandstones and limestones.

Homalozoa

The **Homalozoa** are extinct, Paleozoic echinoderms that lacked the typical pentamer body form. Instead all homalozoans were markedly asymmetric. Homalozoans are extremely variable in forms, but they all were sessile animals. The body (theca) was covered with calcite plates with a number of openings. Their form is in some cases so unusual that it is unclear which openings are to be considered as mouth and anus. Many of them were stalked, similar to sea lilies (crinoids), but often their bodies were bent over, so that the mouth and anus projected forwards rather than upwards. Some forms, especially stylophorans, rested flat on the sea floor. In some forms the single ray (brachiole or aulacophore) possessed an ambulacral groove. It has been claimed that some forms possessed gills and gill slits.

Taxonomy

Homalozoans were traditionally considered to be stem-group echinoderms, but had also been considered to lie in the stem lineage of the chordates (calcichordates). However, it is now generally accepted that homalozoans were echinoderms because their calcite skeleton was composed of the typical stereom crystalline structure.

They include the unusual stylophorans (mitrates and cornutes), Homoiostelea (solutes), the Homostelea (cinctans), and the Ctenocystoidea (ctenoid-bearing homalozoans). They have recently been recognised as a paraphyletic group. The stylophorans are now classified as a clade of the Crinozoa, whereas the other three are classified as clades of the Blastozoa.

Blastoid

Blastoids
Temporal range: Ordovician - Permian

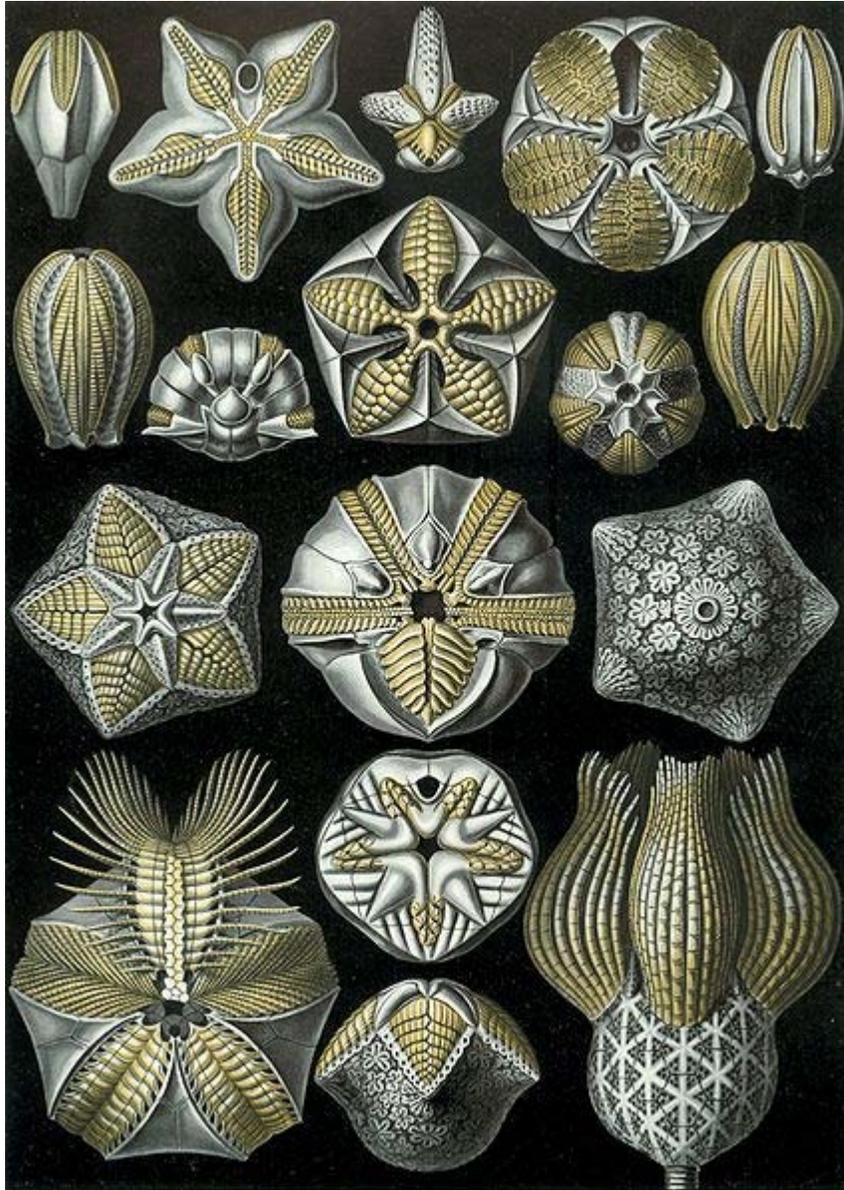Blastoid fossils (*thecae*) attached to matrix.

