Devonian period

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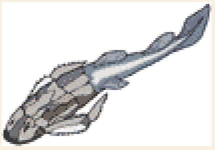
Devonian Period

The Devonian Period - 1

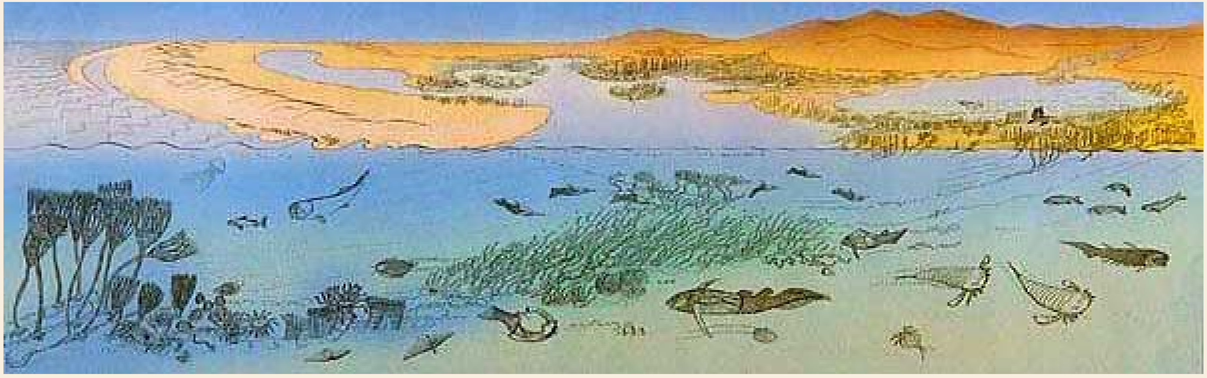
The Devonian Period of the Paleozoic Era: 416 to 359 million years ago

"The Age of Fishes"

Introduction



A time of great transition. In the sea ammonoids and fish evolve and quickly diversify. On land trees and forests appear for the first time. The first insects, spiders, and tetrapods evolve.



To the left a cluster of crinoids wave in the shallow water currents. Nearby are assorted corals and brachiopods. Several types of armoured fish (ostracoderms and Placoderms) swim, or rest on the sandy bottom. To the right are two eurypterids ("sea scorpions"), with an acanthodian fish just above. On land the first primitive plants move ashore.

graphic © from Naturmuseum Senckenberg (Centre for Biodiversity Research)

Geography

image from John A. Long, ed., *Palaeozoic Vertebrate Biostratigraphy and Biogeography*, John Hopkins University Press, Baltimore

In the southern hemisphere the great supercontinent of Gondwanaland (including what is now southern Europe) moves steadily north. But most of the action is happening in the north, where the two continents of Laurentia and Baltica collide, closing Iapetus Ocean and forming a mountain range where sea once was. This is known as the Caledonian Orogeny. At the same time other mountain ranges are thrown up - in southern Laurentia the Acadian/Appalachian, to the west the Antler /Cordillerian, to the north the Ellesmere (along the north margin of

Laurentia) and to the far east the Uralian (in eastern Baltica). The new continent that results from this collision is called Laurussia or Euramerica. During the Devonian the equatorial region was dominated by this newly formed supercontinent, sometimes called the "Old Red continent". It is so called because of its prevailingly reddish, erosion-produced sediments that were deposited in England, Scotland, the Ardennes, and the Rhenish Mountains. The great shallow sandy bays, deltas, and inlets of the Old Red Continent provided a prosperous home for strange armoured jawless fishes, as well as the placoderms which had appeared at this time. To the north again lies the Siberian terraine.

The whole of Euramerica starts to drift northward, whereas Gondwanaland underwent a counterclockwise rotation around the Australian axis. Some of the Chinese blocks and Armorica have started to rift away from the Gondwanan margin. Siberia and the Kazakhstan terranes continued to drift northward.

Both Gondwana and Euramerica are surrounded by subduction zones. They are set on a collision course that will culminate in the formation of a single supercontinent of Pangea during the Permo-Carboniferous.

