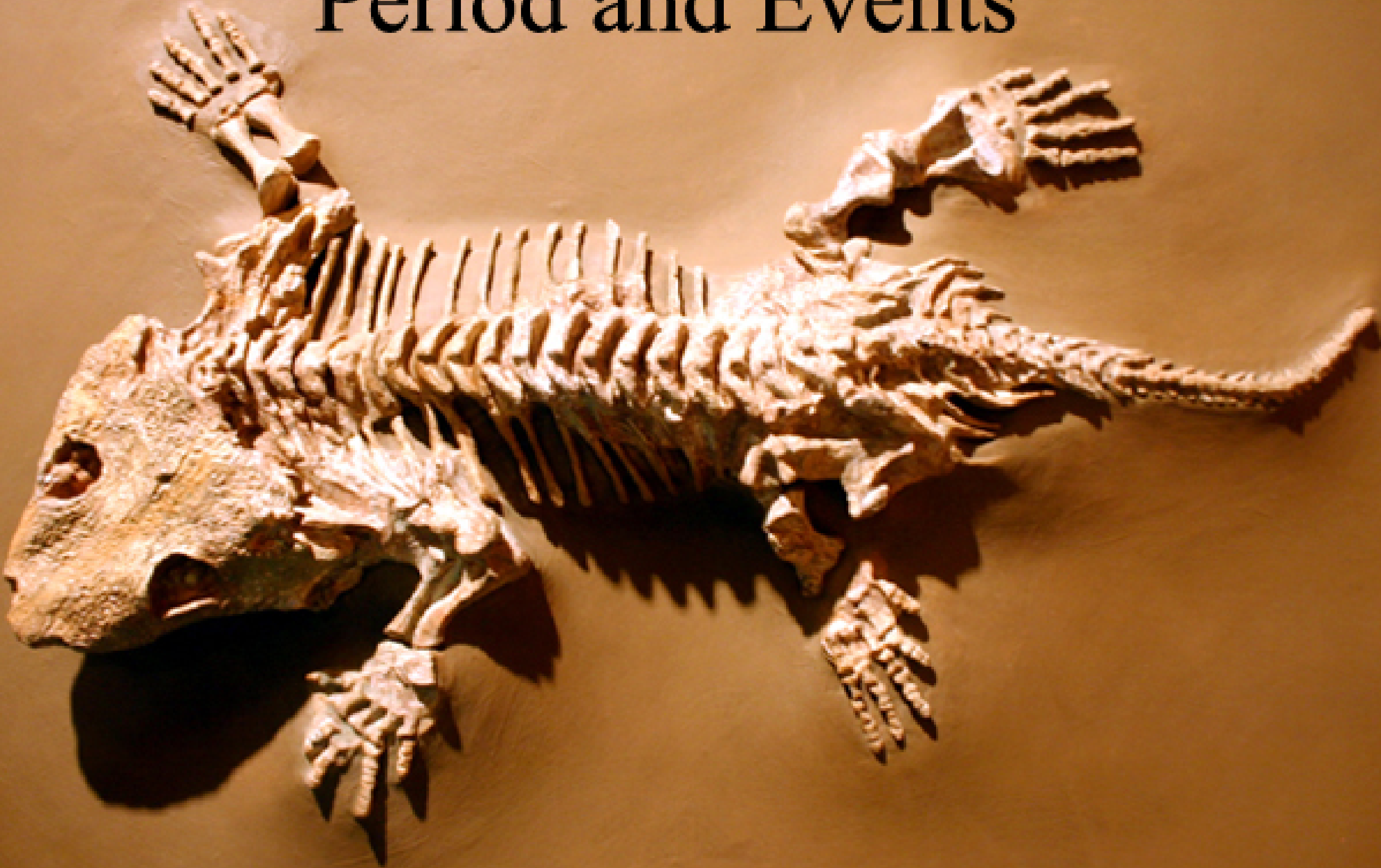
All About

Permian Period and Events



Jack Glasgow

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Permian

The **Permian** is a geologic period and system characterized among land vertebrates by the diversification of the early amniotes into the ancestral groups of the mammals, turtles, lepidosaurs and archosaurs. The Permian Period follows the Carboniferous and extends from 299.0 ± 0.8 to 251.0 ± 0.4 Mya (million years before the present). It is the last period of the Paleozoic Era and famous for its ending epoch event, the largest mass extinction known to science. The Permian Period was named after the kingdom of Permia in modern-day Russia by Scottish geologist Roderick Murchison in 1841.

ICS Subdivisions

Official (ICS, 2004, chart) Subdivisions of the Permian System, from most recent to most ancient rock layers are:

Upper Permian (Late Permian) or Lopingian, Tatarian, or Zechstein, epoch [260.4 ± 0.7 Mya - 251.0 ± 0.4 Mya]

- Changhsingian (Changxingian) [253.8 ± 0.7 Mya - 251.0 ± 0.4 Mya]
- Wuchiapingian (Wujiapingian) [260.4 ± 0.7 Mya - 253.8 ± 0.7 Mya]
- Others:
    - Waiitian (New Zealand) [260.4 ± 0.7 Mya - 253.8 ± 0.7 Mya]
    - Makabewan (New Zealand) [253.8 - 251.0 ± 0.4 Mya]
    - Ochoan (North American) [260.4 ± 0.7 Mya - 251.0 ± 0.4 Mya]

Middle Permian, or Guadalupian epoch [270.6 ± 0.7 - 260.4 ± 0.7 Mya]

- Capitanian stage [265.8 ± 0.7 - 260.4 ± 0.7 Mya]
- Wordian stage [268.0 ± 0.7 - 265.8 ± 0.7 Mya]
- Roadian stage [270.6 ± 0.7 - 268.0 ± 0.7 Mya]
- Others:
    - Kazanian or Maokovian (European) [270.6 ± 0.7 - 260.4 ± 0.7 Mya]
    - Braxtonian stage (New Zealand) [270.6 ± 0.7 - 260.4 ± 0.7 Mya]

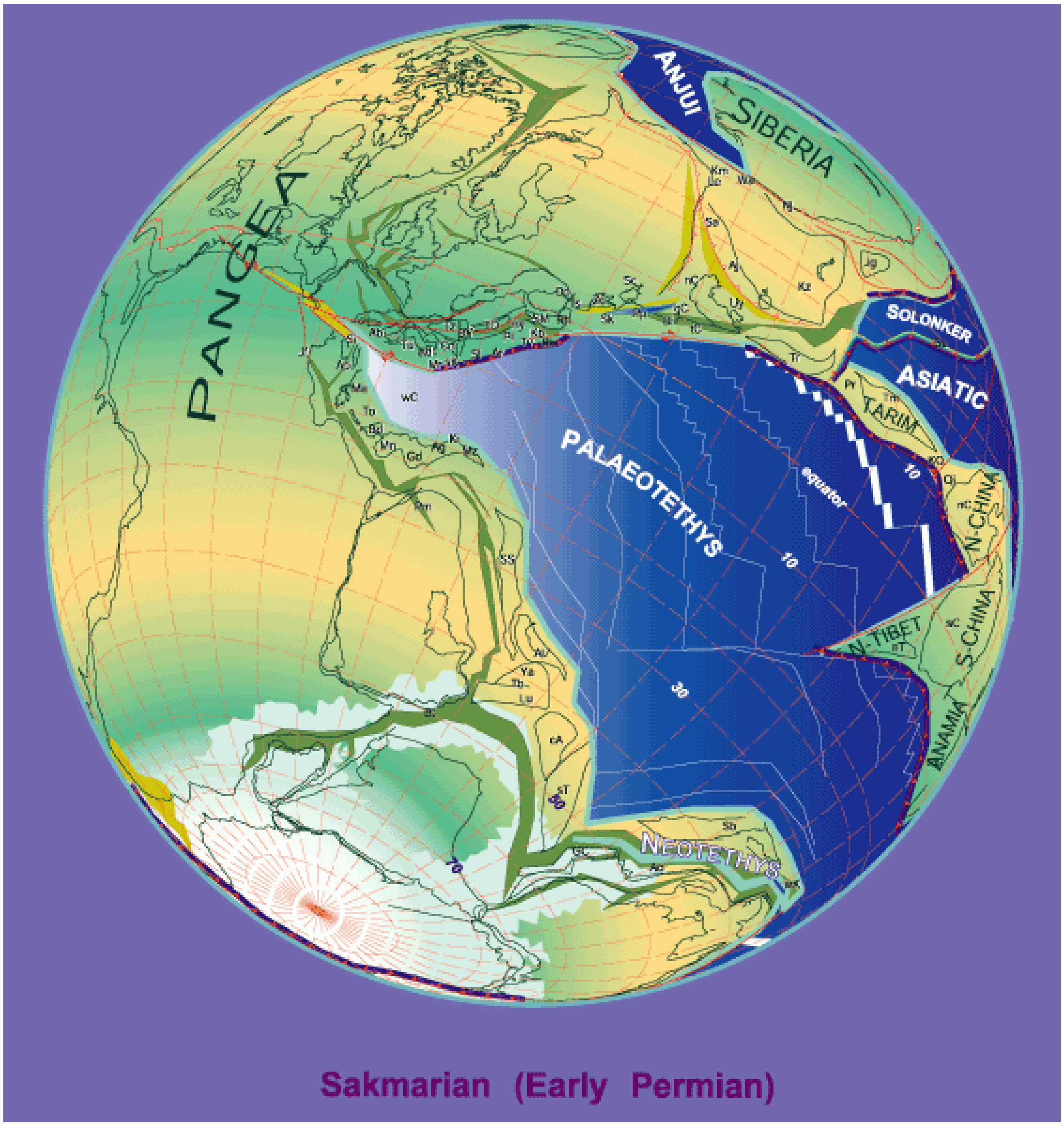
Lower / Early Permian or Cisuralian epoch [299.0 ± 0.8 - 270.6 ± 0.7 Mya]

- Kungurian (Irenian / Filippovian / Leonard) stage [275.6 ± 0.7 - 270.6 ± 0.7 Mya]
- Artinskian (Baigendzinian / Aktastinian) stage [284.4 ± 0.7 - 275.6 ± 0.7 Mya]
- Sakmarian (Sterlitamakian / Tastubian / Leonard / Wolfcamp) stage [294.6 ± 0.8 - 284.4 ± 0.7 Mya]
- Asselian (Krumaian / Uskalikian / Surenian / Wolfcamp) stage [299.0 ± 0.8 - 294.6 ± 0.8 Mya]
- Others:
  - Telfordian (New Zealand) [289 - 278]
  - Mangapirian (New Zealand) [278 - 270.6]

Oceans

Sea levels in the Permian remained generally low, and near-shore environments were limited by the collection of almost all major landmasses into a single continent -- Pangaea. This could have in part caused the widespread extinctions of marine species at the end of the period by severely reducing shallow coastal areas preferred by many marine organisms.

Paleogeography



Geography of the Permian world

During the Permian, all the Earth's major land masses were collected into a single supercontinent known as Pangaea. Pangaea straddled the equator and extended toward the poles, with a corresponding effect on ocean currents in the single great ocean ("Panthalassa", the "universal sea"), and the Paleo-Tethys Ocean, a large ocean that was between Asia and Gondwana. The Cimmeria continent rifted away from Gondwana and drifted north to Laurasia, causing the Paleo-Tethys to shrink. A new ocean was growing on its southern end, the Tethys Ocean, an ocean that would dominate much of the Mesozoic Era. Large continental landmasses create climates with extreme variations of heat and cold ("continental climate") and monsoon conditions with highly seasonal rainfall patterns. Deserts seem to have been widespread on Pangaea. Such dry conditions favored gymnosperms, plants with seeds enclosed in a protective cover, over plants such as ferns that disperse spores. The first modern trees (conifers, ginkgos and cycads) appeared in the Permian.

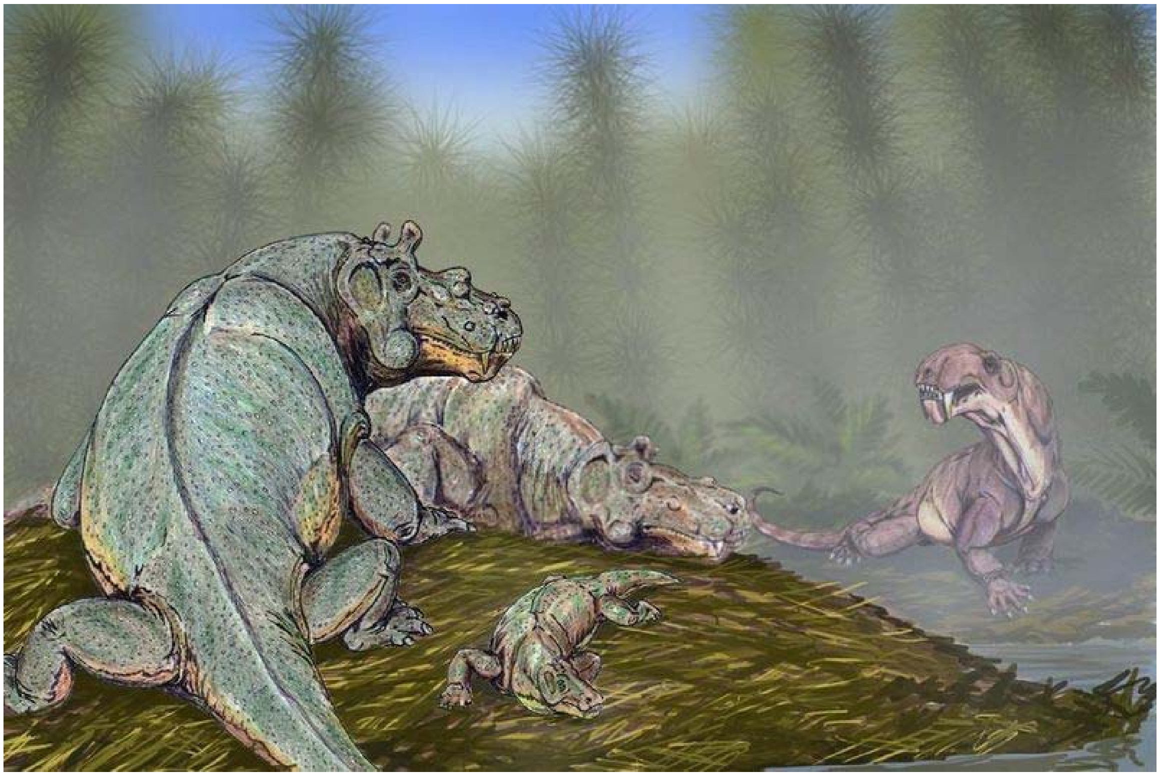
Three general areas are especially noted for their extensive Permian deposits - the Ural Mountains (where Perm itself is located), China, and the southwest of North America, where the Permian Basin in the U.S. state of Texas is so named because it has one of the thickest deposits of Permian rocks in the world.

Climate

The climate in the Permian was quite varied. At the start of the Permian, the Earth was still at the grip of an Ice Age from the Carboniferous. Glaciers receded around the mid-Permian period as the climate gradually warmed, drying the continent's interiors. In the late Permian period, the drying continued although the temperature cycled between warm and cool cycles.

Life

Dimetrodon and *Eryops*- Early Permian, North America



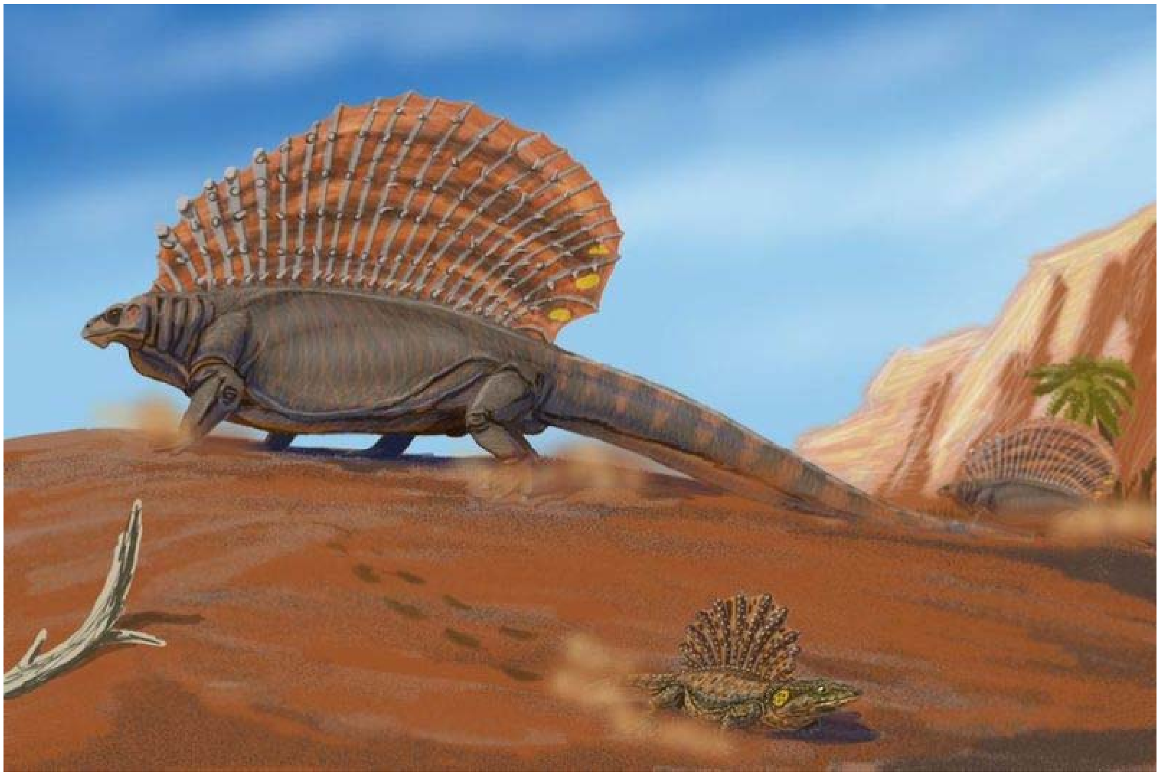
Ocher fauna - Early Middle Permian, Ural Region

Titanophoneus and *Ulemosaurus* - Ural Region

Marine biota

Permian marine deposits are rich in fossil mollusks, echinoderms, and brachiopods. Fossilized shells of two kinds of invertebrates are widely used to identify Permian strata and correlate them between sites: fusulinids, a kind of shelled amoeba-like protist that is one of the foraminiferans, and ammonoids, shelled cephalopods that are distant relatives of the modern nautilus. By the close of the Permian, trilobites and a host of other marine groups became extinct.

Terrestrial biota



Edaphosaurus pogonias and *Platyhystrix* - Early Permian

Terrestrial life in the Permian included diverse plants, fungi, arthropods, and various types of tetrapods. The period saw a massive desert covering the interior of the Pangaea. The warm zone spread in the northern hemisphere, where extensive dry desert appeared. The rocks formed at that time were stained red by iron oxides, the result of intense heating by the sun of a surface devoid of vegetation cover. A number of older types of plants and animals died out or became marginal elements.

The Permian began with the Carboniferous flora still flourishing. About the middle of the Permian a major transition in vegetation began. The swamp-loving lycopod trees of the Carboniferous, such as *Lepidodendron* and *Sigillaria*, were progressively replaced in the continental interior by the more advanced seed ferns and early conifers. At the close of the Permian, lycopod and equicete swamps reminiscent of Carboniferous flora was relegated to a series of equatorial islands in the Paleotethys Sea that later would become the South China.

The Permian saw the radiation of many important conifer groups, including the ancestors of many present-day families. Rich forests were present in many areas, with a diverse mix of plant groups. The southern continent saw extensive seed fern forests of the *Glossopteris* flora. Oxygen levels were probably high there. The ginkgos and cycads also appeared during this period.

Insects of the Permian

By the Pennsylvanian and well into the Permian, by far the most successful were primitive relatives of cockroaches. Six fast legs, two well developed folding wings, fairly good eyes, long, well developed antennae (olfactory), an omnivorous digestive system, a receptacle for storing sperm, a chitin skeleton that could support and protect, as well as form of gizzard and efficient mouth parts, gave it formidable advantages over other herbivorous animals. About 90% of insects were cockroach-like insects ("Blattopterans").

The dragonflies *Odonata* were the dominant aerial predator and probably dominated terrestrial insect predation as well. True Odonata appeared in the Permian and all are amphibious. Their prototypes are the oldest winged fossils, go back to the Devonian, and are different from other wings in every way. Their prototypes may have had the beginnings of many modern attributes even by late Carboniferous and it is possible that they even captured small vertebrates, for some species had a wing span of 71 cm. A number of important new insect groups appeared at this time, including the Coleoptera (beetles) and Diptera (flies).

Reptile and amphibian fauna

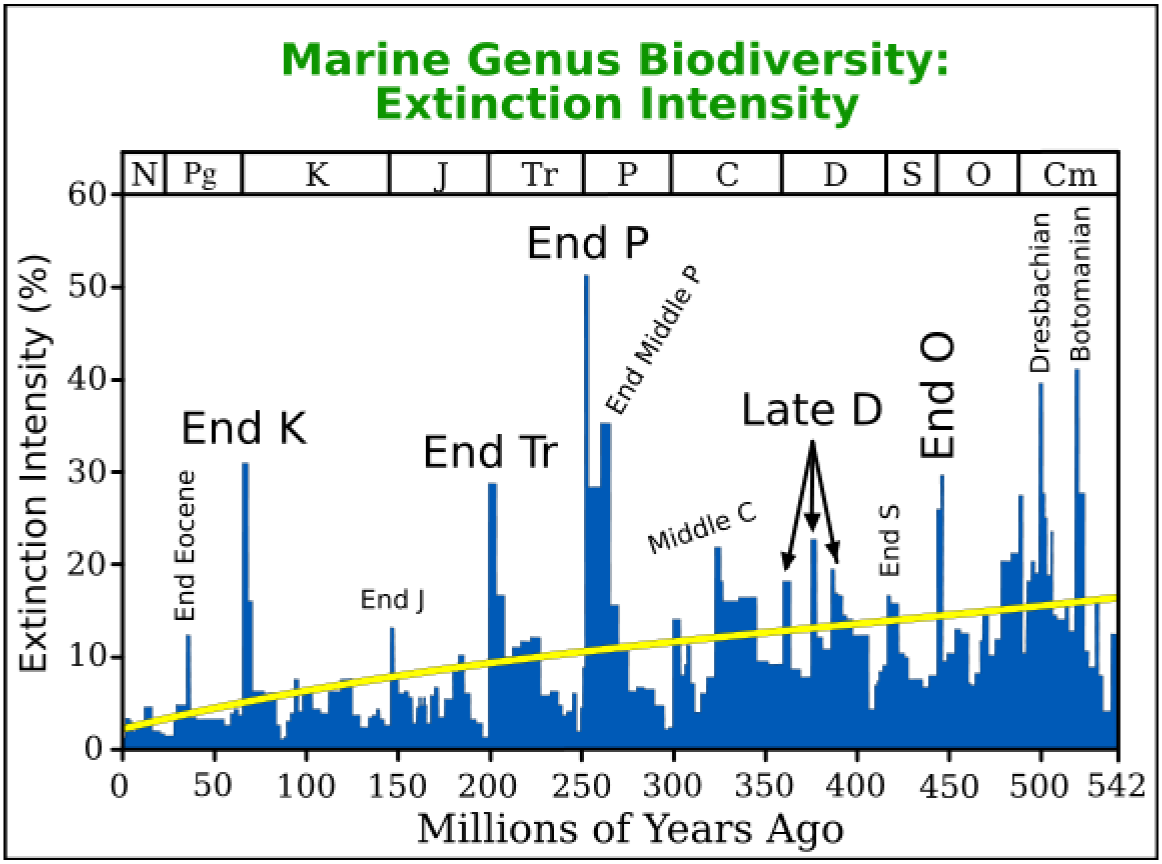
Early Permian terrestrial faunas were dominated by pelycosaurs and amphibians, the middle Permian by primitive therapsids such as the dinocephalia, and the late Permian by more advanced therapsids such as gorgonopsians and dicynodonts. Towards the very end of the Permian the first archosaurs appeared, a group that would give rise to the dinosaurs in the following period. Also appearing at the end of the Permian were the first cynodonts, which would go on to evolve into mammals during the Triassic. Another group of therapsids, the therocephalians (such as *Trochosaurus*), arose in the Middle Permian. There were no aerial vertebrates.

The Permian period saw the development of a fully terrestrial fauna and the appearance of the first large herbivores and carnivores. It was the high tide of the anapsides in the form of the massive Pareiasaurs and host of smaller, generally lizard-like groups. A group of small reptiles, the diapsids started to abound. These were the ancestors to most modern reptiles and the ruling dinosaurs as well as pterosaurs and crocodiles.

Thriving also, were the early ancestors to mammals, the synapsida, which included some large reptiles such as *Dimetrodon*. Reptiles grew to dominance among vertebrates, because their special adaptations enabled them to flourish in the drier climate.