Scientific classification	
Kingdom:	Animalia
Phylum:	Echinodermata
Subphylum:	**Blastozoa**
Class:	**Blastoidea** Say, 1825
Subclasses	
Fissiculata Spiraculata	

"Blastoidea", from Ernst Haeckel's *Artforms of Nature*, 1904

Blastoids (Class Blastoidea) are an extinct type of stemmed echinoderm. Often called *sea buds*, blastoid fossils look like small hickory nuts. They originated, along with many other echinoderm classes, in the Ordovician period and reached their greatest diversity in the Mississippian subperiod of the Carboniferous period. Blastoids persisted until their extinction at the end of Permian, about 250 million years ago. Although never as diverse as their contemporary relatives, the crinoids, blastoids are common fossils, especially in many Mississippian-age rocks.

Description

Like most echinoderms, blastoids were protected by a set of interlocking plates of calcium carbonate, which formed the main body, or *theca*. In life, the theca of a typical blastoid was attached to a stalk or column made up of stacked disc-shaped plates. The other end of the column was attached to the ocean floor by a holdfast, very much like stalked crinoids. The stalk was usually relatively short, and in some species, was absent, with the holdfast being attached directly to the base of the theca.

The mouth was located at the summit of the theca. Radiating like flower petals from the center were five food grooves, or *ambulacra*. Each ambulacrum had many long, thin, fine structures called *brachioles*, which were used to trap food particles and bring them to the mouth. Brachioles were delicate structures, and in fossils are not usually preserved in place. A series of five spiracle plates surrounded the star-shaped mouth, which included the anus, mouth and entrances to a set of five complex, folded respiratory organs known as *hydrospires*. These spiracles prevented mixing of the various fluids. Waste elimination was through the *anispiracle*, an opening formed by the fusing of anus and adjacent spiracles.

Like crinoids, blastoids were high-level, stalked suspension feeders (feeding mainly on planktonic organisms) that inhabited clear-to-silty, moderately-agitated ocean waters from shelf to basin. The food gathering system of blastoids consisted of several types of ambulacra. Food entered the brachiolar ambulacra, was transferred to the side ambulacra through the brachiolar pit, then transferred to the main (median) ambulacra, and finally entered the mouth. Each of these ambulacra were roofed by cover plates. The cover plates of the brachiolar groove were movable and could open, allowing food to enter, or close as needed. Other cover plates may also have been movable.

Taxonomy

Blastoids are subdivided into two subclasses: Fissiculata, which are characterized by direct entrance to the individual hydrospires by way of slits; and Spiraculata, which are characterized by indirect entrance to the hydrospires through canals by way of pores. The earliest blastoid yet found, *Macurdablastus* from the Middle Ordovician of Tennessee, cannot be classified as either subclass.

Chapter 15

List of Prehistoric Annelids

Astreptoscolex anasillosus fossil

This **list of prehistoric annelids** is an attempt to create a comprehensive listing of all genera that have ever been included in Annelida which have been found preserved as fossils. This list excludes purely vernacular terms. It includes all commonly accepted genera, but also genera that are now considered invalid, doubtful (*nomina dubia*), or were

not formally published (*nomina nuda*), as well as junior synonyms of more established names, and genera that are no longer considered acanthodians.