Devonian maps

Earth 390 million years ago

Stratigraphy

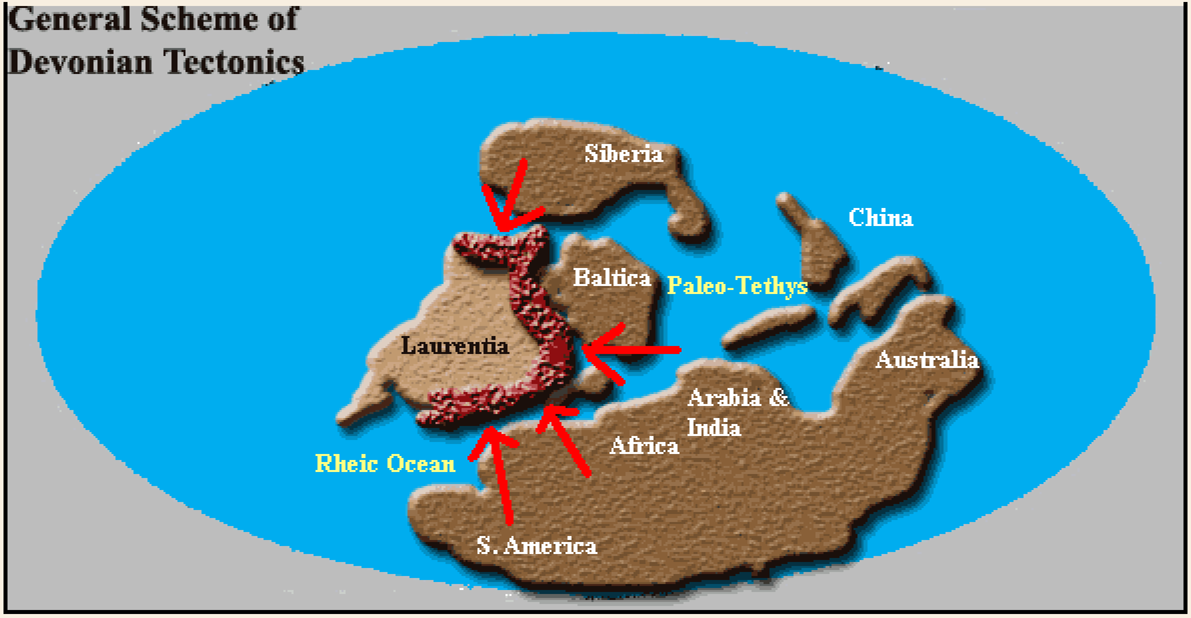
Period	**Epoch**	**Age**	**When began (Harland et al)**	**Duration (Harland et al)**	**When began (ICS)**	**Duration (ICS)**
Carboniferous	**Mississippian**	**Tournasian**	**+362.5 mya**		**359 mya**	**14 my**
Devonian	**Late Devonian**	**Famennian**	**367.0 mya**	**4.5 myr**	**375 mya**	**16 my**
		Frasnian	**377.4 mya**	**10.4 myr**	**385 mya**	**10 my**
	Middle Devonian	**Givetian**	**380.8 mya**	**3.4 myr**	**392 mya**	**7 my**
		Eifelian	**386.0 mya**	**5.2 myr**	**398 mya**	**6 my**
	Early Devonian	**Emsian**	**390.4 mya**	**4.4 myr**	**407 mya**	**9 my**
		Pragian (=Siegenian)	**396.3 mya**	**5.9 myr**	**411 mya**	**4 my**
		Lochkovian (=Gedinnian)	**408.5 mya**	**12.2 myr**	**416 mya**	**5 my**
Silurian	**Pridoli**		**410.7**		**419 mya**	**3 my**

Coccosteus. For a discussion of Devonian paleogeography which ought to be on Palaeos, but isn't, see **Paleogeografica e Orogenesi** from the same site.

Climate

If the Devonian was

the Age of Fishes. Devonian climatology is the Age of Baloney. Reported results vary strongly depending on what climate proxies are used and where they are studied. Historically, the Devonian has been regarded as largely warm and equable, with a disastrous drop in temperatures in the Late Devonian leading to the Frasnian-Famennian "mass extinction(s)." The reason for this impression may be that most work was traditionally done on the "Old Red Continent," *i.e.*, the shallow marine sediments of the seas around Euramerica.



A careful examination of the paleoclimate maps at the **Paleomap Project** site suggests a different global picture. *See* climate maps of the Early Devonian, Middle Devonian, and Late Devonian. The climate of the Early Devonian is rather strongly zonal, with a narrow equatorial tropical belt, broad subtropical arid zones extending to about 35° latitude, and a temperate zones extending essentially to the poles. There is little change in this general picture at any time in the Devonian. In the Late Devonian, the southern "cool temperate" zone expands, with indications of glacial ice in parts of far western Gondwana (northern South America). However, the *northern* temperate zone appears to retreat before a subtropical zone which extends almost to 60° N. So, although parts of the south were cooler, parts of the north, which had very little land area, were becoming warmer. In short, we are not looking at a simple pattern of planetary cooling.