Permian amphibians consisted of temnospondyli, lepospondyli and batrachosaurs.

Permian–Triassic extinction event



The Permian–Triassic extinction event, labeled "End P" here, is the most significant extinction event in this plot for marine genera which produce large numbers of fossils.

The Permian ended with the most extensive extinction event recorded in paleontology: the Permian-Triassic extinction event. 90% to 95% of marine species became extinct, as well as 70% of all land organisms. It is also the only known mass extinction of insects. On an individual level, perhaps as many as 99.5% of separate organisms died as a result of the event. Recovery from the Permian-Triassic extinction event was protracted; on land ecosystems took 30M years to recover.

There is also significant evidence that massive flood basalt eruptions from magma output lasting thousands of years in what is now the Siberian Traps contributed to environmental stress leading to mass extinction. The reduced coastal habitat and highly increased aridity probably also contributed. Based on the amount of lava estimated to have been produced during this period, the worst-case scenario is an expulsion of enough carbon dioxide from the eruptions to raise world temperatures five degrees Celsius.

Another hypothesis involves ocean venting of hydrogen sulfide gas. Portions of deep ocean will periodically lose all of their dissolved oxygen allowing bacteria that live without oxygen to flourish and produce hydrogen sulfide gas. If enough hydrogen sulfide accumulates in an anoxic zone, the gas can rise into the atmosphere.

Oxidizing gases in the atmosphere would destroy the toxic gas, but the hydrogen sulfide would soon consume all of the atmospheric gas available to change it. Hydrogen sulfide levels would increase dramatically over a few hundred years.

Modeling of such an event indicates that the gas would destroy ozone in the upper atmosphere allowing ultraviolet radiation to kill off species that had survived the toxic gas. Of course, there are species that can metabolize hydrogen sulfide.

Another hypothesis builds on the flood basalt eruption theory. Five degrees Celsius would not be enough increase in world temperatures to explain the death of 95% of life. But such warming could slowly raise ocean temperatures until frozen methane reservoirs below the ocean floor near coastlines (a current target for a new energy source) melted, expelling enough methane, among the most potent greenhouse gases, into the atmosphere to raise world temperatures an additional five degrees Celsius. The frozen methane hypothesis helps explain the increase in carbon-12 levels midway into the Permian-Triassic boundary layer. It also helps explain why the first phase of the layer's extinctions was land-based, the second was marine-based (and starting right after the increase in C-12 levels), and the third land-based again.

An even more speculative hypothesis is that intense radiation from a nearby supernova was responsible for the extinctions.

Trilobites, which had thrived since Cambrian times, finally became extinct before the end of the Permian.

Nautiluses, a species of cephalopods, surprisingly survived this occurrence.

In 2006, a group of American scientists from Ohio State University reported evidence for a possible huge meteorite crater (Wilkes Land crater) with a diameter of around 500 kilometers in Antarctica. The crater is located at a depth of 1.6 kilometers beneath the ice of Wilkes Land in eastern Antarctica. The scientists speculate that this impact may have caused the Permian–Triassic extinction event, although its age is bracketed only between 100 million and 500 million years ago. They also speculate that it may have contributed in some way to the separation of Australia from the Antarctic landmass, which were both part of a supercontinent called Gondwana. Levels of iridium and quartz fracturing in the Permian-Triassic layer do not approach those of the Cretaceous-Tertiary boundary layer. Given that a far greater proportion of species and individual organisms became extinct during the former, doubt is cast on the significance of a meteor impact in creating the latter. Further doubt has been cast on this theory based on fossils in Greenland showing the extinction to have been gradual, lasting about eighty thousand years, with three distinct phases.

Many scientists believe that the Permian-Triassic extinction event was caused by a combination of some or all of the hypotheses above and other factors; the formation of Pangaea decreased the number of coastal habitats and may have contributed to the extinction of many clades.

Chapter- 2

Permian–Triassic Extinction Event

The **Permian–Triassic (P–Tr) extinction event**, informally known as the **Great Dying**, was an extinction event that occurred 251.4 million years ago, forming the boundary between the Permian and Triassic geologic periods. It was the Earth's most severe extinction event, with up to 96% of all marine species and 70% of terrestrial vertebrate species becoming extinct It is the only known mass extinction of insects. Some 57% of all families and 83% of all genera were killed. Because so much biodiversity was lost, the recovery of life on Earth took significantly longer than after other extinction events. This event has been described as the "mother of all mass extinctions".

Researchers have variously suggested that there were from one to three distinct pulses, or phases, of extinction. There are several proposed mechanisms for the extinctions; the earlier phase was likely due to gradual environmental change, while the latter phase has been argued to be due to a catastrophic event. Suggested mechanisms for the latter include large or multiple bolide impact events, increased volcanism, and sudden release of methane clathrate from the sea floor; gradual changes include sea-level change, anoxia, increasing aridity, and a shift in ocean circulation driven by climate change.

Dating the extinction

Until about the year 2000 it was thought that rock sequences spanning the Permian-Triassic boundary were too few and contained too many gaps for scientists to estimate reliably when the extinction occurred, how long it took or whether it happened at the same time all over the world. However, a study of uranium/lead ratios of zircons from rock sequences near Meishan, Changxing, Zhejiang Province, China date the extinction to 251.4 ±0.03 Ma, with an ongoing elevated extinction rate occurring for some time thereafter. A large (-9‰), abrupt global change in the ratio of ^{13}C to ^{12}C, denoted $\delta^{13}C$, coincides with this extinction, and is sometimes used to identify the Permian-Triassic boundary in rocks that are unsuitable for radiometric dating.

It has been suggested that the Permian-Triassic boundary is associated with a sharp increase in the abundance of marine and terrestrial fungi, and that this was caused by the sharp increase in the amount of dead plants and animals fed upon by the fungi. For a while this "fungal spike" was used by some paleontologists to identify the Permian-Triassic boundary in rocks that are unsuitable for radiometric dating or lack suitable index fossils, but even the proposers of the fungal spike hypothesis pointed out that "fungal spikes" may have been a repeating phenomenon created by the post-extinction ecosystem in the earliest Triassic. More recently the very idea of a fungal spike has been criticized on several grounds, including that: *Reduviasporonites*, the most common supposed fungal spore, was actually a fossilized alga; the spike did not appear worldwide; and in many places it did not fall on the Permian-Triassic boundary. The algae, which were mis-identified as fungal spores, may even represent a transition to a lake-dominated Triassic world rather than an earliest Triassic zone of death and decay in some terrestrial fossil beds. However, newer chemical evidence agrees better with a fungal origin for *Reduviasporonites*, diluting these critiques.

Uncertainty exists regarding the duration of the overall extinction and about the timing and duration of various groups' extinctions within the greater process. Some evidence suggests that there were multiple extinction pulses or that the extinction was spread out over a few million years, with a very sharp peak in the last 1 million years of the Permian. Statistical analyses of some highly fossiliferous strata in Meishan, South China suggest that the main extinction was clustered around one peak. Recent research shows that different groups became extinct at different times; for example, while difficult to date absolutely, ostracod and brachiopod extinctions were separated by between 0.72 and 1.22 million years. In a well preserved sequence in east Greenland, the decline of animals is concentrated in a period 10 to 60 thousand years long, with plants taking several hundred thousand further years to show the full impact of the event. An older theory, still supported in some recent papers, is that there were two to three major extinction pulses 5 million years apart, separated by a period of extinctions well above the background level; and that the final extinction killed off only about 80% of marine species alive at that time while the other losses occurred during the first pulse or the interval between pulses. According to this theory one of these extinction pulses occurred at the end of the Guadalupian epoch of the Permian. For example, all but one of the surviving dinocephalian genera died out at the end of the Guadalupian, as did the Verbeekinidae, a family of large-size fusuline foraminifera. The impact of the end-Guadalupian extinction on marine organisms appears to have varied between locations and between taxonomic groups - brachiopods and corals had severe losses.

Extinction patterns

Marine extinctions	Genera extinct	Notes
Marine invertebrates		
Foraminifera	97%	Fusulinids died out, but were almost extinct before the catastrophe
Radiolaria (plankton)	99%	
Anthozoa (sea anemones, corals,	96%	Tabulate and rugose corals died out

etc.)		
Bryozoans	79%	Fenestrates, trepostomes, and cryptostomes died out
Brachiopods	96%	Orthids and productids died out
Bivalves	59%	
Gastropods (snails)	98%	
Ammonites (cephalopods)	97%	
Crinoids (echinoderms)	98%	Inadunates and camerates died out
Blastoids (echinoderms)	**100%**	May have become extinct shortly before the P–Tr boundary
Trilobites	**100%**	In decline since the Devonian; only 2 genera living before the extinction
Eurypterids ("sea scorpions")	**100%**	May have become extinct shortly before the P–Tr boundary
Ostracods (small crustaceans)	59%	
Fish		
Acanthodians	**100%**	In decline since the Devonian, with only one living family

Marine organisms

Marine invertebrates suffered the greatest losses during the P–Tr extinction. In the intensively-sampled south China sections at the P-Tr boundary, for instance, 280 out of 329 marine invertebrate genera disappear within the final 2 sedimentary zones containing conodonts from the Permian.

Statistical analysis of marine losses at the end of the Permian suggests that the decrease in diversity was caused by a sharp increase in extinctions instead of a decrease in speciation. The extinction primarily affected organisms with calcium carbonate skeletons, especially those reliant on ambient CO_2 levels to produce their skeletons.

Among benthic organisms, the extinction event multiplied background extinction rates, and therefore caused most damage to taxa that had a high background extinction rate (by implication, taxa with a high turnover). The extinction rate of marine organisms was catastrophic.

Surviving marine invertebrate groups include: articulate brachiopods (those with a hinge), which have suffered a slow decline in numbers since the P–Tr extinction; the Ceratitida order of ammonites; and crinoids ("sea lilies"), which very nearly became extinct but later became abundant and diverse.

The groups with the highest survival rates generally had active control of circulation, elaborate gas exchange mechanisms, and light calcification; more heavily calcified organisms with simpler breathing apparatus were the worst hit. In the case of the brachiopods at least, surviving taxa were generally small, rare members of a diverse community.

The ammonoids, which had been in a long-term decline for the 30 million years since the Roadian (middle Permian), suffered a selective end-Guadalupian extinction pulse. This extinction greatly reduced disparity, and suggests that environmental factors were responsible for this extinction. Diversity and disparity fell further until the P-Tr boundary; the extinction here was non-selective, consistent with a catastrophic initiator. During the Triassic, diversity rose rapidly, but disparity remained low.

The range of morphospace occupied by the ammonoids became more restricted as the Permian progressed. Just a few million years into the Triassic, the original morphospace range was once again occupied, but shared differently between clades.

Terrestrial invertebrates

The Permian had great diversity in insect and other invertebrate species, including the largest insects ever to have existed. The end-Permian is the only known mass extinction of insects, with eight or nine insect orders becoming extinct and ten more greatly reduced in diversity. Palaeodictyopteroids (insects with piercing and sucking mouthparts) began to decline during the mid-Permian; these extinctions have been linked to a change in flora. The greatest decline, however, occurred in the Late Permian and were probably not directly caused by weather-related floral transitions.

Most fossil insect groups found after the Permian–Triassic boundary differ significantly from those that lived prior to the P–Tr extinction. With the exception of the Glosselytrodea, Miomoptera, and Protorthoptera, Paleozoic insect groups have not been discovered in deposits dating to after the P–Tr boundary. The caloneurodeans, monurans, paleodictyopteroids, protelytropterans, and protodonates became extinct by the end of the Permian. In well-documented Late Triassic deposits, fossils overwhelmingly consist of modern fossil insect groups.

Terrestrial plants

Plant ecosystem response

The geological record of terrestrial plants is sparse, and based mostly on pollen and spore studies. Interestingly, plants are relatively immune to mass extinction, with the impact of all the major mass extinctions "negligible" at a family level. Even the reduction observed in species diversity (of 50%) may be mostly due to taphonomic processes. However, a massive rearrangement of ecosystems does occur, with plant abundances and distributions changing profoundly.

At the P–Tr boundary, the dominant floral groups changed, with many groups of land plants entering abrupt decline, such as *Cordaites* (gymnosperms) and *Glossopteris* (seed ferns). Dominant gymnosperm genera were replaced post-boundary by lycophytes - extant lycophytes are recolonizers of disturbed areas.

Palynological or pollen studies from East Greenland of sedimentary rock strata laid down during the extinction period indicate dense gymnosperm woodlands before the event. At the same time that marine invertebrate macrofauna are in decline these large woodlands die out and are followed by a rise in diversity of smaller herbaceous plants including Lycopodiophyta, both *Selaginellales* and *Isoetales*. Later on other groups of gymnosperms again become dominant but again suffer major die offs; these cyclical flora shifts occur a few times over the course of the extinction period and afterwards. These fluctuations of the dominant flora between woody and herbaceous taxa indicate chronic environmental stress resulting in a loss of most large woodland plant species. The successions and extinctions of plant communities do not coincide with the shift in $\delta^{13}C$ values, but occurs many years after. The recovery of gymnosperm forests took 4-5 million years.

Coal gap

No coal deposits are known from the Early Triassic, and those in the Middle Triassic are thin and low-grade. This "coal gap" has been explained in many ways. It has been suggested that new, more aggressive fungi, insects and vertebrates evolved, and killed vast numbers of trees. However these decomposers themselves suffered heavy losses of species during the extinction, and are not considered a likely cause of the coal gap. It could simply be that all coal forming plants were rendered extinct by the P/Tr extinction, and that it took 10 million years for a new suite of plants to adapt to the moist, acid conditions of peat bogs. On the other hand, abiotic factors (not caused by organisms), such as decreased rainfall or increased input of clastic sediments, may also be to blame. Finally, it is also true that there are very few sediments of any type known from the Early Triassic, and the lack of coal may simply reflect this scarcity. This opens the possibility that coal-producing ecosystems may have responded to the changed conditions by relocating, perhaps to areas where we have no sedimentary record for the Early Triassic. For example in eastern Australia a cold climate had been the norm for a long period of time, with a peat mire ecosystem specialising to these conditions. Approximately 95% of these peat-producing plants went *locally* extinct at the P-Tr boundary; Interestingly, coal deposits in Australia and Antarctica disappear significantly *before* the P-Tr boundary.

Terrestrial vertebrates

Even the groups that survived suffered extremely heavy losses of species, and some terrestrial vertebrate groups very nearly became extinct at the end-Permian. Some of the surviving groups did not persist for long past this period, while others that barely survived went on to produce diverse and long-lasting lineages. There is enough evidence to indicate that over two-thirds of terrestrial amphibian, sauropsid ("reptile") and therapsid ("mammal-like reptile") families became extinct. Large herbivores suffered the heaviest losses. All Permian anapsid reptiles died out except the procolophonids (testudines have anapsid skulls but are most often thought to have evolved later, from diapsid ancestors). Pelycosaurs died out before the end of the Permian. Too few Permian diapsid fossils have been found to support any conclusion about the effect of the Permian extinction on diapsids (the "reptile" group from which lizards, snakes, crocodilians, dinosaurs, and birds evolved).

Possible explanations of these patterns

The most vulnerable marine organisms were those that produced calcareous hard parts (i.e., from calcium carbonate) and had low metabolic rates and weak respiratory systems—notably calcareous sponges, rugose and tabulate corals, calciate brachiopods, bryozoans, and echinoderms; about 81% of such genera became extinct. Close relatives without calcareous hard parts suffered only minor losses, for example sea anemones, from which modern corals evolved. Animals with high metabolic rates, well-developed respiratory systems, and non-calcareous hard parts had negligible losses - except for conodonts, in which 33% of genera died out.

This pattern is consistent with what is known about the effects of hypoxia, a shortage but not a total absence of oxygen. However, hypoxia cannot have been the only killing mechanism for marine organisms. Nearly all of the continental shelf waters would have had to become severely hypoxic to account for the magnitude of the extinction, but such a catastrophe would make it difficult to explain the very selective pattern of the extinction. Models of the Late Permian and Early Triassic atmospheres show a significant but protracted decline in atmospheric oxygen levels, with no acceleration near the P-Tr boundary. Minimum atmospheric oxygen levels in the Early Triassic are never less than present day levels - the decline in oxygen levels does not match the temporal pattern of the extinction.

The observed pattern of marine extinctions is also consistent with hypercapnia (excessive levels of carbon dioxide). Carbon dioxide (CO_2) is actively toxic at above-normal concentrations, as it reduces the ability of respiratory pigments to oxygenate tissues, and makes body fluids more acidic, thereby hampering the production of carbonate hard parts like shells. At high concentrations, carbon dioxide causes narcosis (intoxication). In addition to these direct effects, CO_2 reduces the concentration of carbonates in water by "crowding them out," which further increases the difficulty of producing carbonate hard parts.

Marine organisms are more sensitive to changes in CO_2 levels than are terrestrial organisms for a variety of reasons. CO_2 is 28 times more soluble in water than is oxygen. Marine animals normally function with lower concentrations of CO_2 in their bodies than land animals, as the removal of CO_2 in air-breathing animals is impeded by the need for the gas to pass through the respiratory systems membranes (lungs, tracheae, and the like). In marine organisms, relatively modest but sustained increases in CO_2 concentrations hamper the synthesis of proteins, reduce fertilization rates, and produce deformities in calcareous hard parts. In addition, an increase in CO_2 concentration leads to ocean acidification, consistent with the preferential extinction of heavily calcified taxa and signals in the rock record that suggest a more acidic ocean.

It is difficult to analyze extinction and survival rates of land organisms in detail, because there are few terrestrial fossil beds that span across the Permian-Triassic boundary. Triassic insects are very different from those of the Permian, but there is a gap in the insect fossil record spanning approximately 15M years from the late Permian to early Triassic. The best known record of vertebrate changes across the Permian-Triassic boundary occurs in the Karoo Supergroup of South Africa, but statistical analyses have so far not produced clear conclusions.

Biotic recovery

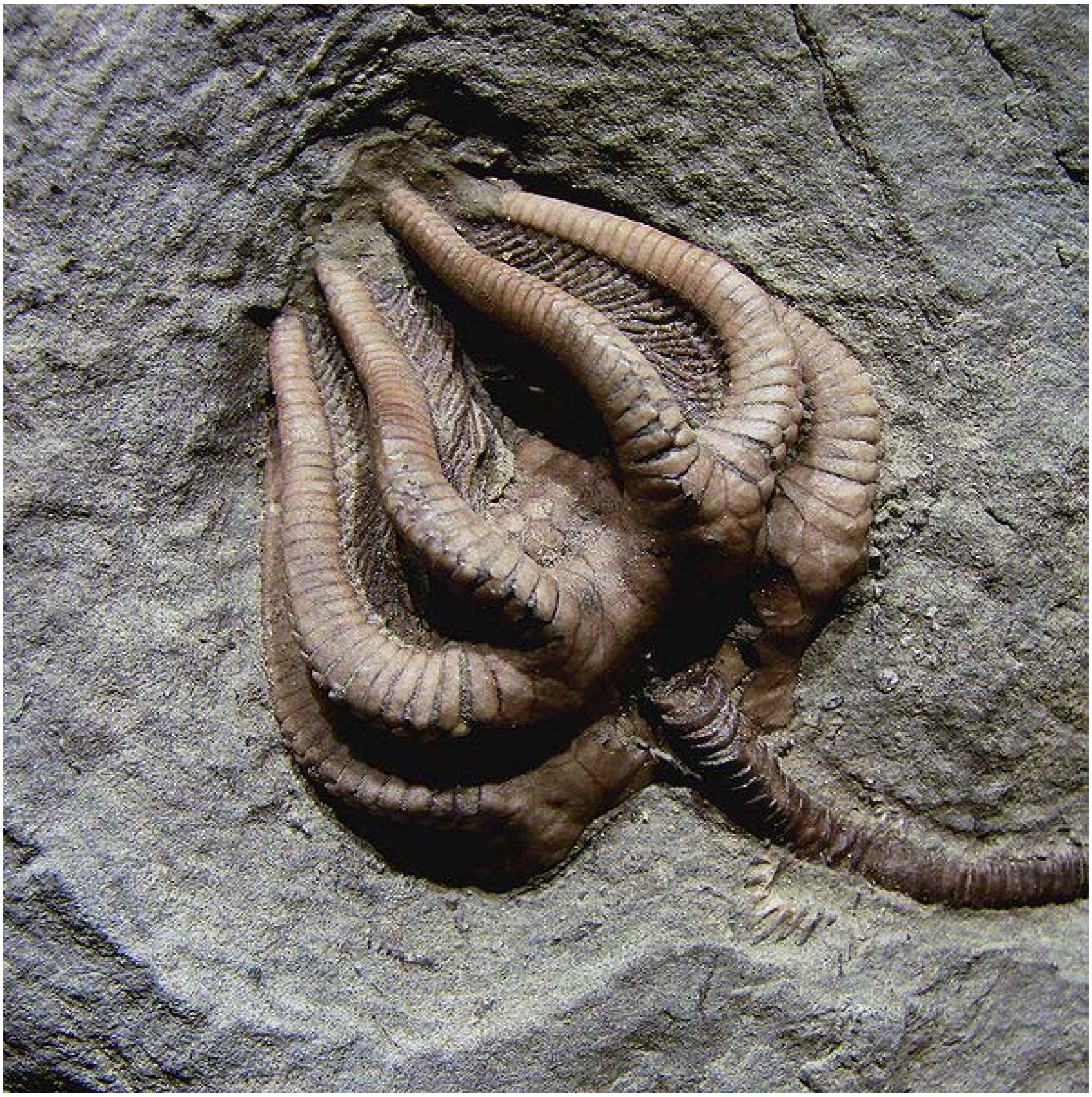
Earlier analyses indicated that life on Earth recovered quickly after the Permian extinctions, but this was mostly in the form of disaster taxa, such as the hardy *Lystrosaurus*. The most recent research indicates that the specialized animals that formed complex ecosystems, with high biodiversity, complex food webs and a variety of niches, took much longer to recover. It is thought that this long recovery was due to the successive waves of extinction, which inhibited recovery, and prolonged environmental stress to organisms, which continued into the Early Triassic. Recent research indicates that recovery did not begin until the start of the mid-Triassic, 4 million to 6 million years after the extinction; and some writers estimate that the recovery was not complete until 30M years after the P-Tr extinction, i.e. in the late Triassic.

A braided river - the Waimakariri River in the South Island of New Zealand.

During the early Triassic (4-6M years after the P-Tr extinction), the plant biomass was insufficient to form coal deposits, which implies a limited food mass for herbivores. River patterns in the Karoo changed from meandering to braided, indicating that vegetation there was very sparse for a long time.

Each major segment of the early Triassic ecosystem — plant and animal, marine and terrestrial — was dominated by a small number of genera, which appeared virtually worldwide, for example: the herbivorous therapsid *Lystrosaurus* (which accounted for about 90% of early Triassic land vertebrates) and the bivalves *Claraia*, *Eumorphotis*, *Unionites* and *Promylina*. A healthy ecosystem has a much larger number of genera, each living in a few preferred types of habitat.

Disaster taxa (opportunist organisms) took advantage of the devastated ecosystem and enjoyed a temporary population boom and increase in their territory. For example: *Lingula* (a brachiopod); stromatolites, which had been confined to marginal environments since the Ordovician; *Pleuromeia* (a small, weedy plant); *Dicroidium* (a seed fern).



Sessile filter feeders like this Crinoid were significantly less abundant after the P-Tr extinction.

Changes in marine ecosystems

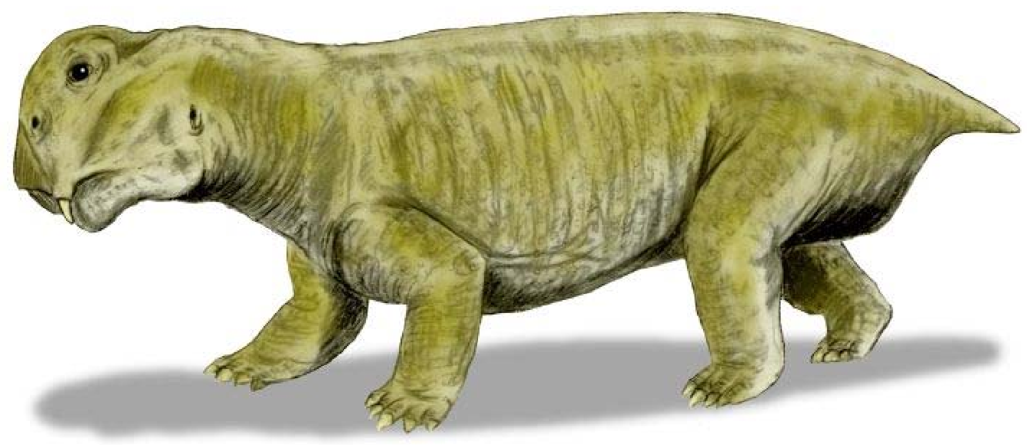
Prior to the extinction, approximately 67% of marine animals were sessile and attached to the sea floor, but during the Mesozoic only about half of the marine animals were sessile while the rest were free living. Analysis of marine fossils from the period indicated a decrease in the abundance of sessile epifaunal suspension feeders, such as brachiopods and sea lilies, and an increase in more complex mobile species such as snails, urchins and crabs.