Naming conventions and terminology

Naming conventions and terminology follow the International Code of Zoological Nomenclature. Technical terms used include:

- **Junior synonym**: A name which describes the same taxon as a previously published name. If two or more genera are formally designated and the type specimens are later assigned to the same genus, the first to be published (in chronological order) is the senior synonym, and all other instances are junior synonyms. Senior synonyms are generally used, except by special decision of the ICZN, but junior synonyms cannot be used again, even if deprecated. Junior synonymy is often subjective, unless the genera described were both based on the same type specimen.
- *Nomen nudum* (Latin for "naked name"): A name that has appeared in print but has not yet been formally published by the standards of the ICZN. *Nomina nuda* (the plural form) are invalid, and are therefore not italicized as a proper generic name would be. If the name is later formally published, that name is no longer a *nomen nudum* and will be italicized on this list. Often, the formally published name will differ from any *nomina nuda* that describe the same specimen.
- *Nomen oblitum* (Latin for "forgotten name"): A name that has not been used in the scientific community for more than fifty years after its original proposal.
- **Preoccupied name**: A name that is formally published, but which has already been used for another taxon. This second use is invalid (as are all subsequent uses) and the name must be replaced. As preoccupied names are not valid generic names, they will also go unitalicized on this list.
- *Nomen dubium* (Latin for "dubious name"): A name describing a fossil with no unique diagnostic features. As this can be an extremely subjective and controversial designation, this term is not used on this list.

A

- *Aglaurides*
- *Albertaprion*
- *Amphictene*
- *Anisocerasites*
- *Arabella*
- *Arabellites*
- *Archaeoprion*
- *Archarenicola*
- *Arenicola*
- *Arites*
- *Asterosalpinx*
- *Astreptoscolex*

B

- *Biconulites*
- *Bipygmaeus*
- *Bohemoscolex*
- *Brochosogenys*
- *Bundenbachochaeta*
- *Burgessochaeta*

C

- *Camptosalpinx*
- *Campylites*
- *Canadia*
- *Carbosesostris*
- *Cementula*
- *Chaetosalpinx*
- *Circeis*
- *Clavulites*
- *Conora*
- *Cowiella*
- *Crininicaminus*
- *Cryptosiphon*
- *Ctenoscolex*
- *Cubiculovinea*
- *Cycloserpula*

D

- *Delosites*
- *Didontogaster*
- *Dinoscolites*
- *Diopatraites*
- *Diploconcha*
- *Discouvermetulus*
- *Ditrupa*
- *Ditrupula*
- *Dodecaceria*
- *Dorvillea*
- *Drilonereis*
- *Dryptoscolex*

E

- *Ebetallites*
- *Elleriprion*
- *Eopolychaetus*
- *Eotomopteris*
- *Eotrophonia*
- *Epitrachys*
- *Esconites*
- *Eunice*
- *Eunicites*
- *Euryprion*

F

- *Falkosites*
- *Fastuoscolex*
- *Filograna*
- *Filogranula*
- *flabelligerid*
- *Flucticularia*
- *Fossundecima*

G

- *Galeolaria*
- *Gammascolex*
- *Genicularia*
- *Gitonia*
- *Glycera*
- *Glycerites*
- *Goniada*
- *Gotlandites*

H

- *Hadimopanella*
- *Hadoprion*
- *Haileyia*
- *Halla*
- *Hammatopsis*
- *Hamulus*
- *Hesionites*
- *Hicetes*
- *Hindenites*
- *Hindeoprion*
- *Hirudopsis*
- *Homaphrodites*
- *Houscolex*
- *Howellitubus*
- *Hydroides*
- *Hystriciola*