Instead, we would suggest that the observed effects can be accounted for by a modest drop in sea level combined with a series of local changes related to the formation of the Pangean supercontinent and the spread of land plants. To appreciate the problems, we need to briefly review the tectonics of the period. As we approach the Late Devonian, Pangea is beginning to take shape. This involved pressure on the Laurentian continent from three sides, as well as gradual closure of the seaway between the Rheic and Paleotethys Oceans. As the pressure on the Laurentian plate increased, huge mountain ranges were thrust up around the periphery of the continent. At about this same time, plants were also beginning to make an impact on the land surface and on atmospheric chemistry. Carbon dioxide levels were still several times higher than in present times, but may have dropped as much as 80% from the Silurian. In addition, the Late Devonian saw the evolution of large trees with deep root systems. These strongly increased terrestrial weathering, with a corresponding draw-down of carbon dioxide.

With these generalities in mind, it is easier to appreciate what was happening on a local level. For most of the Devonian, South America had been invaded by a very shallow sea. Further, the broad connection between the largely equatorial Paleotethys and the deep southern Rheic Oceans probably moderated climates all along the northern coast of Gondwana. In the Late Devonian, that connection remained open, but it was constricted, and deep ocean circulation was probably cut off entirely. The Rheic became colder and more thermally isolated. The flow of warm water from the Paleotethys decreased along the north coast, and the falling sea levels drained the central shallow sea. In addition, as South America began to move north, it emerged from the south polar zone of air circulation into a zone dominated by the trade winds passing east to west. Instead of receiving relatively warm, moist air from the Rheic which might create seasonal rains, northern South America would be exposed to cold air dehydrated by the long passage across the entire Gondwanan continent. Thus, it is not surprising that we observe periods of glaciation at high altitudes in northern South America.

Laurentia was also in the southern trade winds. These winds would carry moisture from the Paleotethys. However the mass of the continent lay in the rain shadow of the mountains raised by the subduction of the Gondwanan and Baltican plates, as well as numerous microplates around the eastern and southern margins. The internal geography of the continent was dominated by desert, with an accumulation of evaporites which, when used as climate proxies, may well suggest a hotter climate than was actually present.

Along the well-studied coasts of Baltica and Laurentia, marine chemistry would have undergone enormous changes. The rain which was *not* falling on central Laurentia and South America *was* falling on the eastern and southern slopes of the ring of mountains around Laurentia. Forests were beginning to grow here, with deep-rooted trees stirring up soil ions which would be swept into the narrow oceans with torrential flows of fresh water. While the precise results of this process are impossible to reconstruct, it almost certainly meant great changes in ocean chemistry and plankton populations, as well as the usual result of excess runoff -- algal blooms.

While it seems unlikely that this extended exercise in geochemical speculation hits very much closer to the truth than anything else, it may serve as a reminder that local conditions often matter a great deal more than global generalities.

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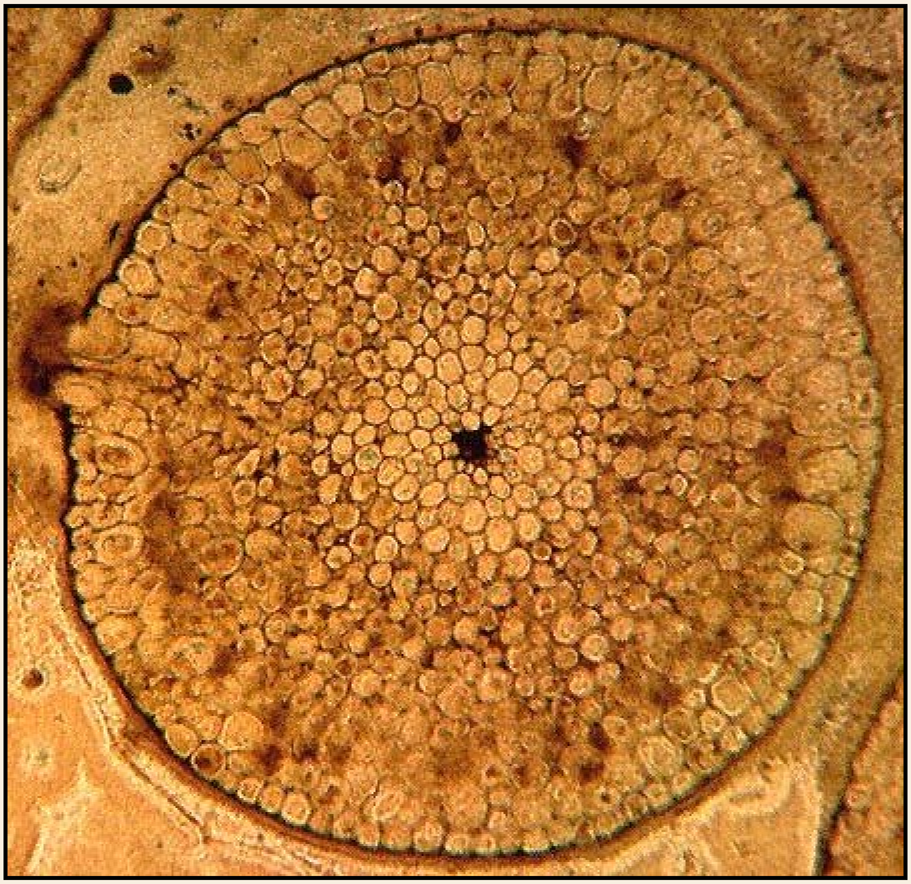
Devonian Sites: the Rhynie Chert