Before the Permian mass extinction event, both complex and simple marine ecosystems were equally common; after the recovery from the mass extinction, the complex communities outnumbered the simple communities by nearly three to one, and the increase in predation pressure led to the Mesozoic Marine Revolution.

Bivalves were fairly rare before the P–Tr extinction but became numerous and diverse in the Triassic and one group, the rudist clams, became the Mesozoic's main reef-builders. Some researchers think much of this change happened in the 5 million years between the two major extinction pulses.

Crinoids ("sea lilies") suffered a selective extinction, resulting in a decrease in the variety of their forms. Their ensuing adaptive radiation was brisk, and resulted in forms possessing flexible arms becoming widespread; motility, predominantly a response to predation pressure, also became far more prevalent.

Land vertebrates



Lystrosaurus was by far the most abundant early Triassic land vertebrate.

Lystrosaurus, a pig-sized herbivorous dicynodont therapsid, constituted as much as 90% of some earliest Triassic land vertebrate faunas. Smaller carnivorous cynodont therapsids also survived, including the ancestors of mammals. In the Karoo region of southern Africa the therocephalians *Tetracynodon*, *Moschorhinus* and *Ictidosuchoides* survived but do not appear to have been abundant in the Triassic.

Archosaurs (which included the ancestors of dinosaurs and crocodilians) were initially rarer than therapsids, but they began to displace therapsids in the mid-Triassic. In the mid to late Triassic the dinosaurs evolved from one group of archosaurs, and went on to dominate terrestrial ecosystems for the rest of the Mesozoic. This "Triassic Takeover" may have contributed to the evolution of mammals by forcing the surviving therapsids and their mammaliform successors to live as small, mainly nocturnal insectivores;

nocturnal life probably forced at least the mammaliforms to develop fur and higher metabolic rates.

Some temnospondyl amphibians made a relatively quick recovery, in spite of nearly becoming extinct. *Mastodonsaurus* and trematosaurians were the main aquatic and semi-aquatic predators during most of the Triassic, some preying on tetrapods and others on fish.

Land vertebrates took an unusually long time to recover from the P-Tr extinction; writer M. J. Benton estimates that the recovery was not complete until 30 million years after the extinction, i.e. not until the Late Triassic, in which dinosaurs, pterosaurs, crocodiles, archosaurs, amphibians and mammaliforms were abundant and diverse.

Causes of extinction event

There are several proposed mechanisms for the extinction event, including both catastrophic and gradualistic processes (similar to those theorized for the Cretaceous–Tertiary extinction event). The former include large or multiple bolide impact events, increased volcanism, or sudden release of methane hydrates from the sea floor. The latter include sea-level change, anoxia, and increasing aridity. Any hypothesis about the cause must explain the selectivity of the event, which primarily affected organisms with calcium carbonate skeletons; the long (4-6 million year) period before recovery started; and the minimal extent of biological mineralization (despite inorganic carbonates being deposited) once the recovery began.

Impact event

Artist's impression of a major impact event. A collision between Earth and an asteroid a few kilometers in diameter would release as much energy as several million nuclear weapons detonating.

Evidence that an impact event may have caused the Cretaceous–Tertiary extinction event has led to speculation that similar impacts may have been the cause of other extinction events, including the P–Tr extinction, and therefore to a search for evidence of impacts at the times of other extinctions and for large impact craters of the appropriate age.

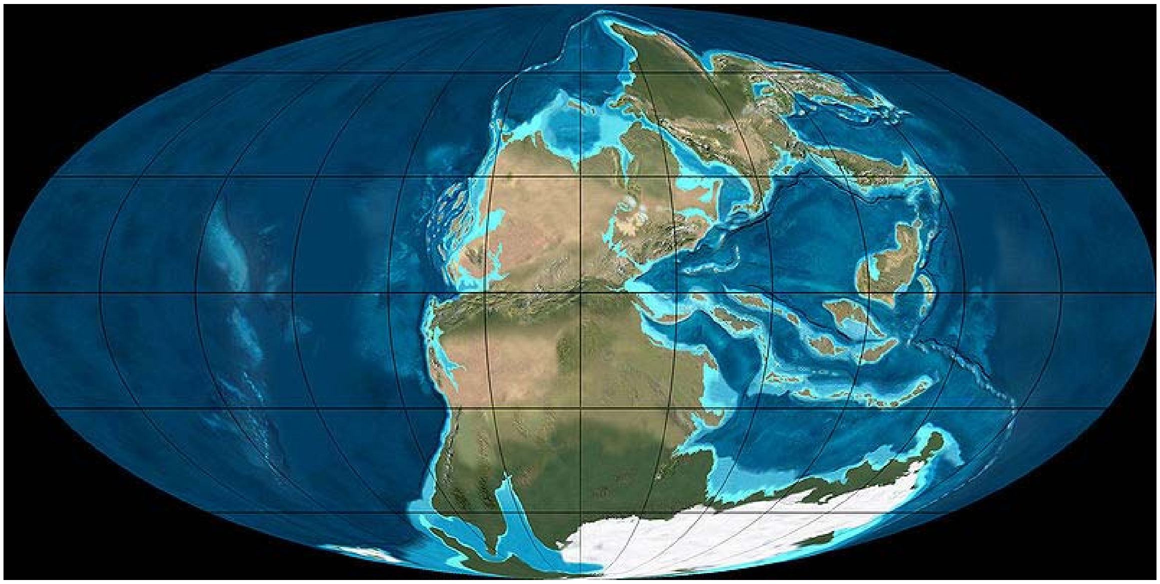
Reported evidence for an impact event from the P–Tr boundary level includes rare grains of shocked quartz in Australia and Antarctica; fullerenes trapping extraterrestrial noble gases; meteorite fragments in Antarctica; and grains rich in iron, nickel and silicon, which may have been created by an impact. However, the accuracy of most of these claims has been challenged. Quartz from Graphite Peak in Antarctica, for example, once considered "shocked," has recently been reexamined by optical and transmission electron microscopy. It was concluded that the observed features were not due to shock, but rather to plastic deformation, consistent with formation in a tectonic environment such as volcanism.

Several possible impact craters have been proposed as possible causes of the P–Tr extinction, including the Bedout structure off the northwest coast of Australia and the hypothesized Wilkes Land crater of East Antarctica. In each of these cases the idea that an impact was responsible has not been proven, and some have been widely criticized. In the case of Wilkes Land, the age of this sub-ice geophysical feature is very uncertain – it may be later than the Permian–Triassic extinction.

If impact is a major cause of the P–Tr extinction, it is likely that the crater would no longer exist. As 70% of the Earth's surface is sea, an asteroid or comet fragment is more than twice as likely to hit ocean as it is to hit land. However, Earth has no ocean-floor crust more than 200 million years old, because the "conveyor belt" process of sea-floor spreading and subduction destroys it within that time. It has also been speculated that craters produced by very large impacts may be masked by extensive lava flooding from below after the crust is punctured or weakened.

One attraction of large impact theories is that theoretically they could trigger other cause-considered extinction-paralleling phenomena, such as the Siberian Traps eruptions (see below) as being either an impact site or the antipode of an impact site. Subduction should not be taken as an excuse that no firm evidence can be found; much like the K-T event, an ejecta blanket stratum rich in siderophilic elements (e.g., iridium) would be found in a great many formations from the time. The abruptness of an impact also explains why species did not rapidly evolve in adaptation to more slowly-manifesting and/or less than global-in-scope phenomena.

Volcanism



The world around the time of the P-Tr extinction. The Siberian Traps eruptions occurred on the eastern shore of the shallow sea (paler blue) at the north of the map. The earlier Emeishan eruptions occurred on the north edge of the almost enclosed shallow sea just north of the equator - at this time the blocks that currently form China and South-East Asia were just emerging.

The final stages of the Permian saw two flood basalt events. A small one, Emeishan Traps in China, occurred at the same time as the end-Guadalupian extinction pulse, in an area close to the equator at the time. The flood basalt eruptions that produced the Siberian Traps constituted one of the largest known volcanic events on Earth and covered over 2,000,000 square kilometers (772,204.3 sq mi) with lava. The Siberian Traps eruptions were formerly thought to have lasted for millions of years, but recent research dates them to 251.2 ± 0.3 Ma — immediately before the end of the Permian.

The Emeishan and Siberian Traps eruptions may have caused dust clouds and acid aerosols—which would have blocked out sunlight and thus disrupted photosynthesis both on land and in the photic zone of the ocean, causing food chains to collapse. These eruptions may also have caused acid rain when the aerosols washed out of the atmosphere. This may have killed land plants and molluscs and planktonic organisms which had calcium carbonate shells. The eruptions would also have emitted carbon dioxide, causing global warming. When all of the dust clouds and aerosols washed out of the atmosphere, the excess carbon dioxide would have remained and the warming would have proceeded without any mitigating effects.

The Siberian Traps had unusual features that made them even more dangerous. Pure flood basalts produce a lot of runny lava and do not hurl debris into the atmosphere. It appears, however, that 20% of the output of the Siberian Traps eruptions was pyroclastic, i.e. consisted of ash and other debris thrown high into the atmosphere, increasing the short-term cooling effect. The basalt lava erupted or intruded into carbonate rocks and into sediments that were in the process of forming large coal beds, both of which would have emitted large amounts of carbon dioxide, leading to stronger global warming after the dust and aerosols settled.

There is doubt, however, about whether these eruptions were enough on their own to cause a mass extinction as severe as the end-Permian. Equatorial eruptions are necessary to produce sufficient dust and aerosols to affect life worldwide, whereas the much larger Siberian Traps eruptions were inside or near the Arctic Circle. Furthermore, if the Siberian Traps eruptions occurred within a period of 200,000 years, the atmosphere's carbon dioxide content would have doubled. Recent climate models suggest that such a rise in CO_2 would have raised global temperatures by 1.5 °C (2.7 °F) to 4.5 °C (8.1 °F), which is unlikely to cause a catastrophe as great as the P-Tr extinction.

Methane hydrate gasification

Scientists have found worldwide evidence of a swift decrease of about 10 ‰ (parts per thousand) in the $^{13}C/^{12}C$ isotope ratio in carbonate rocks from the end-Permian ($\delta^{13}C_{carbonate}$ of -10 ‰). This is the first, largest and most rapid of a series of negative and positive excursions (decreases and increases in $^{13}C/^{12}C$ ratio) that continues until the isotope ratio abruptly stabilises in the middle Triassic, followed soon afterwards by the recovery of calcifying life forms (organisms that use calcium carbonate to build hard parts such as shells).

A variety of factors may have contributed to this drop in the $^{13}C/^{12}C$ ratio, but most turn out to be insufficient to account fully for it:

- Gases from volcanic eruptions have a $^{13}C/^{12}C$ ratio about 5 to 8 ‰ below standard ($\delta^{13}C$ about -5 to -8 ‰). But the amount required to produce a reduction of about 10 ‰ worldwide requires eruptions greater by orders of magnitude than any for which evidence has been found.
- A reduction in organic activity would extract ^{12}C more slowly from the environment and leave more of it to be incorporated into sediments, thus reducing the $^{13}C/^{12}C$ ratio. Biochemical processes use the lighter isotopes, since chemical reactions are ultimately driven by electromagnetic forces between atoms and lighter isotopes respond more quickly to these forces. But a study of a smaller drop of 3 to 4 ‰ in $^{13}C/^{12}C$ ($\delta^{13}C$ -3 to -4 ‰) at the Paleocene-Eocene Thermal Maximum (PETM) concluded that even transferring all the organic carbon (in organisms, soils, and dissolved in the ocean) into sediments would be insufficient: even such a large burial of material rich in ^{12}C would not have produced the *smaller* drop in the $^{13}C/^{12}C$ ratio of the rocks around the PETM.
- Buried sedimentary organic matter has a $^{13}C/^{12}C$ ratio 20 to 25 ‰ below normal ($\delta^{13}C$ -20 to -25 ‰). Theoretically, if the sea level fell sharply, shallow marine sediments would be exposed to oxidization. But 6,500-8,400 gigatons (1 gigaton = 10^9 metric tons) of organic carbon would have to be oxidized and returned to the ocean-atmosphere system within less than a few hundred thousand years to reduce the $^{13}C/^{12}C$ ratio by 10 ‰. This is not thought to be a realistic possibility.
- Rather than a sudden decline in sea level, intermittent periods of ocean-bottom hyperoxia and anoxia (high-oxygen and low- / zero-oxygen conditions) may have caused the $^{13}C/^{12}C$ ratio fluctuations in the Early Triassic; and global anoxia may have been responsible for the end-Permian blip. The continents of the end-Permian and early Triassic were more clustered in the tropics than they are now (see map above), and large tropical rivers would have dumped sediment into smaller, partially enclosed ocean basins in low latitudes. Such conditions favor oxic and anoxic episodes; oxic / anoxic conditions would result in a rapid release / burial respectively of large amounts of organic carbon, which has a low $^{13}C/^{12}C$ ratio because biochemical processes use the lighter isotopes. This, or another organic-based reason, may have been responsible for both this and a late Proterozoic/Cambrian pattern of fluctuating $^{13}C/^{12}C$ ratios.

Other hypotheses include mass oceanic poisoning releasing vast amounts of CO_2 and a long-term reorganisation of the global carbon cycle.

However, only one sufficiently powerful cause has been proposed for the *global* 10 ‰ reduction in the $^{13}C/^{12}C$ ratio: the release of methane from methane clathrates; and carbon-cycle models confirm that it would have been sufficient to produce the observed reduction. Methane clathrates, also known as methane hydrates, consist of methane molecules trapped in cages of water molecules. The methane is produced by methanogens (microscopic single-celled organisms) and has a $^{13}C/^{12}C$ ratio about 60 ‰ below normal ($\delta^{13}C$ -60 ‰). At the right combination of pressure and temperature it gets trapped in clathrates fairly close to the surface of permafrost and in much larger quantities at continental margins (continental shelves and the deeper seabed close to them). Oceanic methane hydrates are usually found buried in sediments where the seawater is at least 300 meters (984 ft) deep. They can be found up to about 2,000 meters (6,562 ft) below the sea floor, but usually only about 1,100 meters (3,609 ft) below the sea floor.

The area covered by lava from the Siberian Traps eruptions is about twice as large as was originally thought, and most of the additional area was shallow sea at the time. It is very likely that the seabed contained methane hydrate deposits and that the lava caused the deposits to dissociate, releasing vast quantities of methane.

One would expect a vast release of methane to cause significant global warming, since methane is a very powerful greenhouse gas. There is strong evidence that global temperatures increased by about 6 °C (10.8 °F) near the equator and therefore by more at higher latitudes: a sharp decrease in oxygen isotope ratios ($^{18}O/^{16}O$); the extinction of *Glossopteris* flora (*Glossopteris* and plants that grew in the same areas), which needed a cold climate, and its replacement by floras typical of lower paleolatitudes.

However, the pattern of isotope shifts expected to result from a massive release of methane do not match the patterns seen throughout the early Triassic. Not only would a methane cause require the release of five times as much methane as postulated for the PETM, but it would also have to be re-buried at an unrealistically high rate to account for the rapid increases in the $^{13}C/^{12}C$ ratio (episodes of high positive $\delta^{13}C$) throughout the early Triassic, before being released again several times.

Sea level fluctuations

Marine regression occurs when areas of submerged seafloor are exposed above sea level. This lowering of sea level causes a reduction in shallow marine habitats, leading to biotic turnover. Shallow marine habitats are productive areas for organisms at the bottom of the food chain, their loss increasing competition for food sources. There is some correlation between incidents of pronounced sea level regression and mass extinctions, but other evidence indicates there is no relationship and that regression may itself create new habitats. It has also been suggested that sea-level changes result in changes in sediment deposition rates and effects water temperature and salinity, resulting in a decline in marine diversity.

Anoxia

There is evidence that the oceans became anoxic (severely deficient in oxygen) towards the end of the Permian. There was a noticeable and rapid onset of anoxic deposition in marine sediments around East Greenland near the end of the Permian. The uranium/thorium ratios of several late Permian sediments indicate that the oceans were severely anoxic around the time of the extinction.

This would have been devastating for marine life, producing widespread die-offs except for anaerobic bacteria inhabiting the sea-bottom mud. There is also evidence that anoxic events can cause catastrophic hydrogen sulfide emissions from the sea floor (see below).

The sequence of events leading to anoxic oceans might have involved a period of global warming that reduced the temperature gradient between the equator and the poles, which slowed or even stopped the thermohaline circulation. The slow-down or stoppage of the thermohaline circulation could have reduced the mixing of oxygen in the ocean.

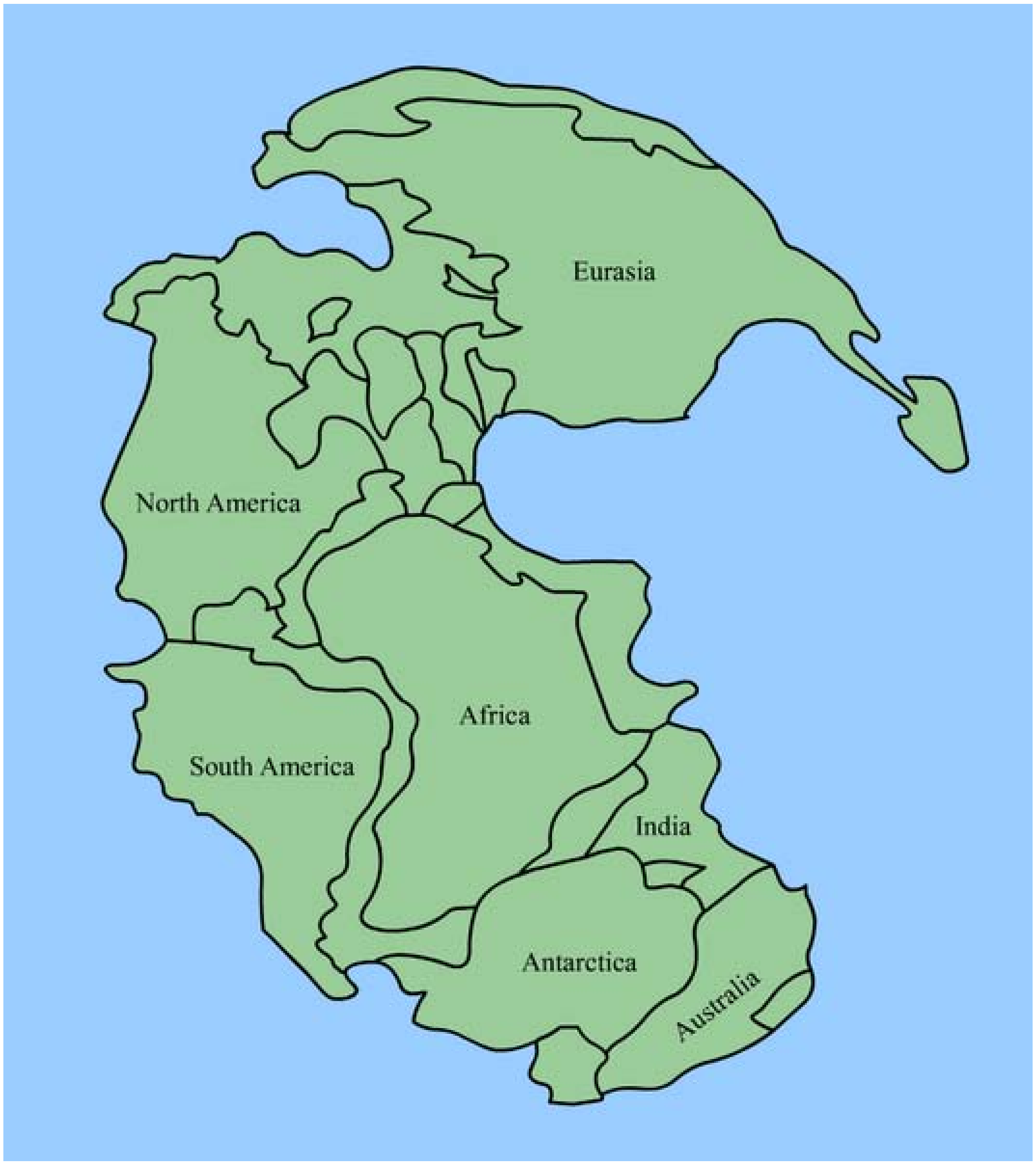
However, one research article suggests that the types of oceanic thermohaline circulation that may have existed at the end of the Permian are not likely to have supported deep-sea anoxia.

Hydrogen sulfide emissions

A severe anoxic event at the end of the Permian could have made sulfate-reducing bacteria the dominant force in oceanic ecosystems, causing vast emissions of hydrogen sulfide that poisoned plant and animal life on both land and sea, as well as severely weakening the ozone layer, exposing much of the life that remained to fatal levels of UV radiation. Indeed, anaerobic photosynthesis by Chlorobiaceae (green sulfur bacteria), and its accompanying hydrogen sulfide emissions, occurred from the end-Permian into the early Triassic. The fact that this anaerobic photosynthesis persisted into the early Triassic is consistent with fossil evidence that the recovery from the Permian–Triassic extinction was remarkably slow.

This theory has the advantage of explaining the mass extinction of plants, which ought otherwise to have thrived in an atmosphere with a high level of carbon dioxide. Fossil spores from the end-Permian further support the theory: many show deformities that could have been caused by ultraviolet radiation, which would have been more intense after hydrogen sulfide emissions weakened the ozone layer.

The supercontinent Pangaea



Map of Pangaea showing where today's continents were at the Permian–Triassic boundary

About half way through the Permian (in the Kungurian age of the Permian's Cisuralian epoch) all the continents joined to form the supercontinent Pangaea, surrounded by the superocean Panthalassa, although blocks that are now parts of Asia did not join the supercontinent until very late in the Permian. This configuration severely decreased the extent of shallow aquatic environments, the most productive part of the seas, and exposed formerly isolated organisms of the rich continental shelves to competition from invaders. Pangaea's formation would also have altered both oceanic circulation and atmospheric weather patterns, creating seasonal monsoons near the coasts and an arid climate in the vast continental interior.

Marine life suffered very high but not catastrophic rates of extinction after the formation of Pangaea almost as high as in some of the "Big Five" mass extinctions. The formation of Pangaea seems not to have caused a significant rise in extinction levels on land, and in fact most of the advance of the therapsids and increase in their diversity seems to have occurred in the late Permian, after Pangaea was almost complete. So it seems likely that Pangaea initiated a long period of increased marine extinctions but was not directly responsible for the "Great Dying" and the end of the Permian.

Combination of causes

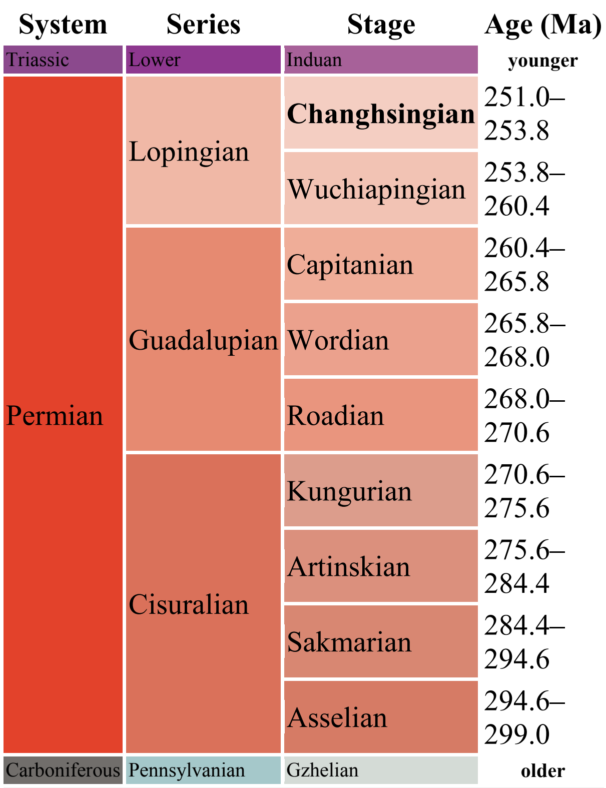
Possible causes supported by strong evidence appear to describe a sequence of catastrophes, each one worse than the previous: the Siberian Traps eruptions were bad enough in their own right, but because they occurred near coal beds and the continental shelf, they also triggered very large releases of carbon dioxide and methane. The resultant global warming may have caused perhaps the most severe anoxic event in the oceans' history: according to this theory, the oceans became so anoxic that anaerobic sulfur-reducing organisms dominated the chemistry of the oceans and caused massive emissions of toxic hydrogen sulfide.

However, there may be some weak links in this chain of events: the changes in the $^{13}C/^{12}C$ ratio expected to result from a massive release of methane do not match the patterns seen throughout the early Triassic; and the types of oceanic thermohaline circulation, which may have existed at the end of the Permian are not likely to have supported deep-sea anoxia.