I

- *Ildraites*
- *Insulicorypha*
- *Iquitosia*

J

- *Janita*
- *Jereminella*
- *Josephella*

K

- *Kaimenella*
- *Kettnerites*
- *Klakesia*
- *Kalloprion*
- *Khemisina*

L

- *Lanceolatites*
- *Lepidenteron*
- *Longitubus*
- *Langeites*
- *Lercaritubus*
- *Lumbriconereis*
- *Laqueoserpula*
- *Levisettius*
- *Lumbricopsis*
- *Lecathylus*
- *Lockportia*
- *Lysaretides*

M

- *Maeandropolydora*
- *Meringosoma*
- *Milaculum*
- *Marlenites*
- *Metalaeospira*
- *Mochtyella*
- *Marphysaites*
- *Metavermilia*
- *Multiprion*
- *Melanoraphia*
- *Microdactylophora*
- *Muroserpula*
- *Mercierella*
- *Microtubus*
- *Myzostomites*

N

- *Nawnites*
- *Neovermilia*
- *Nothrites*
- *Neodexiospira*
- *Nereidavus*
- *Notocirrus*
- *Neomicrorbis*

O

- *Oblongiprion*
- *Ophryotrocha*
- *Ottawella*
- *Oenonites*
- *Ornatoporta*
- *Ottawina*
- *Oliveirania*
- *Orthoconorca*
- *Oxyprion*
- *Onuphis*
- *Orthopelta*

P

- *Palaeoaphrodite*
- *Pectinaria*
- *Praelumbrinereis*
- *Palaeochaeta*
- *Pegmaticula*
- *Processoprion*

- *Palaeodactylophora*
- *Palaeopelyx*
- *Palaeoscolecida*
- *Palaeoscolex*
- *Paleonereites*
- *Paleononites*
- *Paliurus*
- *Palurites*
- *Paradrilonereigenys*
- *Paraglycerites*
- *Paragnathites*
- *Paralaeospira*
- *Paranereites*
- *Paraterebella*
- *Parsimonia*
- *Pentaditrupa*
- *Pernerites*
- *Peronochaeta*
- *Phiops*
- *Phragmosalpinx*
- *Pieckonia*
- *Pileolaria*
- *Pistoprion*
- *Placostegus*
- *Plasmuscolex*
- *Polychaetaspis*
- *Polydora*
- *Pomatoceros*
- *Pontobdellopsis*
- *Praeglycera*
- *Pronereites*
- *Propolynoe*
- *Propomatoceros*
- *Protarabellites*
- *Protectoconorca*
- *Proterebella*
- *Proterula*
- *Protonympha*
- *Protoscolex*
- *Protula*
- *Protulites*
- *Protulophila*
- *Psammosiphon*
- *Pteropelta*
- *Pyrgopolon*

R

- *Ramesses*
- *Ramphoprion*
- *Raphidiophorus*
- *Rhamphegenys*
- *Rhytiprion*
- *Rotularia*
- *Ruedemannella*
- *Rutellifrons*

S

- *Sabellaria*
- *Salmacina*
- *Sarcinella*
- *Sarcionata*
- *Schistomeringos*
- *Schizoproboscina*
- *Sciotoprion*
- *Sclerostyla*
- *Scolecoderma*
- *Semiserpula*
- *Serpentula*
- *Serpula*
- *Serpularia*
- *Serpulopsis*
- *Serratula*
- *Sinuocornu*
- *Siphonostomites*
- *Skalenoprion*
- *Soris*
- *Spiraserpula*
- *Spirographites*
- *Spirorbis*
- *Staurocephalites*
- *Stauronereisites*
- *Stephenoscolex*
- *Sthenelaites*
- *Stom*
- *Streblosoma*
- *Streptindytes*
- *Symmetroprion*

T

- *Terebella*
- *Terebellites*
- *Terebellolites*
- *Tetraprion*
- *Tetraserpula*
- *Thalenessites*
- *Titahia*
- *Torlessia*
- *Tosalorbis*
- *Trentonia*
- *Triadonereis*
- *Trianguligenys*
- *Tubulelloides*
- *Turbinia*

U

- *Uncinogenys*
- *Ungulites*

V

- *Vepreculina*
- *Vermiliopsis*
- *Vermilia*

X

- *Xanioprion*