Chapter- 3

Subdivisions of the Permian

Changhsingian



System	Series	Stage	Age (Ma)
Triassic	Lower	Induan	younger
Permian	Lopingian	**Changhsingian**	251.0–253.8
		Wuchiapingian	253.8–260.4
	Guadalupian	Capitanian	260.4–265.8
		Wordian	265.8–268.0
		Roadian	268.0–270.6
	Cisuralian	Kungurian	270.6–275.6
		Artinskian	275.6–284.4
		Sakmarian	284.4–294.6
		Asselian	294.6–299.0
Carboniferous	Pennsylvanian	Gzhelian	older

Subdivision of the Permian system according to the IUGS, as of July 2009.

In the geologic timescale, the **Changhsingian** or **Changxingian** (from Chinese: 长兴县, Pinyin: *Chángxìng Xiàn*, "Changxing County") is the latest age or uppermost stage of the Permian. It is also the upper or latest of two subdivisions of the Lopingian epoch or series. The Changhsingian lasted from 253.8 ± 0.7 to 251.0 ± 0.7 million years ago (Ma). It was preceded by the Wuchiapingian and followed by the Induan.

The greatest mass extinction event in the Phanerozoic eon occurred during this age. The extinction rate peaked about a million years before the end of this stage.

Stratigraphic definitions

The Changhsingian is named after Changxing County in China (Wades-Giles transcription: *Ch'ang-hsing*). The stage was named for the Changhsing Limestone. The name was first used for a stage in 1970 and was anchored in the international timescale in 1981.

The base of the Changhsingian stage is at the first appearance of conodont species *Clarkina wangi*. The global reference profile is profile D at Meishan, in the type area in Changxing. The top of the Changhsingian (the base of the Induan stage and the Triassic system is at the first appearance of conodont species *Hindeodus parvus*.

The Changhsingian stage contains only one ammonite biozone: that of the genus *Iranites*.

Palaeontology

The Changhsingian ended with the Permian-Triassic Extinction Event when both global biodiversity and alpha diversity (community-level diversity) were devastated. The world after the extinction was almost lifeless, deserted, hot, and dry. Ammonites, fishes, insects, and the tetrapods (cynodonts, amphibians, reptiles, etc.) remained rare and terrestrial ecosystems did not recover for 30M years

Wuchiapingian

System	Series	Stage	Age (Ma)
Triassic	Lower	Induan	**younger**
Permian	Lopingian	Changhsingian	251.0–253.8
		Wuchiapingian	253.8–260.4
	Guadalupian	Capitanian	260.4–265.8
		Wordian	265.8–268.0
		Roadian	268.0–270.6
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		Sakmarian	284.4–294.6
		Asselian	294.6–299.0
Carboniferous	Pennsylvanian	Gzhelian	**older**

Subdivision of the Permian system according to the IUGS, as of July 2009.

In the geologic timescale, the **Wuchiapingian** or **Wujiapingian** (from Chinese: 五家坪, Pinyin: *Wǔ Jiā Píng*, "5 Family Flatland") is an age or stage of the Permian. It is also the lower or earlier of two subdivisions of the Lopingian epoch or series. The Wuchiapingian spans the time between 260.4 ± 0.7 and 253.8 ± 0.7 million years ago (Ma). It was preceded by the Capitanian and followed by the Changhsingian.

Regional stages with which the Wuchiapingian is coeval or overlaps include the Djulfian or Dzhulfian, Longtanian, Rustlerian, Saladoan, and Castile.

Stratigraphic definitions

The Wuchiapingian was first used in 1962, when the Lopingian series of southwestern China was divided in the Changhsingian and Wuchiapingian Formations. In 1973 the Wuchiapingian was first used as a chronostratigraphic unit (i.e. a stage, as opposed to a formation, which is a lithostratigraphic unit).

The base of the Wuchiapingian stage is defined as the place in the stratigraphic record where the conodont species *Clarkina postbitteri postbitteri* first appears. A global reference profile for this boundary (a GSSP) is located near Laibin in the Chinese province of Guangxi.

The top of the Wuchiapingian (the base of the Changhsingian) is at the first appearance of conodont species *Clarkina wangi*.

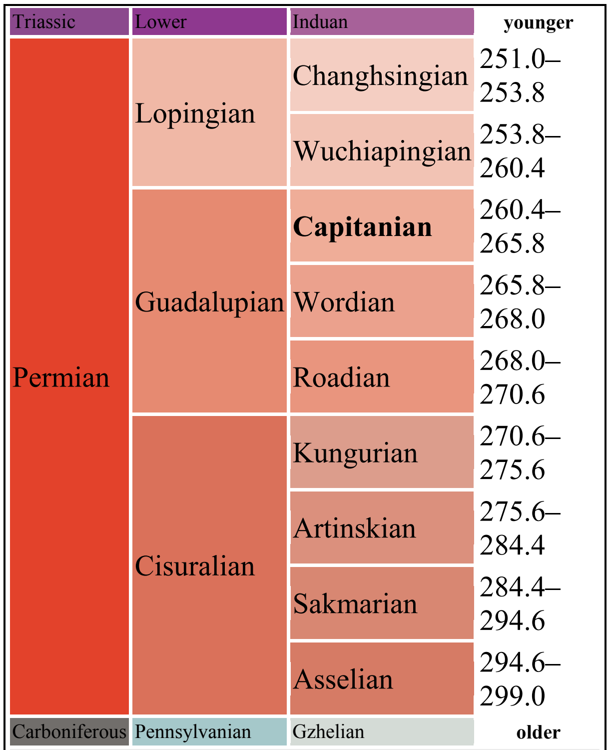
The Wuchiapingian contains two ammonite biozones: that of the genus *Araxoceras* and that of the genera *Roadoceras* and *Doulingoceras*.

Biodiversity

An extinction pulse occurred during the Wuchiapingian, faunas were recovering when another larger extinction pulse, the Permian-Triassic Extinction Event devastated life. .

Capitanian

System	Series	Stage	Age (Ma)



Triassic	Lower	Induan	**younger**
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		Asselian	294.6– 299.0
Carboniferous	Pennsylvanian	Gzhelian	**older**

Subdivision of the Permian system according to the IUGS, as of July 2009.

In the geologic timescale, the **Capitanian** is an age or stage of the Permian. It is also the uppermost or latest of three subdivisions of the Guadalupian epoch or series. The Capitanian lasted between 265.8 ± 0.7 Ma and 260.4 ± 0.7 million years ago (Ma). It was preceded by the Wordian and followed by the Wuchiapingian.

A significant mass extinction event occurred at the end of this stage which may be related to the much larger Permian-Triassic extinction event that followed about 10 million years later.

Stratigraphy

The Capitanian stage was introduced into scientific literature by George Burr Richardson in 1904. The name comes from the Capitan Reef in the Guadalupe Mountains (Texas, USA). The Capitanian was first used as a stratigraphic subdivision of the Guadalupian in 1961, when both names were still only used regionally in the southern US. The stage was added to the internationally used ISC timescale in 2001.

Definitions

The base of the Capitanian stage is defined as the place in the stratigraphic record where fossils of conodont species *Jinogondolella postserrata* first appear. The global reference profile for this stratigraphic boundary is located at Nipple Hill in the southern Guadalupe Mountains of Texas.

The top of the Capitanian (the base of the Wuchiapingian and Lopingian series) is defined as the place in the stratigraphic record where the conodont species *Clarkina postbitteri postbitteri* first appears.

The Capitanian stage was part of the time in which the Zechstein was deposited in Europe. It is coeval with the old European regional Saxonian stage. In the eastern Tethys domain, the Capitanian overlaps the regional Murgabian stage, the Midian stage and the lower part of the Laibinian stage. In Russia the Capitanian equals the lower part of the regional Severodvinian stage.

Biostratigraphy

The Capitanian contains one ammonite biozone (*Timorites*) and three conodont biozones:

- zone of *Clarkina postbitteri hongshuiensis*
- zone of *Jinogondolella altudaensis*
- zone of *Jinogondolella postserrata*

Larger fusulinid species permit a division in two biozones:

- zone of *Rausserella*
- zone of *Afganella schenki*

Biodiversity

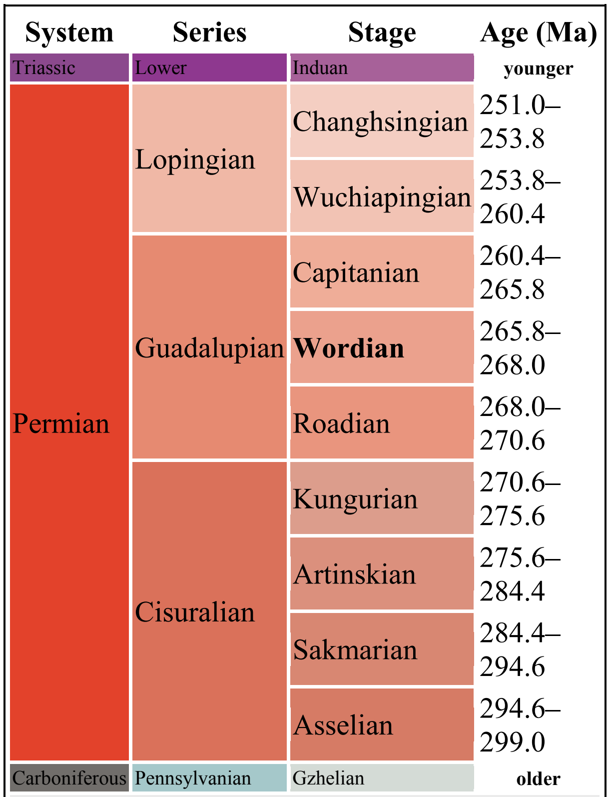
Olson’s Extinction, in the Early Guadalupian (Roadian, Wordian), reveals an extended period of low diversity when worldwide two-thirds of terrestrial vertebrate life was lost. Global diversity rose dramatically in the Capitanian, probably the result of disaster taxa filling empty guilds, only to fall again when the end-Guadalupian event caused a diversity drop in the Wuchiapingian. .

Events

Carbon isotopes in marine limestone from of Capitanian age show an increase in $\delta^{13}C$ values. The change in carbon isotopes in the sea water reflects cooling of global climates.

This climatic cooling may have caused the end-Capitanian extinction event among species that lived in warm water, like larger fusulinids (Verbeekninidae), large bivalves (Alatoconchidae and Rugosa corals, and Waagenophyllidae.

Wordian



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	Guadalupian	Capitanian	260.4–265.8
		Wordian	265.8–268.0
		Roadian	268.0–270.6
	Cisuralian	Kungurian	270.6–275.6
		Artinskian	275.6–284.4
		Sakmarian	284.4–294.6
		Asselian	294.6–299.0
Carboniferous	Pennsylvanian	Gzhelian	older

Subdivision of the Permian system according to the IUGS, as of July 2009.

In the geologic timescale, the **Wordian** is an age or stage of the Permian. It is the middle of three subdivisions of the Guadalupian epoch or series. The Wordian lasted between 268.0 ± 0.7 and 265.8 ± 0.7 million years ago (Ma). It was preceded by the Roadian and followed by the Capitanian.

Stratigraphy

The Wordian stage was introduced into scientific literature by Johan August Udden in 1916 and was named after the Word Formation of the North American Permian Basin. The Capitanian was first used as a stratigraphic subdivision of the Guadalupian in 1961, when both names were still only used regionally in the southern US. The stage was added to the internationally used ISC timescale in 2001.

The base of the Wordian stage is defined as the place in the stratigraphic record where fossils of conodont species *Jinogondolella aserrata* first appear. The global reference profile for this stratigraphic boundary is located at Getaway Ledge in the Guadalupe Mountains of Texas.

The top of the Wordian (the base of the Capitanian stage) is defined as the place in the stratigraphic record where the conodont species *Jinogondolella postserrata* first appears.

The Wordian stage was part of the time in which the Zechstein was deposited in Europe.

Biostratigraphy

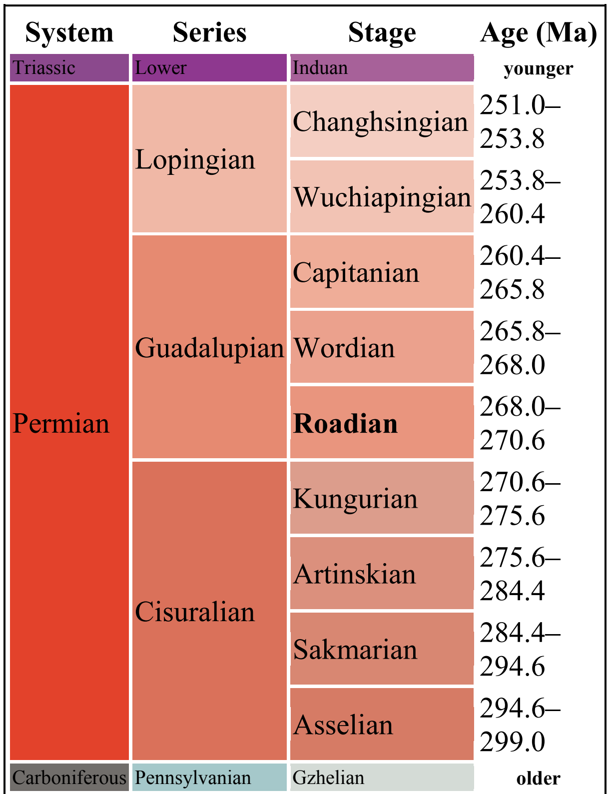
The Wordian spans the entire conodont biozone of *Jinogondolella aserrata*. It contains two fusulinid biozones:

- zone of *Afganella tereshkovae*
- zone of *Neoschwagerina tenuis*

Biodiversity

Olson's Extinction, a worldwide loss of terrestrial vertebrate life occurred during the Early Guadalupian (Roadian, Wordian).

Roadian



System	Series	Stage	Age (Ma)
Triassic	Lower	Induan	younger
Permian	Lopingian	Changhsingian	251.0–253.8
		Wuchiapingian	253.8–260.4
	Guadalupian	Capitanian	260.4–265.8
		Wordian	265.8–268.0
		Roadian	268.0–270.6
	Cisuralian	Kungurian	270.6–275.6
		Artinskian	275.6–284.4
		Sakmarian	284.4–294.6
		Asselian	294.6–299.0
Carboniferous	Pennsylvanian	Gzhelian	older

Subdivision of the Permian system according to the IUGS, as of July 2009.

In the geologic timescale, the **Roadian** is an age or stage of the Permian. It is the earliest or lower of three subdivisions of the Guadalupian epoch or series. The Roadian lasted between 270.6 ± 0.7 and 268.0 ± 0.7 million years ago (Ma). It was preceded by the Kungurian and followed by the Wordian.

Stratigraphy

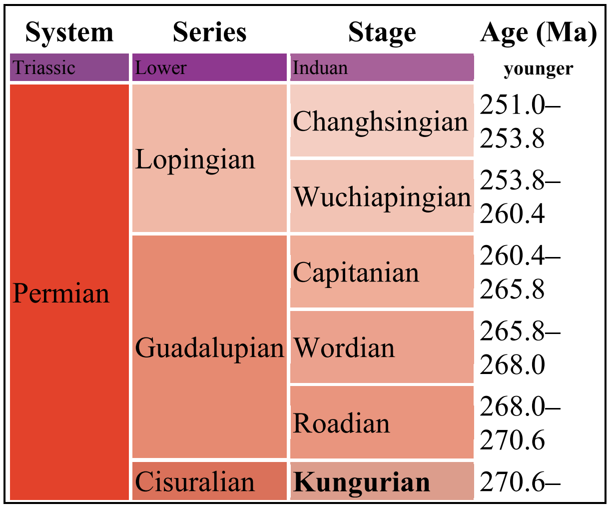
The Wordian stage was introduced into scientific literature in 1916 and was named after the Word Formation of the North American Permian Basin. In 1961, the regional timescale used for the southeastern US had the Wordian and Capitanian as subdivisions of the Guadalupian. Efforts to correlate the Permian stratigraphy of the southeastern US with that of Russia led to the conclusion that between the Wordian stage and the Russian Artinskian stage, another stage needed to be introduced. This stage, the Roadian stage, was established in 1968 and took its name from the Road Canyon Member, the lower (oldest) part of the Word Formation. The stage was added to the internationally used IUGS timescale in 2001.

The base of the Roadian is defined as the place in the stratigraphic record where fossils of conodont species *Jinogondolella nanginkensis* first appear. The global reference profile for the base (the GSSP) is located in Stratotype Canyon in the Guadalupe Mountains, Texas (31° 52' 36,1" N, 104° 52' 36,5" W). The top of the Roadian (the base of the Wordian stage) is at the first appearance of fossils of conodont species *Jinogondolella aserrata*.

Biodiversity

Olson's Extinction, a worldwide loss of terrestrial vertebrate life occurred during the Early Guadalupian (Roadian, Wordian).

Kungurian



System	Series	Stage	Age (Ma)
Triassic	Lower	Induan	younger
Permian	Lopingian	Changhsingian	251.0–253.8
		Wuchiapingian	253.8–260.4
	Guadalupian	Capitanian	260.4–265.8
		Wordian	265.8–268.0
		Roadian	268.0–270.6
	Cisuralian	**Kungurian**	270.6–

			275.6
		Artinskian	275.6–284.4
		Sakmarian	284.4–294.6
		Asselian	294.6–299.0
Carboniferous	Pennsylvanian	Gzhelian	**older**

Subdivision of the Permian system according to the IUGS, as of July 2009.

In the geologic timescale, the **Kungurian** is an age or stage of the Permian. It is the latest or upper of four subdivisions of the Cisuralian epoch or series. The Kungurian lasted between 275.6 ± 0.7 and 270.6 ± 0.7 million years ago (Ma). It was preceded by the Artinskian and followed by the Roadian.

Stratigraphy

The Kungurian is named after the Russian city of Kungur in the vicinity of Perm. The stage was introduced into scientific literature by Alexander Stuckenberg in 1890.

The base of the Kungurian stage is defined as the place in the stratigraphic record where fossils of conodont species *Neostreptognathodus pnevi* and *Neostreptognathodus exculptus* first appear. As of 2009, there was no agreement yet on a global reference profile (a GSSP) for the base of the Kungurian. The top of the Kungurian (the base of the Roadian and the Guadalupian series) is defined as the place in the stratigraphic record where fossils of conodont species *Jinogondolella nanginkensis* first appear.

The Kungurian contains three conodont biozones:

- zone of *Neostreptognathodus sulcoplicatus*
- zone of *Neostreptognathodus prayi*
- zone of *Neostreptognathodus pnevi*

Artinskian

System	Series	Stage	Age (Ma)
Triassic	Lower	Induan	**younger**
Permian	Lopingian	Changhsingian	251.0–253.8
		Wuchiapingian	253.8–260.4
	Guadalupian	Capitanian	260.4–

			265.8
		Wordian	265.8– 268.0
		Roadian	268.0– 270.6
	Cisuralian	Kungurian	270.6– 275.6
		Artinskian	275.6– 284.4
		Sakmarian	284.4– 294.6
		Asselian	294.6– 299.0
Carboniferous	Pennsylvanian	Gzhelian	**older**

Subdivision of the Permian system according to the IUGS, as of July 2009.

In the geologic timescale, the **Artinskian** is an age or stage of the Permian. It is a subdivision of the Cisuralian epoch or series. The Artinskian lasted between 284.4 ± 0.7 and 275.6 ± 0.7 million years ago (Ma). It was preceded by the Sakmarian and followed by the Kungurian.

Stratigraphy

The Artinskian is named after the small Russian city of Arti (formerly *Artinsk*), situated in the southern Ural mountains, about 200 km southwest of Yekaterinburg. The stage was introduced into scientific literature by Alexander Karpinsky in 1874.

The base of the Artinskian stage is defined as the place in the stratigraphic record where fossils of conodont species *Sweetognathus whitei* and *Mesogondolella bissell* first appear. As of 2009, there was no agreement yet on a global reference profile (a GSSP) for the base of the Artinskian. The top of the Artinskian (the base of the Kungurian) is defined as the place in the stratigraphic record where fossils of conodonts *Neostreptognathodus pnevi* and *Neostreptognathodus exculptus* first appear.

Sakmarian

System	Series	Stage	Age (Ma)
Triassic	Lower	Induan	**younger**
Permian	Lopingian	Changhsingian	251.0– 253.8
		Wuchiapingian	253.8– 260.4

	Guadalupian	Capitanian	260.4–265.8
		Wordian	265.8–268.0
		Roadian	268.0–270.6
	Cisuralian	Kungurian	270.6–275.6
		Artinskian	275.6–284.4
		Sakmarian	284.4–294.6
		Asselian	294.6–299.0
Carboniferous	Pennsylvanian	Gzhelian	**older**

Subdivision of the Permian system according to the IUGS, as of July 2009.

In the geologic timescale, the **Sakmarian** is an age or stage of the Permian. It is a subdivision of the Cisuralian epoch or series. The Sakmarian lasted between 294.6 ± 0.8 and 284.4 ± 0.7 million years ago (Ma). It was preceded by the Asselian and followed by the Artinskian.

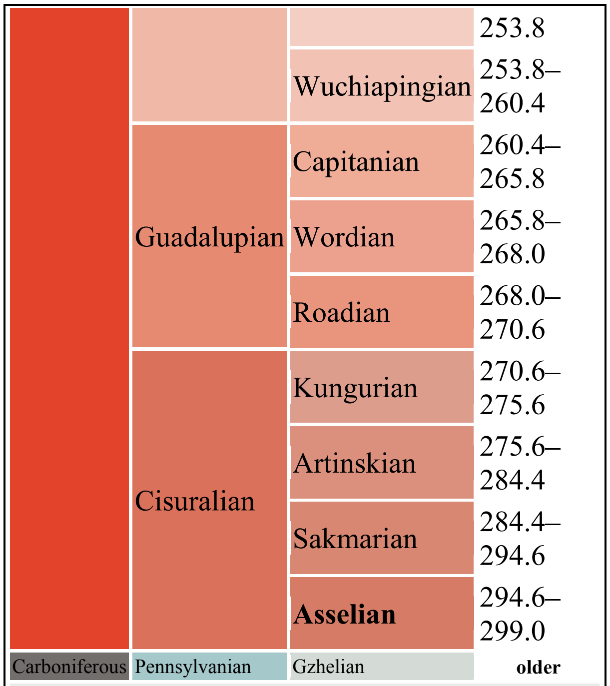
Stratigraphy

The Sakmarian stage is named after the Sakmara River in the Ural Mountains, a tributary to the Ural River. The stage was introduced into scientific literature by Alexander Karpinsky in 1874. In Russian stratigraphy, it originally formed a substage of the Artinskian stage. Currently, the ICS uses it as an independent stage in its international geologic timescale.

The base of the Sakmarian stage is laid with the first appearance of conodont species *Streptognathodus postfusus* in the fossil record. A global reference profile for the base (a GSSP) had in 2009 not yet been appointed. The top of the Sakmarian (the base of the Artinskian) is defined as the place in the stratigraphic record where fossils of conodont species *Sweetognathus whitei* and *Mesogondolella bissell* first appear.

Asselian

System	Series	Stage	Age (Ma)
Triassic	Lower	Induan	**younger**
Permian	Lopingian	Changhsingian	251.0–



			253.8
		Wuchiapingian	253.8–260.4
	Guadalupian	Capitanian	260.4–265.8
		Wordian	265.8–268.0
		Roadian	268.0–270.6
	Cisuralian	Kungurian	270.6–275.6
		Artinskian	275.6–284.4
		Sakmarian	284.4–294.6
		Asselian	294.6–299.0
Carboniferous	Pennsylvanian	Gzhelian	**older**

Subdivision of the Permian system according to the IUGS, as of July 2009.

In the geologic timescale, the **Asselian** is the earliest geochronologic age or lowermost chronostratigraphic stage of the Permian. It is a subdivision of the Cisuralian epoch or series. The Asselian lasted between 299.0 ± 0.8 and 294.6 ± 0.8 million years ago (Ma). It was preceded by the Gzhelian (the latest or uppermost subdivision in the Carboniferous) and followed by the Sakmarian.

Stratigraphy

The Asselian stage was introduced into scientific literature in 1954, when the Russian stratigrapher V.E. Ruzhenchev split it from the Artinskian. At that moment the Artinskian still encompassed most of the lower Permian - its current definitions are more restricted. The Asselian is named after the Assel River in the southern Ural Mountains of Kazakhstan.

The base of the Asselian stage is at the same time the base of the Cisuralian series and the Permian system. It is defined as the place in the stratigraphic record where fossils of the conodont *Streptognathodus isolatus* first appear. The global reference profile for the base (the GSSP or golden spike) is located in the valley of the Aidaralash River, near Aqtöbe in the Ural Mountains of Kazakhstan. The top of the Asselian stage (the base of the Sakmarian stage) is at the first appearance of conodont species *Streptognathodus postfusus*.

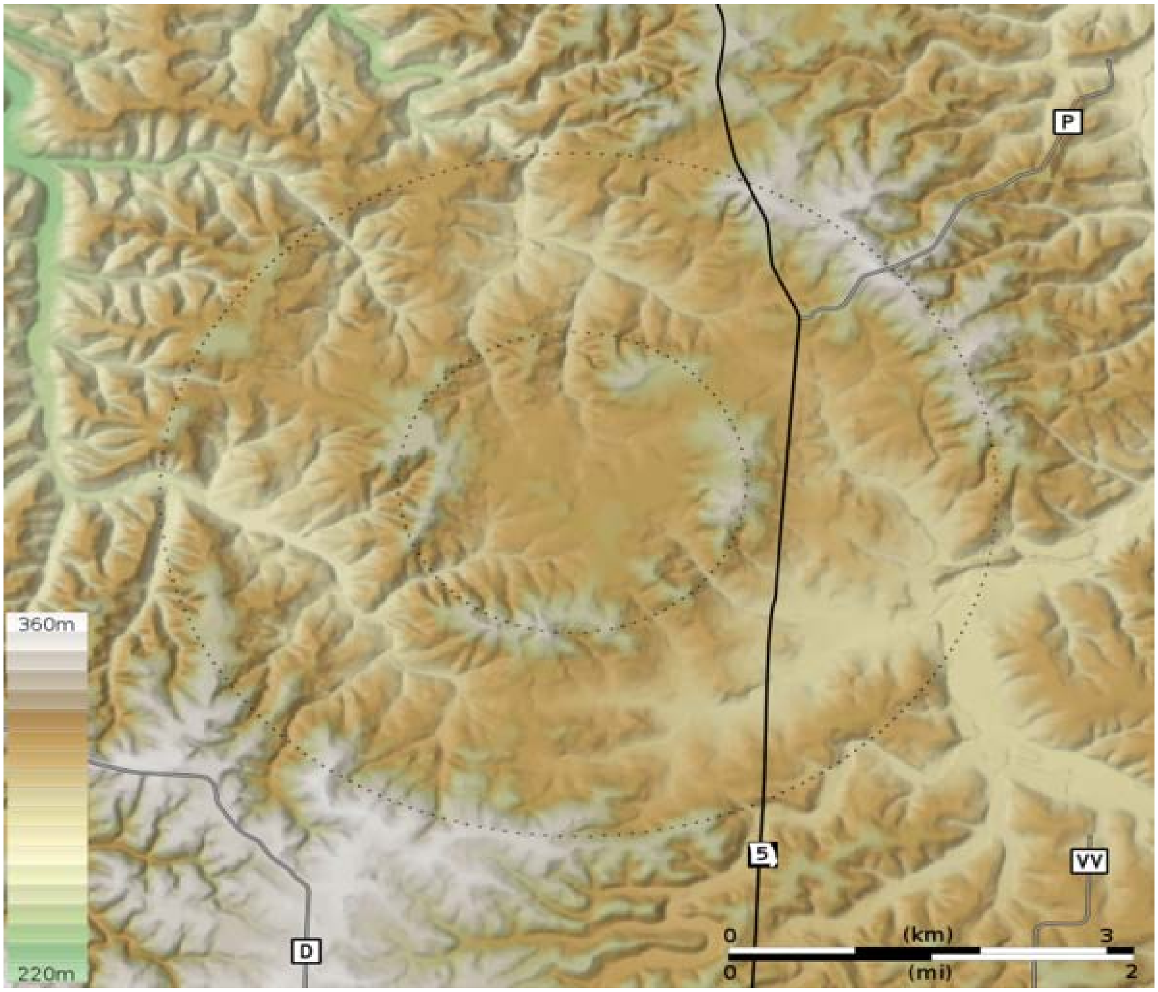
The Asselian contains five conodont biozones:

- zone of *Streptognathodus barskovi*
- zone of *Streptognathodus postfusus*
- zone of *Streptognathodus fusus*
- zone of *Streptognathodus constrictus*
- zone of *Streptognathodus isolatus*

Chapter- 4

Permian Impact Craters

Decaturville crater



The topography of the Decaturville crater is highly eroded.

The **Decaturville crater**, also referred to as the **Decaturville Dome**, is an impact crater in Missouri, United States, and is one of the 38th parallel structures.

It is 6 km in diameter and the age is estimated to be less than 300 million years (Permian or younger). The crater is exposed at the surface.

The effect that this impact had on the surrounding bedrock can be seen in a roadcut that runs along highway 5 about 16 miles north of Lebanon.

Des Plaines crater

Des Plaines is an impact crater in Illinois, United States. It is located in the city of Des Plaines, which is a suburb of Chicago.

It is 8 kilometres (5mi) in diameter and the age is estimated to be less than 280 million years (Permian or younger). The crater is buried beneath 75 to 200 feet (23–60 m) of glacial till and can only be seen as a series of faults and deformation in logs and seismic surveys.

Dobele crater

Dobele crater is an impact crater in central Latvia. The town of Dobele is built over the site of the crater.

It is 4.5 km in diameter and the age is estimated to be 290 ± 35 million years (Cisuralian epoch of the Permian period). The impact structure is buried and is not visible.

Île Rouleau crater

Île Rouleau is an impact crater in Quebec, Canada, located on a small, uninhabited island in Lake Mistassini in the centre of the province.

The crater is is 4 km in diameter and the age is estimated to be less than 300 million years (Permian or earlier). Part of the crater is exposed to the surface, but most of it is under the waters of the lake.

Kursk crater

Kursk is an impact crater in Russia.

It is 6 km in diameter and the age is estimated to be 250 ± 80 million years old (Late Permian or Early Triassic). The crater is not exposed to the surface.

Middlesboro crater

The **Middlesboro crater** is a meteorite crater in Kentucky, United States. It is named after the city of Middlesborough (both spellings are used), which today occupies much of the crater.

The crater is approximately 3 miles (about 5 km) in diameter and its age is estimated to be less than 300 million years (Permian).

History

The Middlesboro crater is located in the Appalachian Mountains, between the Cumberland Mountains and Pine Mountain. It forms part of the string of geological features that made the Cumberland Gap a critical westward passage during the settlement of Kentucky and the Ohio Valley in the late 18th and early 19th centuries.

The town of Middlesborough, built in the crater, was established in 1886 to exploit iron and coal deposits, although the town's founder, Alexander A. Arthur, apparently did not know of the crater's extraterrestrial origin. While coal mining is still the town's primary economic driver, local leaders hope to turn the crater into a tourist destination. In 2003, the Kentucky Society of Professional Geologists designated the area a Distinguished Geologic Site, and the construction of the Cumberland Gap Tunnel makes the town a convenient source of supplies for visitors to Cumberland Gap National Historical Park.

Mishina Gora crater

Mishina Gora is an impact crater in European Russia, 180 kilometres southwest of St. Petersburg.

It is 2.5 km (1.5 mi) in diameter and the age is estimated to be 300 ± 50 million years old, dating to the beginning of the Permian. The crater is exposed at the surface, but is not easily distinguishable from overhead imagery.

Ternovka crater

Ternovka is a meteorite crater in Ukraine (Dnipropetrovsk Oblast).

It is 11 km in diameter and the age is estimated to be 280 ± 10 million years (Permian). The crater is not exposed at the surface.

Clearwater Lakes

Clearwater Lakes *Lac à l'Eau Claire*	
	
Clearwater Lakes as seen from a Space Shuttle (North is up)	
Location	Quebec
Coordinates	56°08′N 74°18′W / 56.133°N 74.3°WCoordinates: 56°08′N 74°18′W / 56.133°N 74.3°W
Lake type	impact crater lake
Primary outflows	Clearwater River
Basin countries	Canada
Surface area	1,383 km^2 (534 sq mi)
Max. depth	178 meters (584 ft)
Surface elevation	241 meters (791 ft)

Clearwater Lakes, imagery by NASA World Wind

The **Lac à l'Eau Claire** (the official name, in French), also called the **Clearwater Lakes** in English, **Wiyasakami** in Cree and **Allait Qasigialingat** by the Inuit, are a pair of circular lakes on the Canadian Shield in Quebec, Canada, near Hudson Bay.

The lakes are actually a single body of water with a sprinkling of islands forming a "dotted line" between the eastern and western parts. The name is due to the clear water it holds. There are actually 25 lakes with that name in the province (26 if the *Petit lac à l'Eau Claire* — the Small Clearwater Lake — is included). These are the largest and northernmost, and the second largest natural lake in Quebec after Lake Mistassini.

In 1896, the explorer and geologist Albert Peter Low, a member of the Geological Survey of Canada, provided the probable origin of the lakes descriptive name by highlighting the extraordinary clarity and depth of its icy waters.

Impact craters

The lakes fill circular depressions that are interpreted as paired impact craters (astroblemes). The eastern and western craters are 26 km and 36 km in diameter, respectively. Both craters have the same age, 290 ± 20 million years (Permian), and it is believed that they formed simultaneously. The impactors may have been gravitationally bound as a binary asteroid, a suggestion first made by Thomas Wm. Hamilton in a 1978 letter to Sky & Telescope magazine in support of the then-controversial theory that asteroids may possess moons.

Micro climate

Because of its size, Clearwater Lake can affect the local climate, as attested to by the distribution of plant species. Although the lake’s shorelines are populated mainly by boreal species, the flora of the central islands in the western basin of the lake is characteristically arctic, making the islands an arctic enclave.

Proposed national park

A vast area surrounding the lakes, Richmond Gulf (*Lac Guillaume-Delisle*), and Iberville Lake (*Lac D'Iberville*) is being studied for inclusion in a new Quebec park, Lacs-Guillaume-Delisle-et-à-l'Eau-Claire National Park. This proposed park of 15,549 square kilometers (6,004 sq mi) would become Quebec's largest park (excluding wilderness reserves).

Chapter- 5

Permian Life

Annularia

Annularia **Fossil range: Carboniferous**	

Annularia stellata

Scientific classification	
Kingdom:	Plantae
Division:	Pteridophyta
Class:	Equisetopsida
Order:	Equisetales
Family:	Calamitaceae
Genus:	***Annularia***

Specimen of *Annularia* on display at the State Museum of Pennsylvania

Annularia is a Carboniferous plant fossil. It is a form taxon. Its radiating structures are most likely the leaves of *Calamites*.

Calamites

Calamites **Fossil range: Carboniferous–early Permian**	
 A range of *Calamites* specimens, illustrating the different appearance of fossils preserved under different taphonomic modes.	
Scientific classification	
Kingdom:	Plantae
Division:	Pteridophyta
Class:	Equisetopsida
Order:	Equisetales
Family:	Calamitaceae
Genus:	***Calamites***
Species	

Calamites is a genus of extinct arborescent (tree-like) horsetails to which the modern horsetails (genus *Equisetum*) are closely related. Unlike their herbaceous modern cousins, these plants were medium-sized trees, growing to heights of more than 30 meters (100 feet). They were components of the understories of coal swamps of the Carboniferous period.

Taphonomy

A number of organ taxa have been identified as part of a united organism, which has inherited the name *Calamites* in popular culture. *Calamites* correctly refers only to casts of the stem of Carboniferous/Permian sphenophytes, and as such is a form genus of little taxonomic value. There are two forms of casts, which can give mistaken impressions of the organisms. The most common is an internal cast of the hollow (or pith-filled) void in the centre of the trunk. This can cause some confusion: firstly, it must be remembered that a fossil was probably surrounded with 4-5 times its width in (unpreserved) vascular tissue, so the organisms were much wider than the internal casts preserved. Further, the fossil gets narrower as it attaches to a rhizoid, a place where one would expect there to be the highest concentration of vascular tissue (as this is where the peak transport occurs). However, because the fossil is a cast, the narrowing in fact represents a constriction of the *cavity*, into which vascular tubes encroach as they widen.

Further organ genera belonging to sphenophytes include:

- *Arthropitys* (stems which are preserved in a mineralised form)
- *Astromyelon* (permineralised rhizomes, distinguished from *Arthropitys* by the absence of a carinal canal)
- *Annularia* and *Asterophylites* (form genera of leaf-whorls which are paraphyletic).

Anatomy

The foliage of *Calamites*

The trunks of *Calamites* had a distinctive segmented, bamboo-like appearance and vertical ribbing. The branches, leaves and cones were all borne in whorls. The leaves were needle-shaped, with up to 25 per whorl.

Their trunks produced secondary xylem, meaning they were made of wood. The vascular cambium of *Calamites* was *unifacial*, producing secondary xylem towards the stem center, but not secondary phloem.

The stems of modern horsetails are typically hollow or contain numerous elongated air-filled sacs. *Calamites* was similar in that its trunk and stems were hollow, like wooden tubes. When these trunks buckled and broke, they could fill with sediment. This is the reason pith casts of the inside of *Calamites* stems are so common as fossils.

Reproduction

A *Calamites* rhizoid

Calamites reproduced by means of spores, which were produced in small sacs organized into cones. They are also known to have possessed massive underground rhizomes, which allowed for the production of clones of one tree. This is the only group of trees of their period known to have a clonal habit. This type of asexual reproduction would allow them to spread quickly into new territory, and help to anchor them firmly in the unstable ground along rivers and in newly deposited delta sediments. The rhizomes of *Calamites* look quite similar to the stems in most cases, but have nodes that get progressively closer together as they approach the apical area (the growth tip that spreads outward through the soil).

Different forms

Calamites come in a variety of different "form genera". One type, *Calamites suckowi*, is distinguishable from other *Calamites* forms by its prominent, swollen nodes and relatively wide-spaced longitudinal ribs. Another example, *Calamites cisti*, has much smaller nodes and the ribs are typically closer together.

In addition, the distance between successive node lines on a *Calamites suckowi* specimen is typically much wider than the diameter. In other forms like *Calamites cisti*, the opposite is true or the specimen is just slightly wider than the diameter.

However, the value of these form taxa is limited. The distance between nodes, for example, is highly variable, and an intercalary meristem means that this distance varied as the organisms grew.

Extinction and classification

The genus *Calamites* has been placed in the plant division Equisetophyta (formerly known as Sphenophyta) and family Calamitaceae. They finally became extinct in the Lower Permian, a time which, however, also saw the origin of the family Equisetaceae, to which the only living sphenophyte genus *Equisetum* belongs.

Cladophlebis

Cladophlebis **Fossil range: Permian - Cretaceous**	
Scientific classification	
Kingdom:	Plantae
Class:	Filicopsida
Order:	Filicales
Genus:	***Cladophlebis*** **Brongniart (1849)**

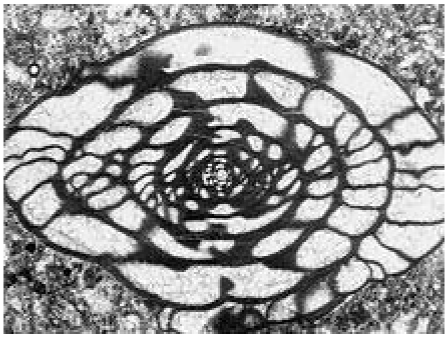
Cladophlebis is an extinct genus of fern which grew during the Mesozoic and late Paleozoic eras. It was a common plant during that time (284.4 to 70.6 million years ago) in both the northern and southern hemispheres, and belonged to the order of plants called Filicales.

There were many species of *Cladophlebis*, including: *C. akhtashensis, C. arctica, C. browniana, C. denticulata, C. dunberi, C. haiburnensis, C. heterophylla, C. hirta, C. impressa, C. kurtzi, C. lobifolia, C. nebbensis, C. patagonica, C. phlebopteris, C.*

porsildi, C. readi, C. remota, C. roessertii, C. septentrionalis, C. simplicima, C. spectabilis, C. tenuis, C. wyomingensis, and *C. yanschinii*.

Fusulinid

Fusulinid



Scientific classification

Domain:	Eukaryota
Kingdom:	Protista
Phylum:	Foraminifera
Order:	**Fusulinida**

Superfamilies

Archaediscacea
Colaniellacea
Earlandiacea
Endothyracea
Fusulinacea
Geinitzinacea
Moravamminacea
Nodosinellacea
Palaeotextulariacea
Parathuraminacea
Ptychocladiacea
Tetrataxacea
Tournayellacea

The **fusulinids** are an extinct group of foraminiferan protozoa. They produced calcareous shells, which are of fine calcite granules packed closely together; this distinguishes them from other calcareous forams, where the test is usually hyaline. Their fossils are so abundant that they have formed entire limestone formations. The fusulinid Cottonwood Limestone formation in Kansas is an example of this. Fusulinids are important guide fossils.

Fusulinids appeared late in the Mississippian subperiod. They were a part of the Carboniferous and Permian marine communities. They are excellent guide fossils for Pennsylvanian and Permian rocks. However, fusulinids became extinct at the end of the Permian Period.

Gigantopterid

Gigantopterids **Fossil range: late Permian**	
Scientific classification	
Domain:	Eukaryota
(unranked):	Archaeplastida
Kingdom:	Plantae
Superdivision:	Spermatophyta
Order:	**Gigantopteridales** (disputed)
Family:	**Gigantopteridaceae** (disputed) Koidz.
Genera	
Synonyms	
Gigantonomiales S.Meyen	

Gigantopterids (**Gigantopteridales**) is the name given to fossils of a group of plants existing in the Late Permian, until some 250 million years ago. Gigantopterids were among the most advanced land plants of the Paleozoic and disappeared soon after the massive Permian–Triassic extinction event 251.4 million years ago. Though some lineages of these plants managed to persist initially, they either disappeared entirely or adapted radically, evolving into undetermined descendants, as surviving life prospered again in much-altered ecosystems. One hypothesis proposes that at least some "gigantopterids" became the ancestors of angiosperms and/or Bennettitales and/or Caytoniales.

Gigantopterid fossils were documented as early as 1883, but only investigated more thoroughly in the early 20th century. Some of their most significant evidence has been initially found in Texas, but they may have been present worldwide: another key region for gigantopterid fossils is in China, and the consolidation of all major continents into Pangea would have allowed for easy global dispersal. They were among the most striking and important plants of the Cathaysian flora of Sino-Malaya, also called *Gigantopteris* flora to reflect this.

Description

They bore many of the traits of flowering plants, but are not known to have flowered themselves. Gigantopterid plants had simple, bilaterally symmetrical leaf structures, woody stems and spines. They grew new parts by producing shoots, like flowering plants. Judging from the fossil remains, they were probably robust plants with fronds that resembled fern fronds when young. When mature they were more like flowering plant leaves with reticulate venation arranged in a frond. *Gigantopteris nicotianaefolia* for example is named thus because each of its leaflets resembles a tobacco leaf in shape.

They grew at least over 20 cm (around 10 in), probably over 50 cm (20 in) tall, depending on whether it grew as a scrambling vine (the initial assumption) or erect (nowadays considered more likely). Some were apparently amphibious, while others thrived in rather arid habitat.

The vascular tissue contains vessel elements and in at least some taxa resembles that of the Gnetophyta. They had a cuticula similar to that of other seed plants. Some male sporangia (*Gigantotheca*) and seeds (*Gigantonomia*, *Cornucarpus*) have been tentatively referred to this group. While the sporangia are certainly not flowers, they differ from other sporangia of Permian plants.

Chemical analysis of fossil remains indicates that gigantopterids produced oleananes, chemical compounds otherwise known to be used by flowering plants, for which they function as a suppressant of insect pests. They are apparently also found in certain modern ferns however.

Systematics

It is probable that the gigantopterids are a non-monophyletic form taxon. Plant life from their era is very difficult to document and organize. They have been variously allied with the "seed ferns" (another paraphyletic group of early seed plants) Peltaspermales and Callistophytales, *Gnetum*, and the Magnoliophyta. All that can be said at present is that they were spermatophytes. It is also highly unlikely that they were close relatives of gymnosperms, cycads or ginkgos, because these lineages were already established and distinct in the Late Permian.

Vegetative leaves of *Emplectopteris* were at one time included in this group. However, they had ovules attached to the underside of the fronds and are now placed in their own family (Emplectopteridaceae) within the Callistophytales.

Some prefer to refer to the presumed "core" taxa of this group as **Gigantonomiales**. However, many experts remain skeptical of the new name, because they consider such a move premature until more is known about the interrelationships of the genera of "gigantopterids" and the relationships of these to other plants.

Several genera have been named. Those then known were assigned to a family **Gigantopteridaceae** and numerous subfamilies by Gen-ichi Koidzumi. It appears as if at least some of his divisions ought to prove useful when a more definite phylogenetic, systematic and taxonomic arrangement for this group is eventually found. On the other hand, the Gigantopteridaceae would with near certainty have to be more narrowly circumscribed even if the Gigantopteridales are by and large verified as a clade; they might even become limited to the two or so genera now placed in the Gigantopteridieae.

Proposed subfamilies and genera

Cathaysiopteridieae - may be synonym of Palaeogoniopteridieae

- *Cathaysiopteris*
- *Cathaysiopteridium*

Gigantopteridieae (including Cardioglossieae)

- *Gigantonoclea* - includes *Cardioglossum* and apparently*Progigantopteris*
- *Gigantopteris*

Gothanopteridieae - may be synonym of Cathaysiopteridieae/Palaeogoniopteridieae

- *Gothanopteris*

Palaeogoniopteridieae

- *Gigantopteridium*
- *Palaeogoniopteris*
- *Zeilleropteris*

Unresolved

- *Delnortea*
- *Emplectopteridium*
- *Emplectopteris*
- *Neogigantopteridium* - probably Cathaysiopteridieae/Palaeogoniopteridieae
- *Vasovinea*

Sigillaria

Sigillaria
Fossil range: Carboniferous to Permian

Sigillaria root (*Stigmaria*) from the Llewellyn Formation.

Scientific classification

Kingdom:	Plantae
Division:	Lycopodiophyta
Class:	Isoetopsida
Order:	Lepidodendrales
Family:	Lepidodendraceae
Genus:	***Sigillaria***

Sigillaria is a genus of extinct, spore-bearing, arborescent (tree-like) plants which flourished in the Late Carboniferous period but dwindled to extinction in the early Permian period. It was a lycopodiophyte, and is related to the lycopsids, or club-mosses, but even more closely to quillworts, as was its associate *Lepidodendron*. *Sigillaria* was a tree-like plant, with a tall, occasionally forked trunk that lacked wood. Support came from a layer of closely packed leaf bases just below the surface of the trunk, while the center was filled with pith. The old leaf bases expanded as the trunk grew in width, and left a diamond-shaped pattern, which is evident in fossils. The trunk had photosynthetic tissue on the surface, meaning that it was probably green.

Sigillaria on display at State Museum of Pennsylvania, from Sharon, Mercer County, Pennsylvania

Sigillaria (bark) on display at State Museum of Pennsylvania, from Scranton, Lackawanna County, Pennsylvania

Replica of *Sigillaria* sp. in a laboratory of practices of the Faculty of Sciences of the University of A Coruña

The trunk was topped with a plume of long, grass-like, microphyllous leaves, so that the plant looked somewhat like a tall, forked bottlebrush. The plant bore its spores (not seeds) in cone-like structures attached to the stem. *Sigillaria*, like many ancient lycopods, had a relatively short life cycle - growing rapidly and reaching maturity in a few years.

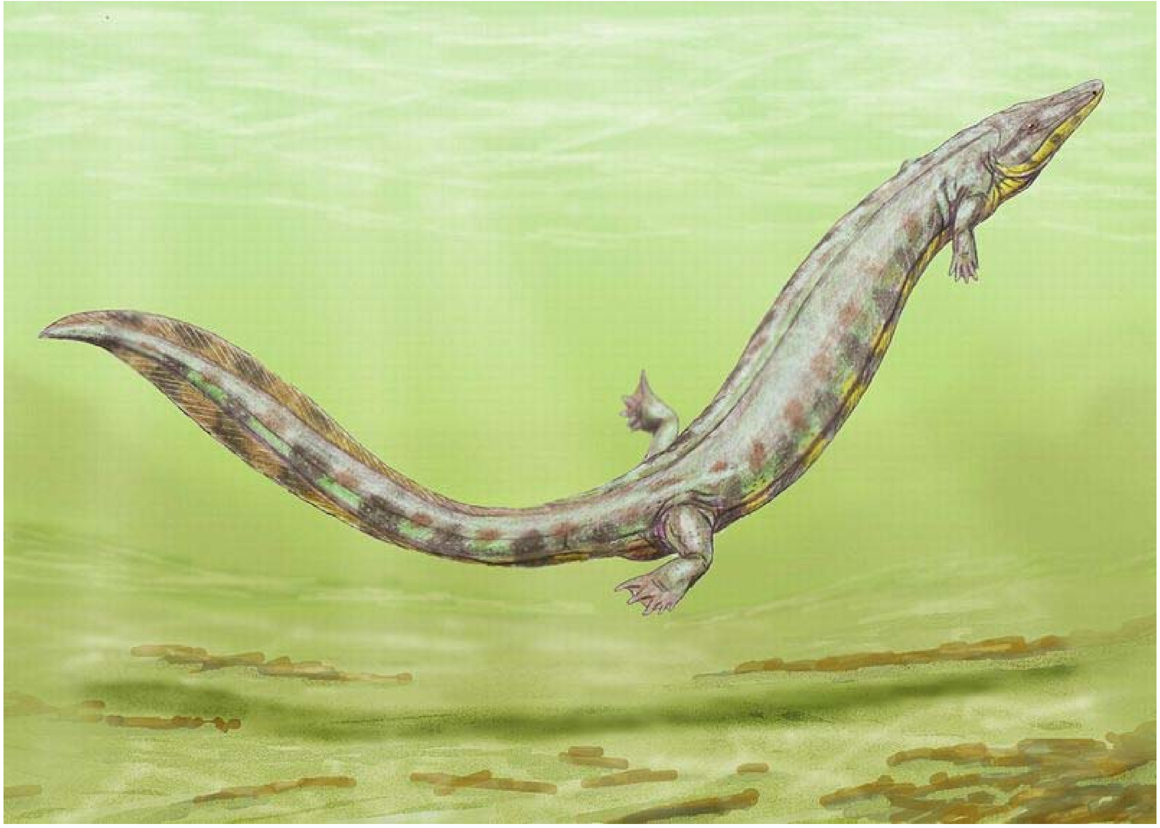
Some have suggested that *Sigillaria* was monocarpic, meaning that it died after reproduction, though this is not proven. It was associated with *Lepidodendron*, the scale tree, in the Carboniferous coal swamps.

Chapter- 6

Permian Animals

Archeria (animal genus)

Archeria was an eel-like anthracosaur which lived in the Early Permian. It was medium-sized aquatic predator.

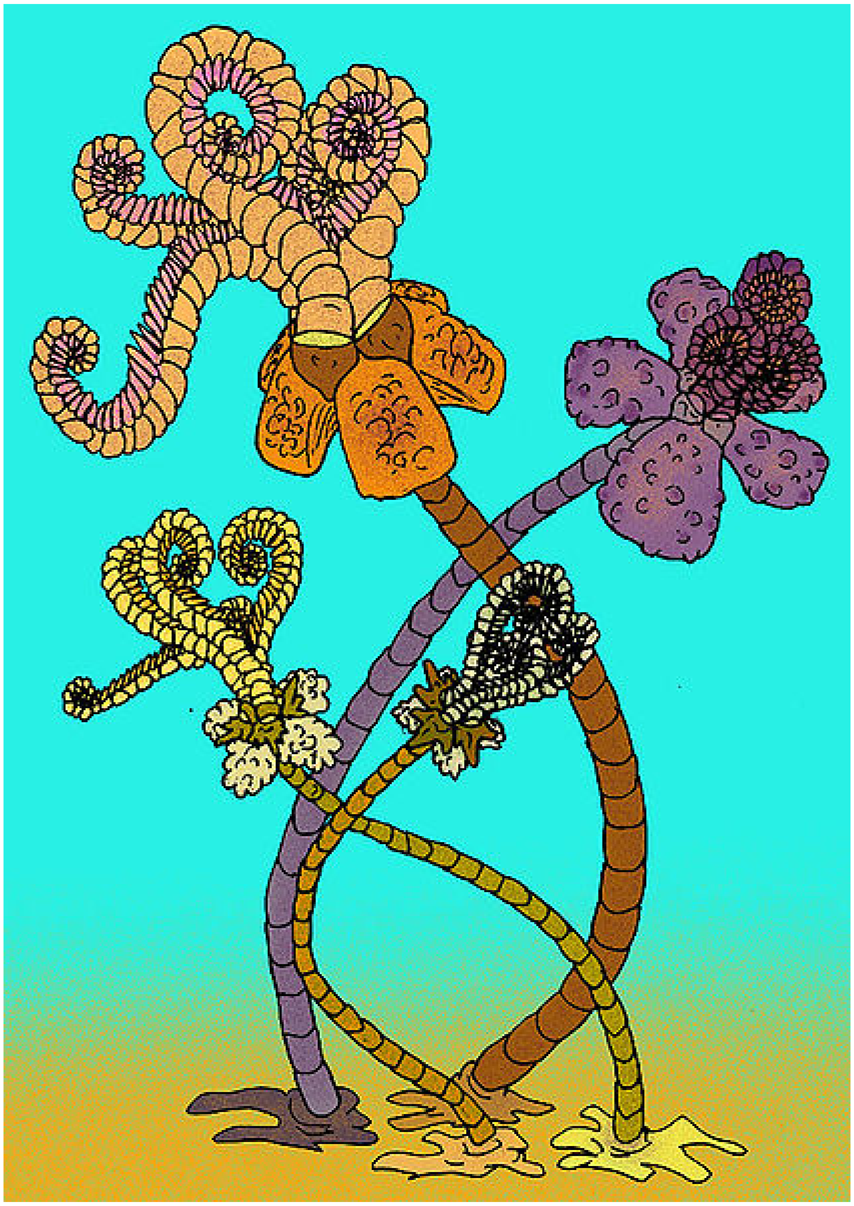


Archeria crassidisca.

Calceolispongia

Calceolispongia (literally "Shoe Sponge") is a diverse genus of cladid crinoids that lived along the shores of eastern Gondwanaland that correspond to Timor and Western Australia, today.

Calceolispongia
Fossil range: Permian



When the first fossils were discovered, they were mistakenly thought to be sponges, hence the generic name. Later, similarly shaped fossils were found, and (correctly) identified as those of a crinoid, and named "*Dinocrinus*." ("Terrible Lily") It was soon realized that *Dinocrinus* and *Calceolispongia* were the same, and *Dinocrinus* is now regarded as a junior synonym.

Chroniosaurus

Chroniosaurus

Fossil range: 255 Ma

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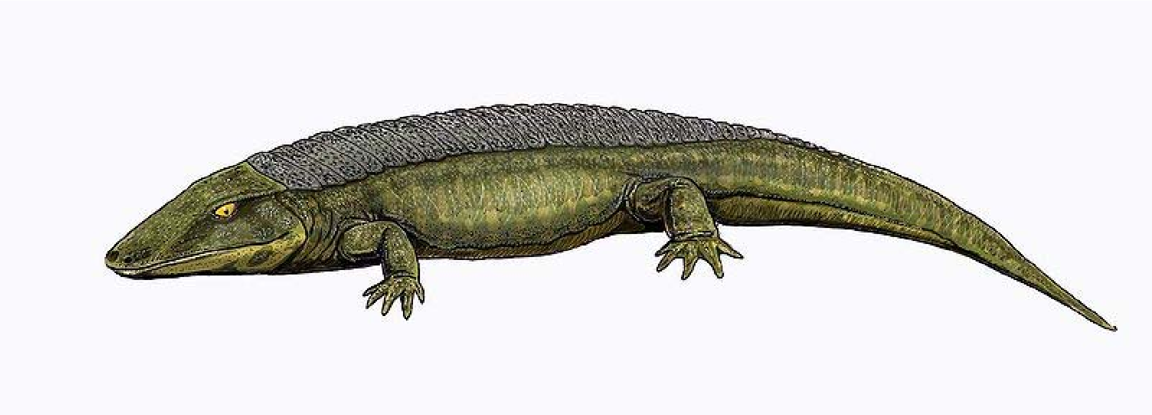
Upper Permian

Chroniosaurus dongusensis

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Superclass:	Tetrapoda
Superorder:	Reptiliomorpha
Order:	Chroniosuchia
Family:	Chroniosuchidae
Genus:	***Chroniosaurus*** Tverdochlebova, 1972

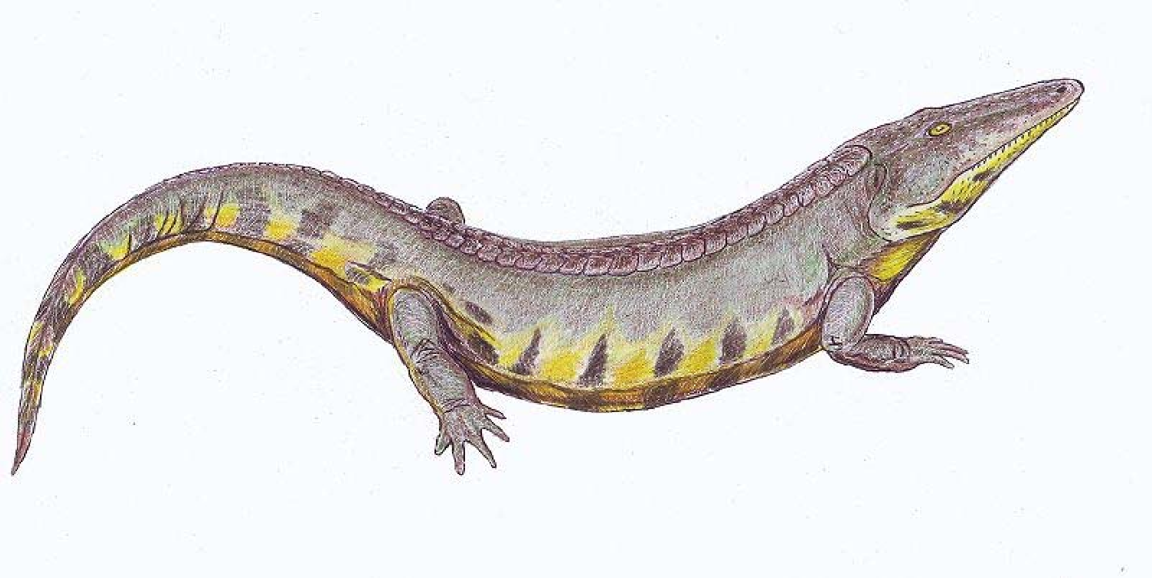
Chroniosaurus is an extinct genus of chroniosuchid reptiliomorph from upper Permian (upper Tatarian age) deposits of Novgorod, Orenburg and Vologda Regions, Russia. It was first named by Tverdokhlebova in 1972 and the type species is *Chroniosaurus dongusensis*.

Chroniosuchia

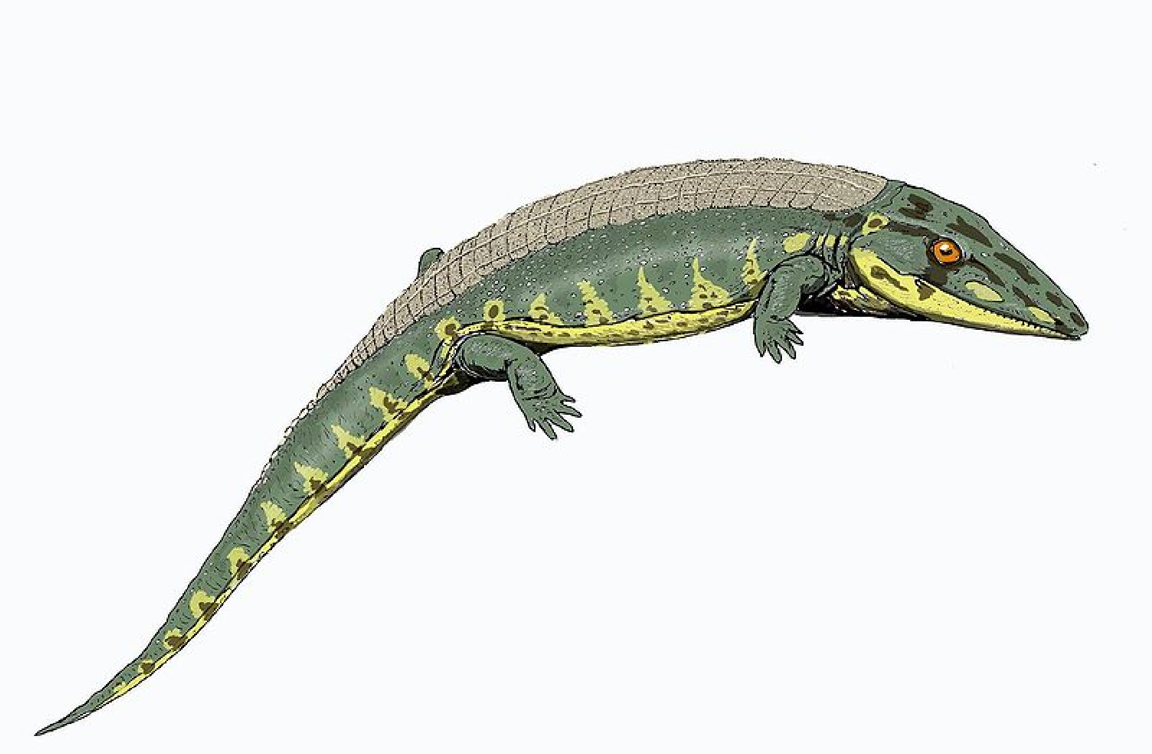


Chroniosuchus

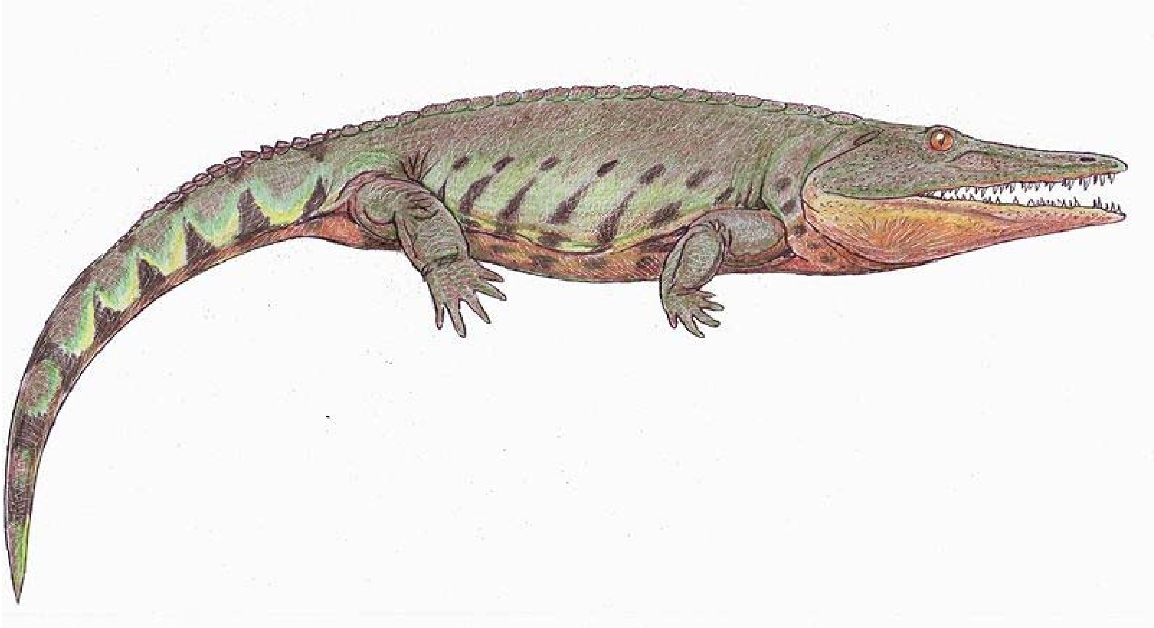
The **Chroniosuchia** are a order of tetrapods that lived in the middle Permian and the upper Triassic periods of Eastern Europe, Kyrgyzstan , China and Germany.



Bystrowiana permira



Chroniosaurus dongusensis



Uralerpeton tverdokhlebovae

Taxonomy

- **Reptiliomorpha**
- Order **Chroniosuchia**
    - Family **Bystrowianidae**
        - *Axitectum*
        - *Bystrowiana*
        - *Bystrowiella*
        - *Dromotectum*
        - *Synesuchus*
    - Family **Chroniosuchidae**
        - *Chroniosaurus*
        - *Chroniosuchus*
        - *Ingentidens*
        - *Jarilinus*
        - *Madygenerpeton*
        - *Phratochronis*
        - *Uralerpeton*
        - *Suchonica*

Chroniosuchus

Chroniosuchus
Fossil range: 255 Ma
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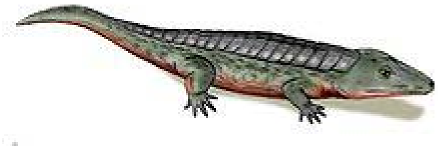
Upper Permian

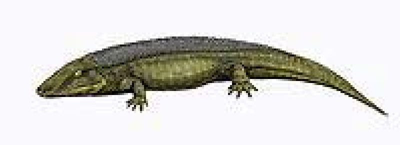


Chroniosuchus paradoxus

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Superclass:	Tetrapoda
Superorder:	Reptiliomorpha
Order:	Chroniosuchia
Family:	Chroniosuchidae
Genus:	***Chroniosuchus*** Vjuschkov, 1957

Species

- *C. paradoxus* Vjuschkov, 1957 (type)
- *C. licharevi* (Riabinin, 1962)



Chroniosuchus paradoxus.

Chroniosuchus is an extinct genus of chroniosuchid reptiliomorph from upper Permian (upper Tatarian age) deposits of Arkhangelsk, Orenburg and Vologda Regions, Russia. It was first named by Vjuschkov in 1957 and the type species is *Chroniosuchus*

Claraia

Claraia

Fossil range: 266–237 Ma

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Scientific classification	
Kingdom:	Animalia

Phylum:	Mollusca
Class:	Bivalvia
Order:	Pectinoida
Superfamily:	Pterinopectinoidea
Family:	Pterinopectinidae
Genus:	***Claraia*** Bittner, 1901

Claraia is an extinct genus of scallop-like bivalve mollusk that lived from the Capitanian stage of the Late Permian to the Anisian stage of the Middle Triassic, 266-237 million years ago. Fossils have been found worldwide in North America, Europe, Asia, Africa, and Australia. It is a common fossil following the Permian-Triassic boundary, suggesting that it experienced rapid diversification during and after the Permian–Triassic extinction event around 251.4 million years ago.

Claraia may have been an opportunistic genus that filled the niche of many benthic invertebrates such as brachiopods that were heavily impacted by the extinction. A narrowing of the byssal notch and a trend towards a smoother shell in species of *Claria* over time may have led to increased mobility. This increase in mobility may have been an advantage over more sessile animals during the extinction event . It is thought to have lived in anoxic waters at great depths, and therefore may have been better adapted for the anoxic event that may have occurred during the Permian–Triassic extinction event.

Diadectes

Diadectes
Fossil range: Early Permian

D. phaseolinus

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata

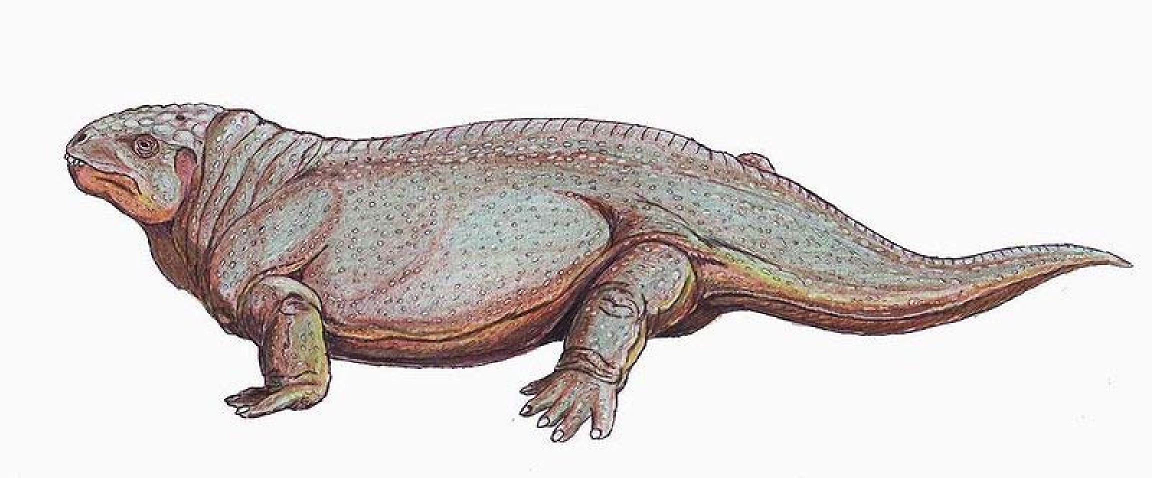
Superclass:	Tetrapoda
Superorder:	Reptiliomorpha
Order:	Diadectomorpha
Family:	Diadectidae
Genus:	***Diadectes***

Species

D. absitus Berman *et al.*, 1998
D. maximus
D. tenuitectus

Diadectes (meaning *biter-through* or *penetrating bite*) was a genus of large, very reptile-like tetrapods that lived during the Early Permian. It is one of the very first herbivorous tetrapods, and also one of the first fully terrestrial animals to attain large size.

Description



Restoration

Diadectes was a heavily built animal, 1.5 to 3 meters long, with a thick-boned skull, heavy vertebrae and ribs, massive limb girdles and short, robust limbs. The nature of the limbs and vertebrae clearly indicate a terrestrial animal.

Paleobiology

It possesses some characteristics of reptilians and amphibians, combining a reptile-like skeleton with a more primitive, seymouriamorph-like skull. *Diadectes* has been classified as a stem-amniote close to the ancestry of amniotes.

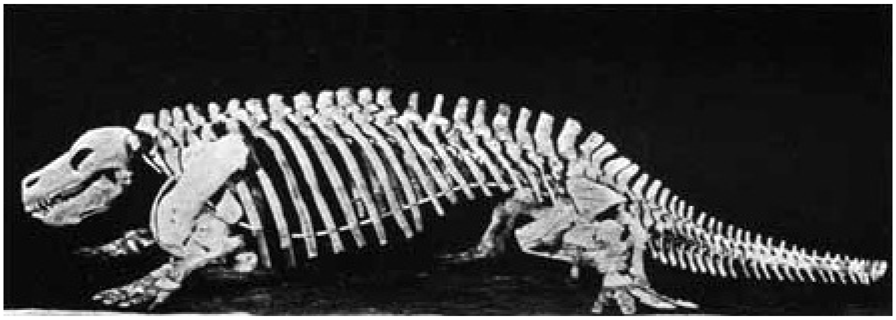
Among its primitive features, *Diadectes* has a large otic notch (a feature found in Paleozoic amphibians) with an ossified tympanum.

Fossil

At the same time its teeth show advanced specialisations for a herbivorous diet that are not found in any other type of early Permian animal. The eight front teeth are spatulate and peg-like, and served as incisors that were used to nip off mouthfuls of vegetation. The broad blunt cheek teeth show extensive wear associated with occlusion, and would have functioned as molars, grinding up the food.

It also had a partial secondary palate, which meant it could chew its food and breath at the same time, something many even more advanced reptiles were unable to do.

Discovery

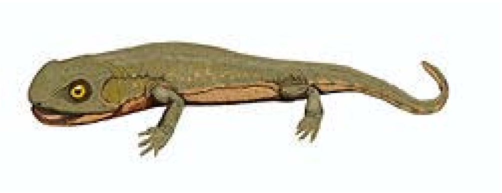


Skeleton in profile

Diadectes fossil remains are known from a number of locations across North America, especially the Texas Red Beds (Wichita and Clear Fork).

Discosauriscus

Discosauriscus
Fossil range: Early Permian



Discosauriscus austriacus

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	Vertebrata
Class:	Amphibia *sensu lato*
Order:	Seymouriamorpha
Family:	Discosauriscidae
Genus:	***Discosauriscus*** Kuhn, 1933

Species

- *D. austriacus* (Makowsky, 1876)
- *D. pulcherrimus* (Fritsch, 1879) (type)

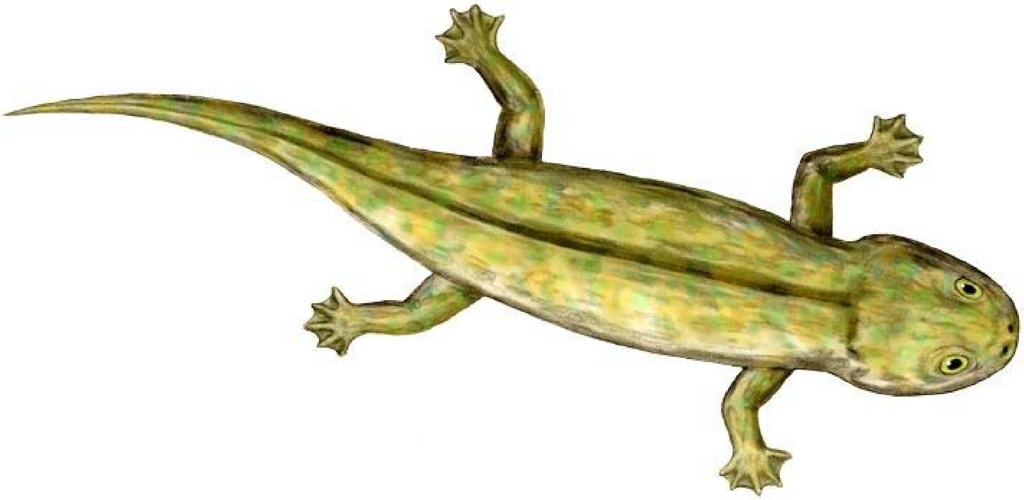
Synonyms

- *Letoverpeton* Spinar, 1952

Discosauriscus was a small reptiliomorph that lived in Central and Western Europe in the Lower Permian Period. Its best fossils have been found in Boskovice Furrow, in the Czech Republic.

Classification

Discosauriscus fossil



Discosauriscus

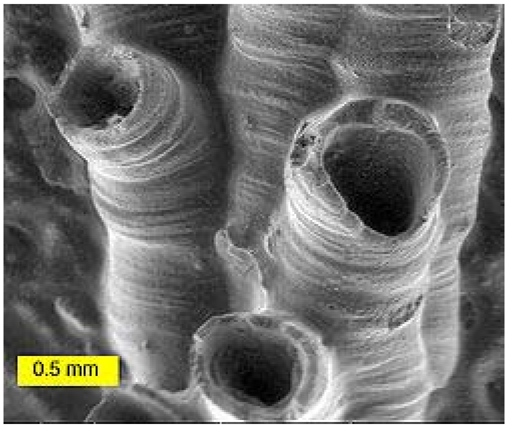
Discosauriscus belongs in alternative classifications to the order Anthracosauria or Seymouriamorpha, and is the type genus of the family Discosauriscidae. Currently recognised are two valid species - *Discosauriscus austriacus* and *Discosauriscus pulcherrimus*. *Letoverpeton* is a junior synonym of *Discosauriscus*.

Characteristics

Discosauriscids are only known from larval or neotenic forms, and three ontogenetic stages can be distinguished. *Discosauriscus* had wide jaws with sharp teeth, short limbs and relatively long tail. The phalangeal formula was 2-3-4-5-3 for both hind- and forelimbs. The body was covered with rounded scales with concentric rings, and a well preserved lateral-line system has been described.

Discosauriscus may have had electroreceptive organs.

Hederellid

Hederelloids **Fossil range: Silurian - Permian**	
	
Scanning electron microscope image of a hederelloid from the Devonian of Michigan.	
Scientific classification	
Kingdom:	Animalia
Phylum:	*incertae sedis* (possibly Phoronida)
Genera	

Hederellids are extinct colonial animals with calcitic tubular branching exoskeletons. They range from the Silurian to the Permian and were most common in the Devonian period. They are more properly known as "hederelloids" because they were originally defined as a suborder by Bassler (1939), who described about 130 species. Although they have traditionally been considered bryozoans, they are clearly not because of their branching patterns, lack of an astogenetic gradient, skeletal microstructure, and wide range in tube diameters (Wilson and Taylor, 2001). Work continues on assessing the true affinities of hederelloids, but they appear to be most closely related to phoronids and other lophophorates (Taylor and Wilson, 2008; Taylor et al., 2010).

Classification

- **Family Hederellidae**
    - Genus *Diversipora*
    - Genus *Hederella*
- **Family Reptariidae**
    - Genus *Cystoporella*
    - Genus *Hederopsis*
    - Genus *Hernodia*

Lycosuchus

Lycosuchus

Lycosuchus Sp. skull at the Museum für Naturkunde, Berlin

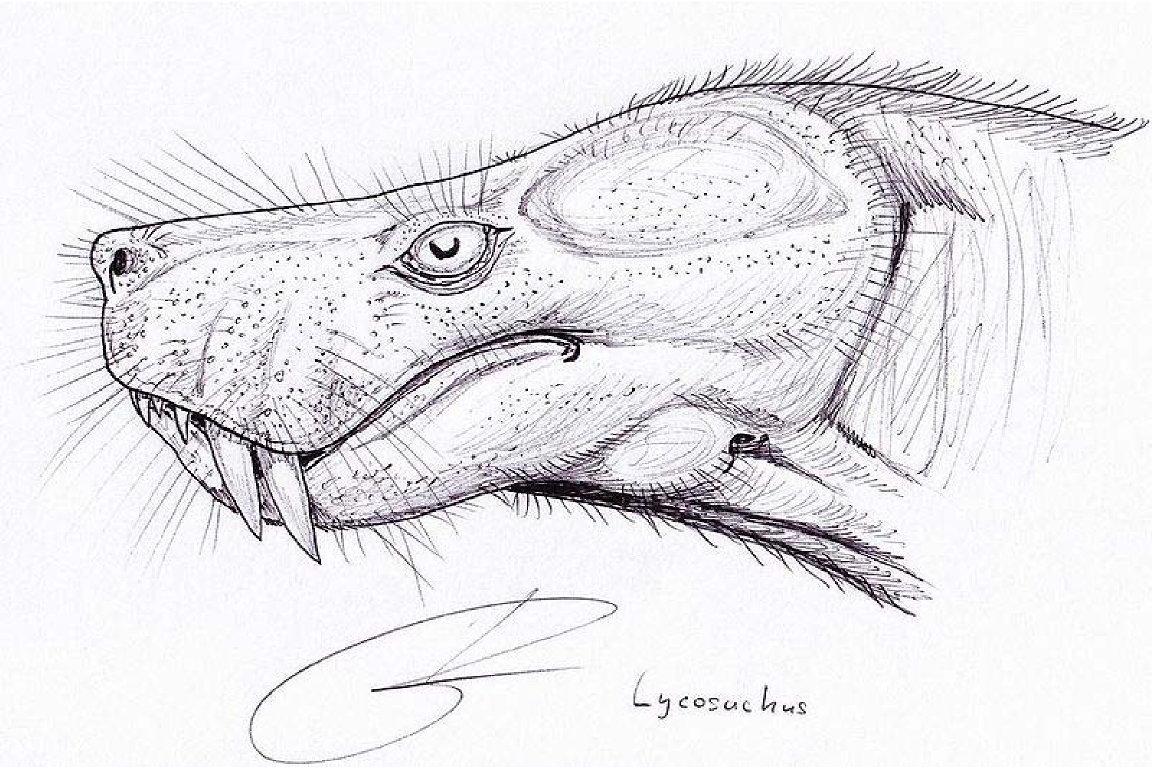
Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Synapsida
Order:	Therapsida
Suborder:	Therocephalia
Family:	Lycosuchidae
Genus:	***Lycosuchus***

Species

- *L. mackayi*

- *L. vanderrieti*

Lycosuchus ("wolf crocodile") is an extinct carnivorous genus of therocephalian which lived in the late Permian 265—245 Ma existing for approximately 20 million years.



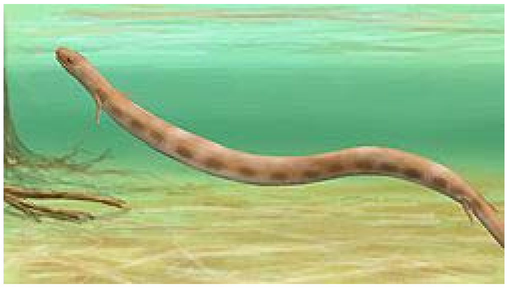
Head

Lycosuchus in environment

Discovered in South Africa, it was named by paleontologist Robert Broom in 1903 and later assigned by him to Therocephalia.

Lysorophia

Lysorophians
Fossil range: Carboniferous to Permian



Brachydectes newberryi

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	Vertebrata
Superclass:	Tetrapoda
Class:	Amphibia
Subclass:	Lepospondyli

Order: **Lysorophia**
Family: **Lysorophidae**

Genera

- ?*Brachydectes*
- ?*Megamolgophis*
- *Cocytinus*
- *Lysorophus*
- *Molgophis*

Lysorophia is an order of aquatic Carboniferous and Permian amphibians within the extinct subclass Lepospondyli. Lysorophians resembled small snakes, as their bodies are extremely elongate. There is a single family, the **Lysorophidae**. Currently there are around five genera included within Lysorophia.

Description

The skull is lightly built and open, with large orbits and fenestrae. The intertemporal, supratemporal, postfrontal, and jugal bones of the skull have disappeared. The mandibles are short, and the maxilla and premaxilla freely movable.

Life restoration of *Lysorophus tricarinatus* showing speculative egg-coiling behavior.

The torso is very elongate, the limbs diminutive or absent, and the tail short. There are up to 99 pre-sacral (i.e. not including the hips and tail) vertebrae.

Based on morphology of the cranio-vertebral articulation, Lysorophids are usually considered to be related to the Microsauria, although the pattern of bones of the skull is very different.

Distribution

🟩 **Pennsylvanian (Upper Carboniferous) sites**
🟥 **Permian sites**
🟨 **Doubtful lysorophian site**

Geographic distribution of Lysorophia after Wellstead (1991)

Lysorophians are known mainly from the Late Pennsylvanian and Early Permian of North America. In North America, fossils of lysorophians have been found from places such as the Chinle Formation in San Juan County, Utah and the Mazon Creek fossil beds in Grundy County, Illinois. Carboniferous lysorophians are also known from Europe, having been found from England and Ireland. Possible remains of a lysorophian have also been found from La Machine, France, although they may belong to an aïstopod.

Macroleter

Macroleter

Fossil range: Late Permian, 264 Ma

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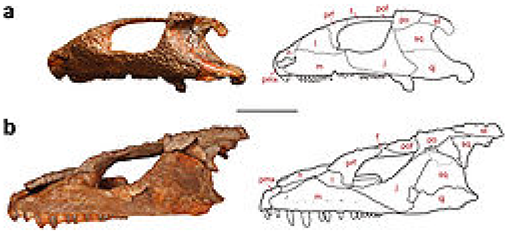


Skull photo and diagram of *Bashkyroleter mesensis* and *Macroleter poezicus*

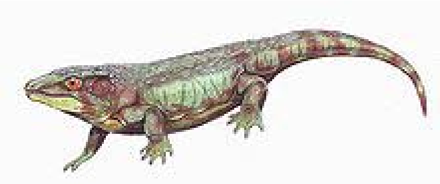
Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	Vertebrata
Class:	Sauropsida
Subclass:	Parareptilia
Family:	Nycteroleteridae
Genus:	***Macroleter*** Tverdochlebova & Ivachnenko, 1984

Species

- *M. poezicus* Tverdochlebova & Ivachnenko, 1984 (type)
- *M. agilis* (Olson, 1980 [originally

Seymouria agilis]) Reisz & Laurin, 2001



Restoration

Macroleter is an extinct genus of parareptile which existed in Oklahoma and Russia during the upper Permian period. It was first named by paleontologists Tverdochlebova and Ivachnenko in 1984. The type species is *Macroleter poezicus* from Upper Permian of Russia. *Seymouria agilis* (Olson, 1980) that is known from only one specimen (holotype UCMP 143 277), a nearly complete skeleton from the Chickasha Formation of Oklahoma, was reassigned by Michel Laurin and Robert R. Reisz to this genus.

Rutocerina

Rutoceratina **Fossil range: Devonian - L Permian**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	Nautiloidea
Order:	Nautilida
Suborder:	**Rutoceratina** (Shinskiy 1957)

The **Rutocertina** is one of only three suborders in Shimankiy's (1957) classification of the Nautilida, the other two being the Lirocerina and Nautilina. Genera in the Rutocerina are redistributed (Kummel 1964) in the Rutoceratina, Tainoceratina, and Centroceratina. The Lirocerina is redefined as the Liroceratina, and Nautilina.remains as is. In general terms these are similar to the simpler classification proposed by Kummel 1964, wherein the Nautilida is divided into five superfamilies, the **Tainocerataceae**, **Trigonocerataceae**, **Clydonautilacea**, **Aipocerataceae**, and **Nautilaceae**. Shimanskiy's classification involves 34 families, Kummel's only twenty-seven.

The Rutoceratina (Shmanskiy 1957) is divided into two unequal superfamilies which do not correspond with the superfamiles of Kummel, 1964. They are the Rutoceratacea and the Solenochilaceae.

The Rutoceratacea is essentially the Rutoceratidae of Kummel 1964, elevted and expanded to contain two families, the Rutoceratidae in the Devonian, and the Neptunoceratidae in the late Carboniferous.

The Solenochilaceae is more or less equivalent to Kummel's Aipoceratacеae

Description

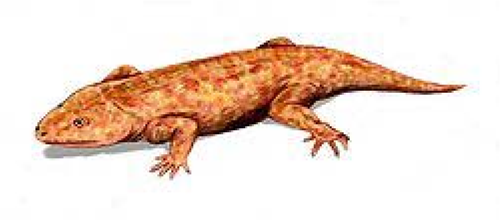
Based on descriptions of the Rutoceratidae and Aipocerataceae in Kummel 1964, the Rutoceratina are characterized as having longiconic, curved, and coiled shells which develop solid, nollow, and spoutlike wings, frills, and spines; the siphuncle being ventral, mostly orthochaonitic and empty, but in some the septal necks may be long ventrally and recumbent dorsally.

Range

The Rutoceratina lived during the Devonian , Carboniferous, and early Permian, derived from the Oncocerida. They gave rise (Shimanskiy) through the Rutoceratidae in the Devonian to the Tainoceratina and the Centroceratina and through a family of the Solenochilaceae the at the end of the Devonian to the Liroceratina.

Seymouria

Seymouria
Fossil range: Early Permian



Seymouria baylorensis from the Early Permian of North America

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Superclass:	Tetrapoda

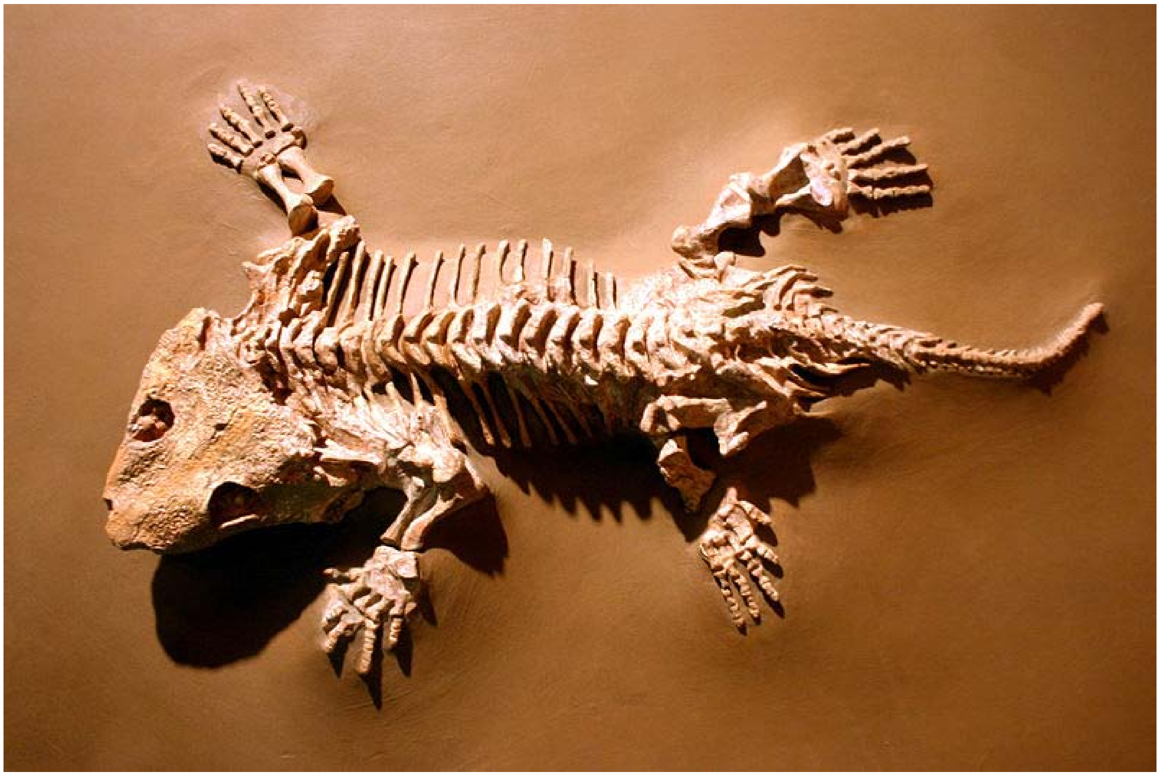
Superorder:	Reptiliomorpha
Order:	Seymouriamorpha
Family:	Seymouriidae
Genus:	***Seymouria*** Broili, 1904

Species

- *S. baylorensis* Broili, 1904 (type)
- *S. sanjuanensis* Vaughn, 1966
- *S. grandis* Olson, 1979

Synonyms

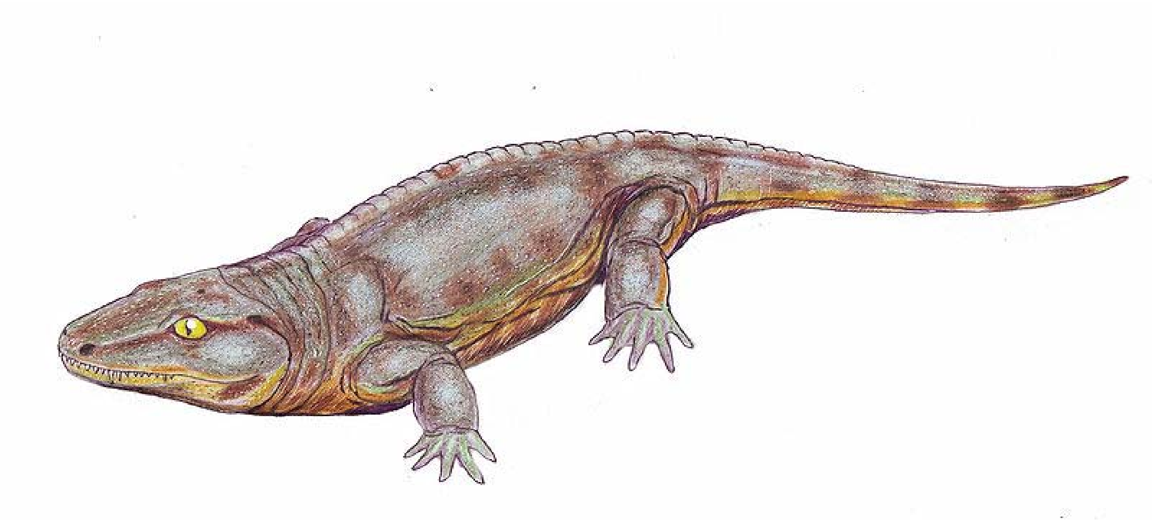
Seymouria was a reptile-like tetrapod from the early Permian of North America and Europe (approximately 280 to 270 million years ago). It was small, only 2 ft (60 cm) long. *Seymouria* was well adapted to life on land, with many reptilian features--so many, in fact, that it was first thought to be a primitive reptile.



Seymouria skeleton, Museum of Natural History, Washington.

Description

The dry climate of the Permian suited reptiles better than amphibians and other more primitive tetrapods, but *Seymouria* had many reptilian features that helped it in this harsh environment. It had long and muscular legs, and may have had dry skin and the ability to conserve water. It may have been able to excrete excess salt from its blood through a gland in its nose, like modern reptiles. All of this meant that *Seymouria*, unlike amphibians and other early tetrapods, might have lived for extended periods of time away from water. If so, this would have allowed it to move about the landscape in search of insects, small amphibians, and other possible preys, such as the eggs of reptiles.



Seymouria baylorensis.

Seymouria sanjuanensis

Male *Seymouria* had thick skulls that may have been used to batter rivals in mating contests. After mating, the females would have had to return to water to lay their eggs. As in amphibians, the larvae would develop in water, hunting for worms and insects until they were strong enough to live on land. While no larvae are known from *Seymouria* itself, fossil larvae of its relative *Discosauriscus* and other species in the order Seymouriamorpha have been found, with impressions of external gill structures as in some amphibians.

Fossils of *Seymouria* were first found in Seymour, Baylor County, Texas (hence the name of the type species, *Seymouria baylorensis*, or "Baylor County Seymour one"). Over the years, many well preserved fossils have been found in North America and Germany, including the "Tambach Lovers", two individuals of *S. sanjuanensis* fossilized lying next to each other (though of course it cannot be determined whether they really were a couple killed during mating). *Seymouria agilis* (Olson, 1980) that is known from only one specimen (holotype UCMP 143 277), a nearly complete skeleton from the Chickasha Formation of Oklahoma, was reassigned by Michel Laurin and Robert R. Reisz as a Macroleter.

Chapter- 7

Temnospondyli

Temnospondyls
Fossil range: Carboniferous–Early Cretaceous

Skeleton of *Eryops*, Gallerie de Paléontologie, MNHN, Paris.

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Amphibia
Subclass:	Labyrinthodontia †(?)
Order:	**Temnospondyli** Zittel, 1888

Suborders

Temnospondyli (from Greek τέμνειν, *temnein* = "to cut" + σπόνδυλος, *spondylos* = "vertebra") is an important and extremely diverse taxon of small to giant primitive amphibians that flourished worldwide during the Carboniferous, Permian, and Triassic periods. A few stragglers continued into the Cretaceous. During their evolutionary history they adapted to a very wide range of habitats, including fresh-water aquatic, semi-aquatic, amphibious, terrestrial, and in one group even near-shore marine, and their fossil remains have been found on every continent. Authorities disagree over whether some specialised forms were ancestral to some modern amphibians, or whether the whole group died out without leaving any descendants.

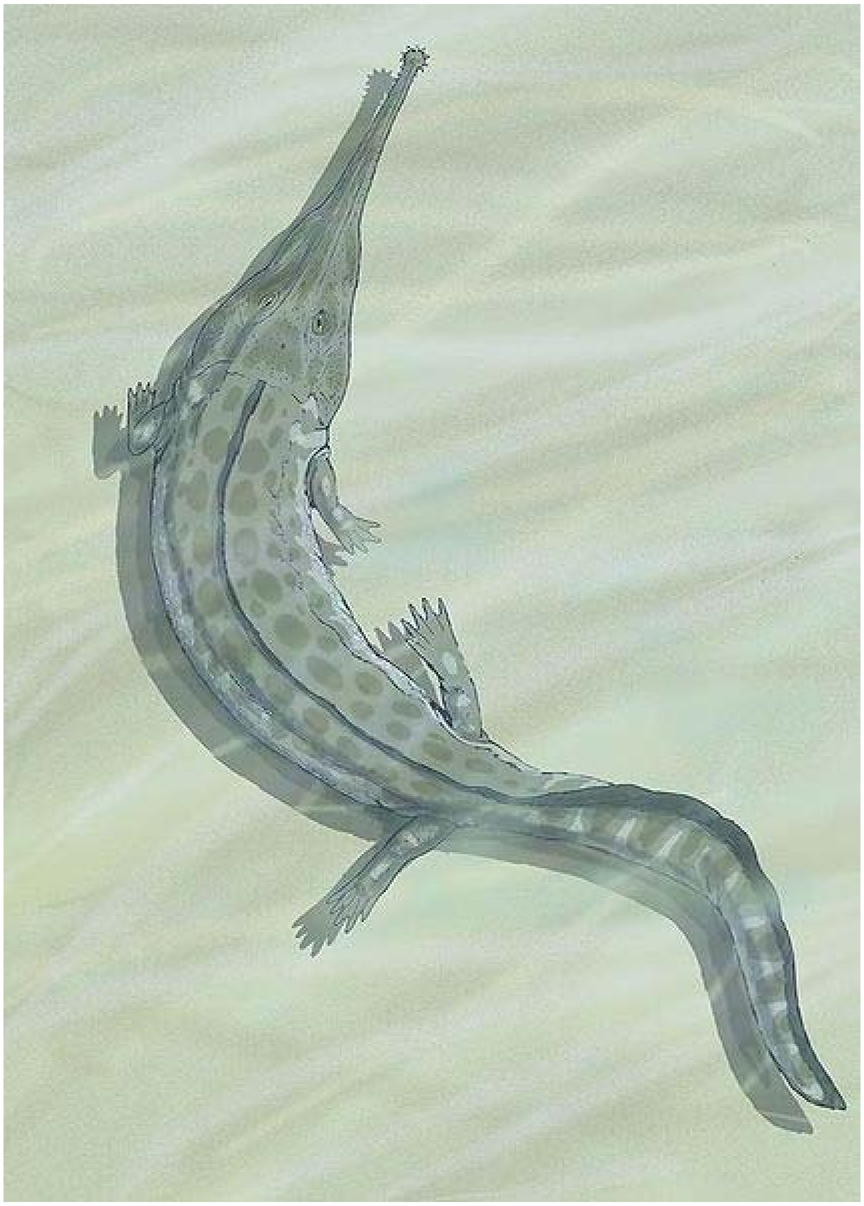
Evolutionary History

Carboniferous and early Permian Temnospondyli

Capetus, a basal temnospondyl.

During the Carboniferous, Temnospondyli included basal medium-sized (*Dendrerpeton*) or large (*Cochleosaurus*, about 1.5 metres (4.9 ft) long) semi-aquatic forms. Others such as the amphibamids were smaller and more derived, resembling newts or salamanders, and some taxa, such as the genus *Branchiosaurus*, even retained external gills like the modern-day axolotl. During the latest Carboniferous and early Permian (ca. 300 Ma), several groups such as the dissorophoids evolved strong, robust limbs and vertebrae and became adapted to life on land while others such as the eryopids and trematopids developed into large (c. 1.5 metres (4.9 ft) long) and heavy-bodied semi-aquatic predators.

Late Permian Temnospondyli

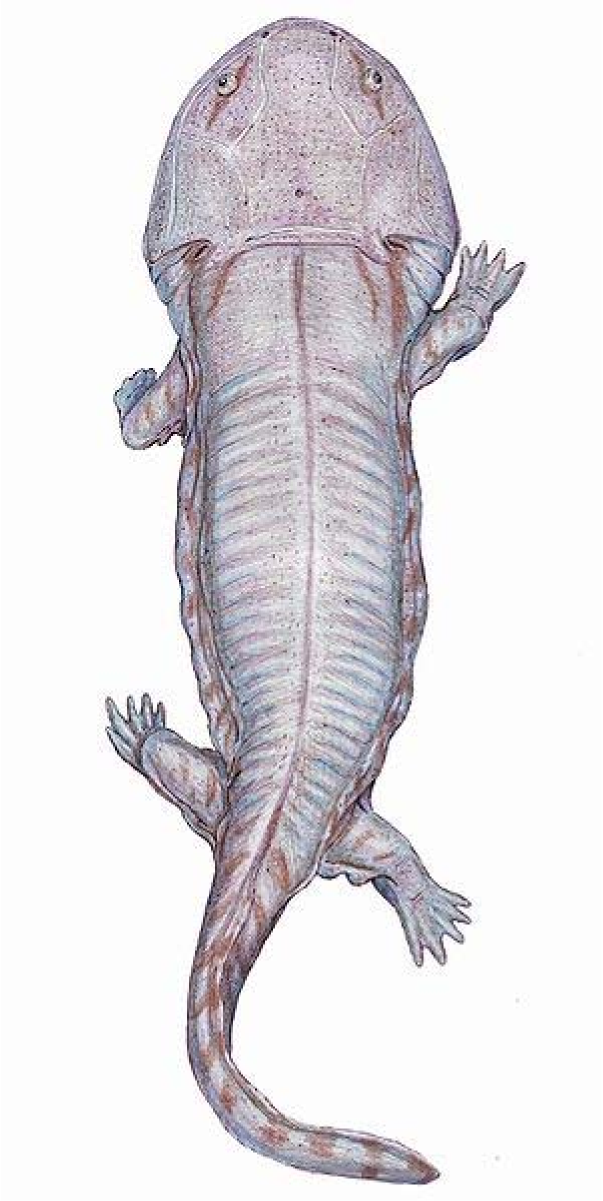


Prionosuchus from the Permian, the largest amphibian ever described.

During the later Permian, increasing aridity and more successful reptiles meant the end of the terrestrial temnospondyls, but semi- and fully aquatic animals continued to flourish, including the large *Melosaurus* of Eastern Europe. Other temnospondyls such as archegosaurids developed long snouts and an astonishing similarity to crocodiles, although they lacked the armour characteristic of the latter group. These temnospondyls included the largest known amphibian, the 9 metres (30 ft) long *Prionosuchus* of Brazil.

As these amphibians continued to flourish and diversify in the lakes and rivers of the late Permian (260.4 - 251.0 Ma), a number of groups became more dependent on life in the water. The vertebrae became weak, the limbs small and vestigal, and the heavy skull large and flat, with the eyes looking upwards. These include the classic Stereospondyli, and other related types. During the Triassic period these animals dominated the fresh-water ecosystems, evolving in a range of both small and large forms. During the Early Triassic (251.0 - 245.0 Ma) one group of successful long-snouted fish eaters, the trematosaurs, even adapted to a life in the sea, the only known amphibians to do so with the exception of the modern Crab-eating frog). Another group, the Capitosauroidea, included not only medium-sized but also many giant species, 2.3 to 4 metres (7.5 to 13 ft) or more in length (e.g. *Paracyclotosaurus*, *Cyclotosaurus*), with huge and extraordinarily flat skulls, over a meter long in the largest forms (*Mastodonsaurus*). These animals seem to have lived on the river bottom, perhaps spending most or all their entire lives in water, and catching their prey by a sudden opening of the upper jaw, sucking in fish or smaller tetrapods that happened to swim past.

Mesozoic survivors



Siderops, a Jurassic temnospondyl.

In the Carnian stage of the late Triassic (228.0 - 216.5 Ma) capitosauroids were joined by the superficially very similar Metoposauridae (1.5 metres (4.9 ft) long—and distinguished mainly by the different position of the eye-sockets), and the curious wide-headed plagiosaurs (about a meter in length), with external gills.

The Triassic-Jurassic extinction event (ca. 199.6 Ma) killed all the giant temnospondyls. Only the smaller Brachyopidae and Chigutisauridae survived. These grew to large size during the Jurassic, with the brachyopids flourishing in China, and the chigutisaurs in Gondwana.

The most recent known temnospondyl was the giant chigutisaur *Koolasuchus*, known from the Early Cretaceous of Australia where it seems to have survived in rift valleys that were too cold in the winter for crocodiles, co-existing with dinosaurs. At around 2.5 to 5 meters in length , this was one of the largest of its kind, as well as the last.

Relationship to modern amphibians

The Lissamphibia, the modern amphibians, appear to have risen in the Permian. The root of the group is controversial, but may be with the Temnospondyli. Skull morphology of some of the smaller later form has been compared to those of modern frogs and salamanders. The presence of bicuspid, pedicellate teeth in small, paedomorphic or immature temnospondyls like the genus *Doleserpeton* has been cited as the most convincing argument in favor of the temnospondyl origin of lissamphibians. Other analysis indicate that another fossil group, the Lepospondyli, are more likely candidates for lissamphibian origin, leaving the Temnospondyli an extinct group.

Systematics

Two types of vertebrae

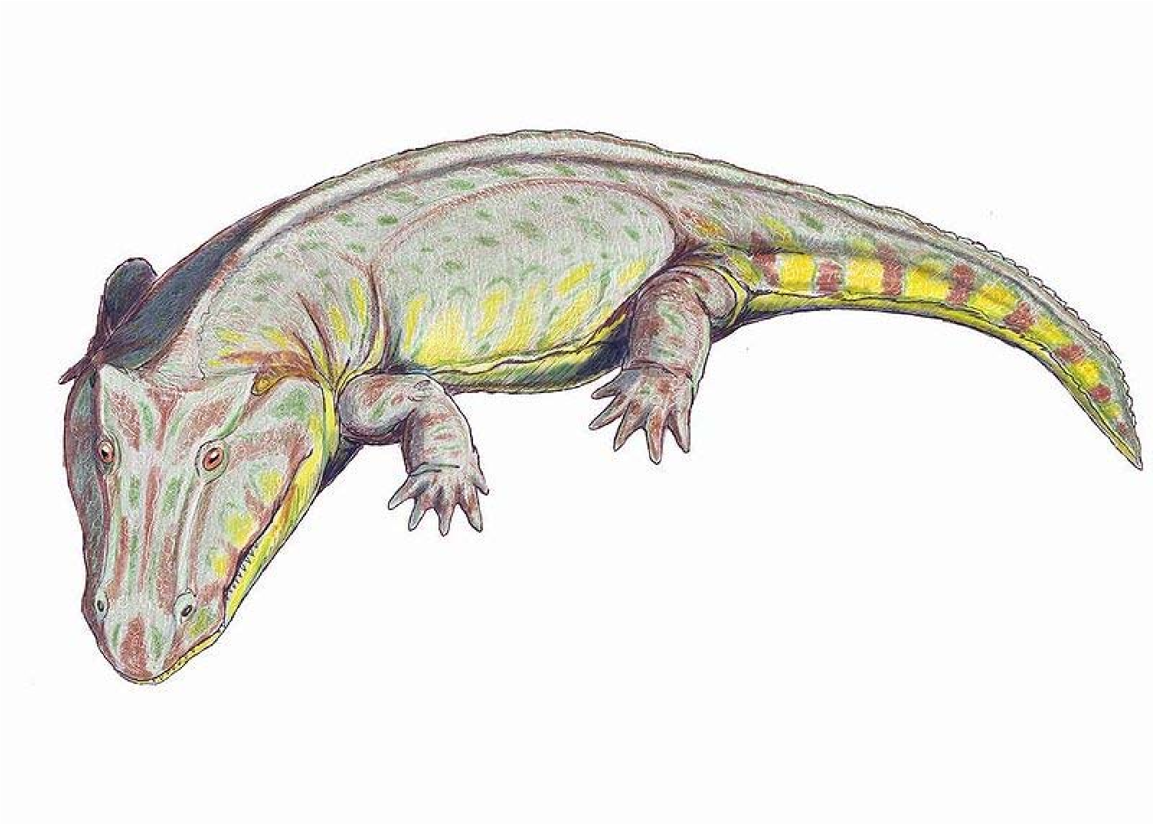
Originally, Temnospondyli were classified according to the structure of the vertebrae. Earlier forms, with complex vertebrae consisting of a number of separate elements, were called "Rachitomi", and large Triassic aquatic forms with simpler weaker vertebrae were called "Stereospondyli"; and these two types were considered suborders of the order Temnospondyli.

In the Rachitomous condition the intercentra were large and wedge-shaped, and the pleurocentra were relatively small blocks that fitted between them. Both elements supported the neural arch, and well-developed interlocking zygapophyses strengthened the connections between the vertebrae. The strong backbone and strong limbs let many ratchitomes be at least partially, and in some cases fully, terrestrial.

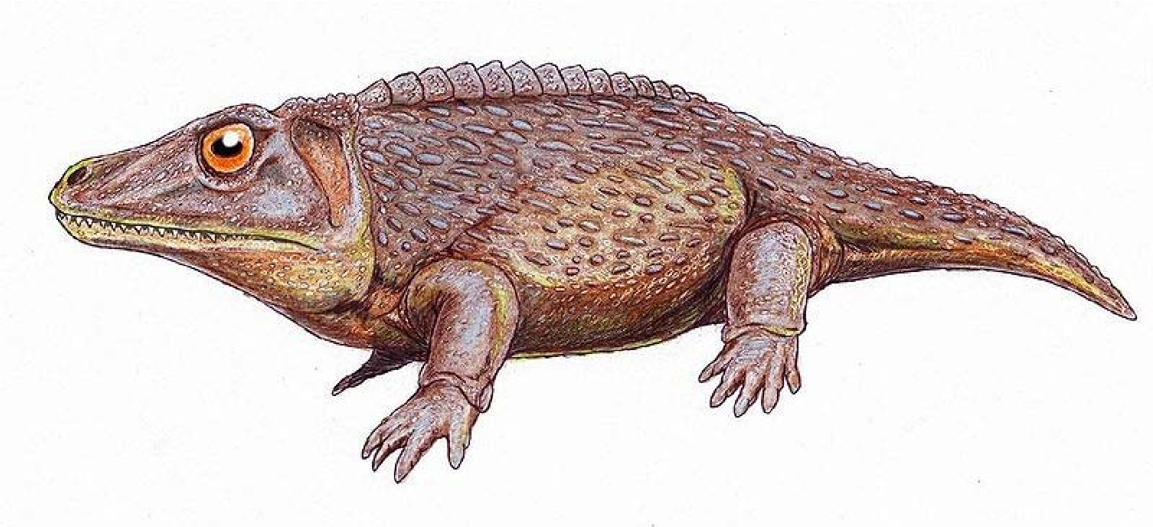
In the stereospondylous condition the pleurocentra have been lost, and the vertebral centra reduced to simple blocks made up of the intercentra only. This weaker type of backbone indicates a more fully aquatic existence.

More recent research has shown that this classification is no longer viable. The basic rachitomous condition is primitive for amphibians (tetrapods) in general. The pure stereospondyls seem to have arisen from different ancestors. Some temnospondyls have rachitomous, semi-rachitomous, and sterospondylous vertebrae at different points the vertebral column of the same individual. Other taxa have intermediate morphologies that do not fit into one or the other category. However, at least according to some analyses, the stereospondyls (minus some ambiguous taxa) can still be considered a clade.

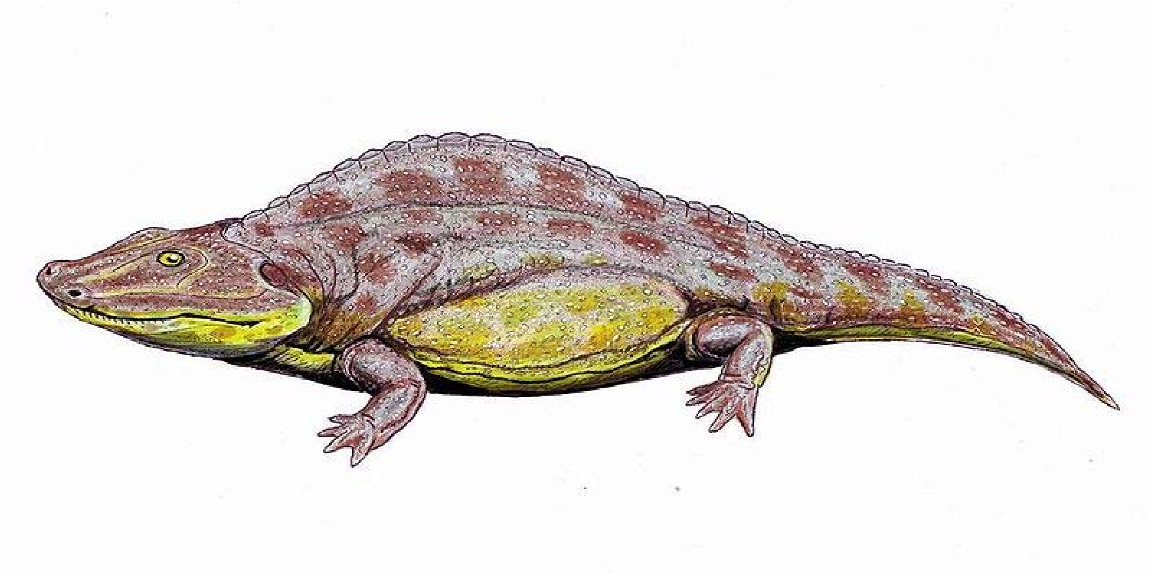
Taxonomy



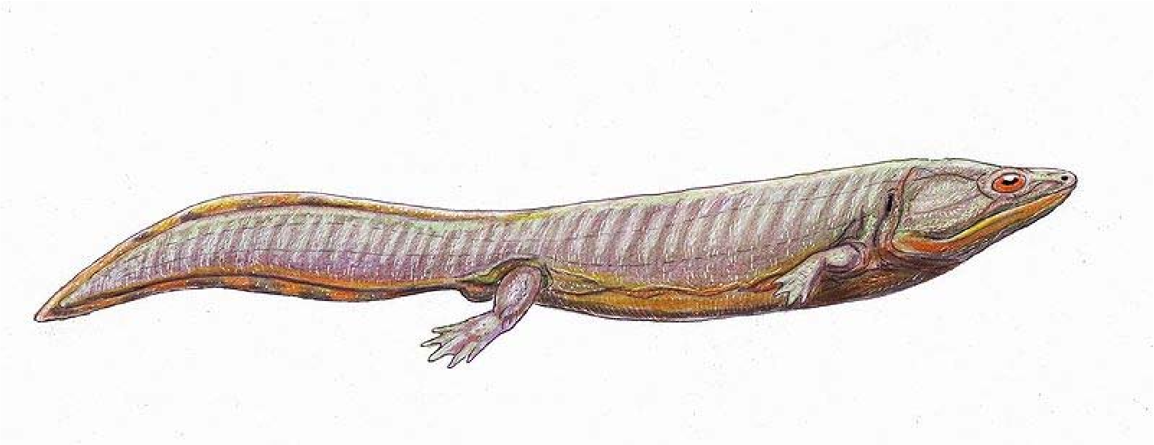
Edops, a basal edopoid.



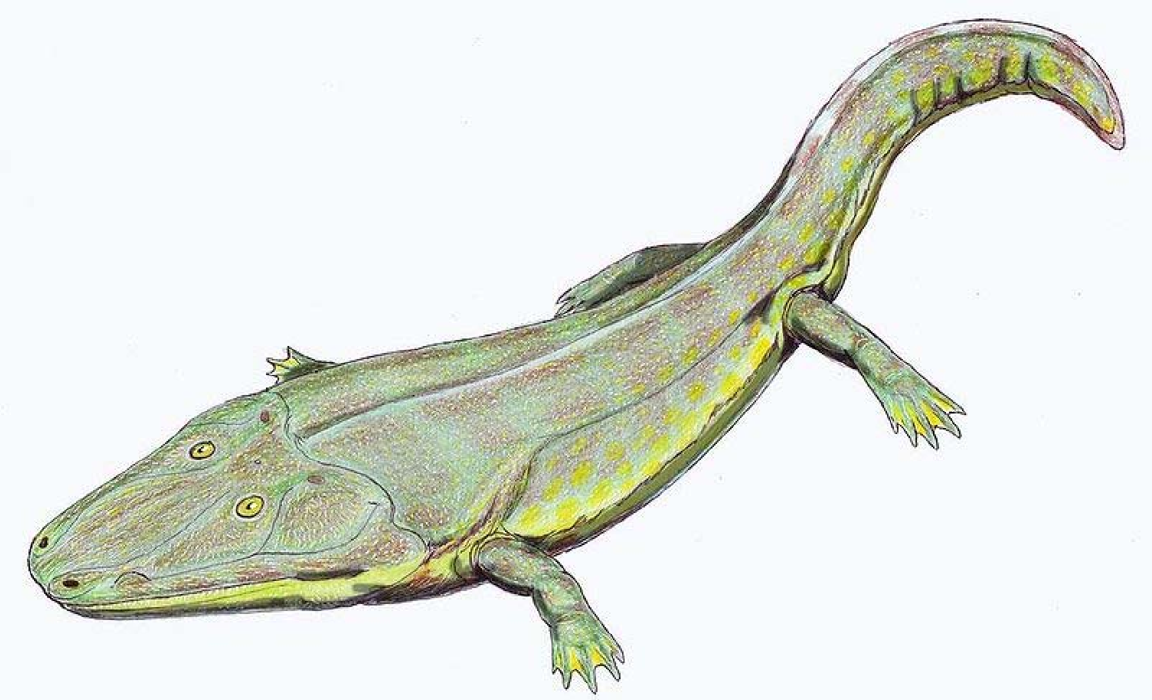
Zygosaurus, a dissorophid.



Sclerothorax, a basal limnarchian.



Dvinosaurus, a dvinosaurid.



Cyclotosaurus, a capitosaurid.

Class Amphibia

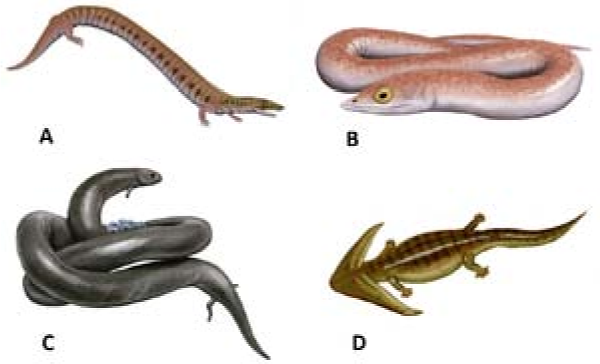
- **Order Temnospondyli**
    - *Saharastega*
    - Superfamily Edopoidea
        - Family Cochleosauridae (Chenoprosopidae)
        - Family Edopidae
    - *Capetus*
    - *Iberospondylus*
    - Family Dendrerpetontidae
    - **Suborder Euskelia**
    - **Clade Limnarchia**
        - Suborder Dvinosauria
        - Clade Stereospondylomorpha
            - Superfamily Archegosauroidea
                - Family Actinodontidae
                - Family Archegosauridae
                - Family Intasuchidae?
            - Suborder Stereospondyli
                - Family Peltobatrachidae
                - Family Lapillopsidae
                - Family Rhinesuchidae
                - Family Lydekkerinidae
                - Clade Capitosauria

        - Superfamily Mastodonsauroidea (Capitosauroidea)
            - Family Heylerosauridae
            - Family Mastodonsauridae
            - Family Sclerothoracidae
    - Infraorder Trematosauria
        - Superfamily Trematosauroidea
        - Superfamily Metoposauroidea
        - Superfamily Plagiosauroidea
        - Superfamily Brachyopoidea
        - Superfamily Rhytidosteoidea

Chapter- 8

Lepospondyli

Lepospondyls
Fossil range: Carboniferous - Permian



Lepospondyli diversity. (*Rhynchonkos* (A), *Phlegethontia* (B), *Lysorophus* (C) & *Diplocaulus* (D))

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	Vertebrata
Superclass:	Tetrapoda
Class:	Amphibia
Subclass:	**Lepospondyli** Zittel, 1888

Lepospondyli are a group of small but diverse Carboniferous to early Permian tetrapods. Six different groups are known, the Acherontiscidae, Adelospondyli, Aïstopoda, Lysorophia, Microsauria and Nectridea, and between them they include newt-like, eel- or snake-like, and lizard-like forms, along with species that don't fit any current category. Various species were aquatic, semi-aquatic, or terrestrial. None were large (the biggest genus, the keraterpetontid *Diplocaulus*, reached a meter in length, but most were much smaller), and it can be assumed that they lived in specialised ecological niches not taken by their more numerous Temnospondyl contemporaries.

Classification

All lepospondyls are characterised by having simple, spool-shaped vertebra, which were not preformed as cartilage, but rather grew as bony cylinders around the notochord. In addition, the upper portion of the vertebra, the neural arch, is usually fused to the centra (the main body of the vertebra) (Colbert 1969).

No clear common ancestors are known, since each of the known clades are already highly specialised when they first appear in the fossil record. It is not known whether the lepospondyls are an artificial (polyphyletic) group which independently evolved similar characteristics of the vertebra, or whether they descended from a single common ancestor.

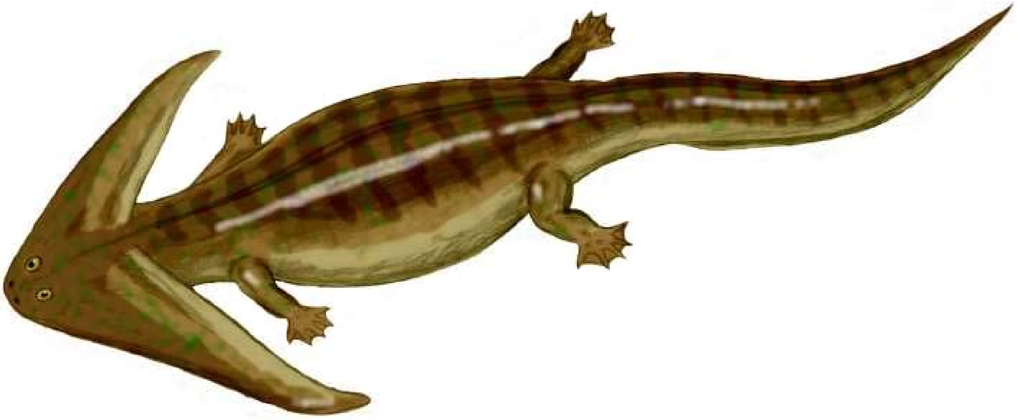
At one time it was thought that some lepospondyls are related or perhaps ancestral to modern Urodela, but not the other modern amphibians, although this view is no longer held. For a long time they were considered one of the three subclasses of amphibians (Romer 1966, Colbert 1969, Carroll 1988). More recently, it has been suggested that the lepospondyls may be related or ancestral to modern amphibians as well as to amniotes (reptiles etc) (Laurin 1996), that they are an artificial grouping with some members related to both extinct and living amphibians (Batrachomorpha) but not amniotes (Benton 2000), or alternatively are a monophyletic group closely related to the ancestry of amniotes but not to recent amphibians (Benton 2004).

Apart from the Nectridea, lepospondyls are limited in distribution to Europe and North America (Carroll 1988).

Taxonomy

Adelospondylus, an adelospondyl.

Ophiderpeton, an aïstopod.



Diplocaulus, a nectridean.

Pelodosotis, a microsaur.

Class Amphibia

- **Subclass LEPOSPONDYLI**
  - **Order Adelospondyli**
  - Family Acherontiscidae
  - **Order Aïstopoda**
    - Family Lethiscidae
    - Family Ophiderpetontidae
    - Family Oestocephalidae
    - Family Pseudophlegethontiidae

        - Family Phlegethontiidae
    - **Order Nectridea**
        - *Arizonerpeton*
        - Family Scincosauridae
        - Family Keraterpetontidae
        - Family Urocordylidae
    - **Superorder Microsauria**
        - Family Odonterpentontidae
        - **Tuditanomorpha**
            - Family Pantylidae
            - Family Tuditanidae
            - Family Hapsidopareiontidae
            - Family Gymnarthridae
            - Family Ostodolepidae
            - Family Trihecatontidae
            - Family Goniorhynchidae
        - Family Brachystelechidae
        - **Order Lysorophia**
            - Family Lysorophidae