The most famous of the Devonian Lagerstätten is the Rhynie Chert from Scotland. This deposit is dated as from the Pragian Age of the early Devonian. Paleogeographic reconstructions and other evidence suggest the environment was tropical to subtropical. This deposit is a petrified peat bog preserving the plants in exquisite anatomical detail in the place where they grew and died.

Fossils from the Rynie Chert were buried in short-lived freshwater deposits that later were subjected to replacement of organic material with silica, forming a chert deposit that preserved even details of the cells of the organisms.

The peat species include *Aglaophyton* (formerly *Rhynia major*), *Horneophyton*, *Nothia* and the lycopsid *Asteroxylon*, but the only plant preserved exactly in its growth position is *Rhynia gwynne-vaughanii*.

The preservation of all these plants is so fine that individual cells can be seen. The detail of preservation shows, for example, that the stomata of *Rhynia* were connected to an extensive intercellular system of air spaces, essential for the ventilation of a land plant, and that groundwater was absorbed through unicellular hairs on the horizontal stems. The plant assemblage itself is interesting for the Early Devonian in that its members are not recognized or recorded elsewhere in Euramerica.

It is impossible to determine how typical the Rhynie Chert flora was of the wetter areas of Euramerica. Other Early Devonian assemblages contain plants with far greater amounts of thick-walled structural tissues, and are thus thought to have lived in places subjected to much drier periods.

As well as a number of types of land-plants, Fungi, including mycorhizal fungi, have been recovered from the Rhynie Chert. Wefts of fine, sparingly septate hyphae, some terminating in vesicles, which occur within degraded tissue of vascular plants, are usually identified as a saprotrophic fungus (*Phycomycetes*), but thick-walled spore-like bodies superficially similar to those of endomycorrhiza (*Endogone*) suggest that the fungal hyphae lived in symbiotic association with the vascular plants even at that early stage of terrestrial evolution, just as they do today.

Also found are algae, including mats of filamentous blue-green algae, a charophyte green alga called *Palaconitella*, and filamentous green algae.

Small arthropods are exquisitely preserved between the plant stems and within sporangia. They include crustaceans, a springtail (Class Colembella), several small mites, the first spider and numerous larger extinct mite-like arachnids called trigonotarbids. The trigonotarbids probably preyed on other arthropods while the insects and mites ate spores, leaf-litter, and microorganisms or sucked plant sap, as the associated wounded plant stems suggest.

Image: *Rhynia gwynne-vaughanii* stem cross section, from the Rhynie Chert in Scotland. Image cropped and reduced by M.J. Farabee, originally from rhynie.html. MAK021023

For more Devonian sites: **Coccosteus site**

Rhynie Chert Links

The Biota of Early Terrestrial Ecosystems: The Rhynie Chert - Ongoing research into the stratigraphy, sedimentology and paleontology of an Early Devonian hot spring, by The Rhynie Chert Research Group: Aberdeen - **Best on the Web**

The Rhynie Chert - good coverage by University of California Museum of Paleontology site. MAK021023

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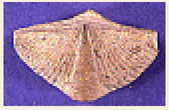
The Devonian Period - 2

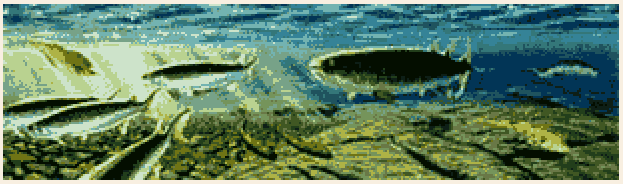
Devonian Life

image from Earth History Resources

The warm tropical oceans of the Devonian period abound in fish, nautiloids, corals, echinoderms, trilobites, and conodonts. A typical reef of this time is shown here. The yellow flower-like organisms are crinoids, an echinoderm only distantly related to starfish and sea urchins. The sea anemone like organisms with the thick stems (including the big one in the center) are Rugose corals. At the bottom right a trilobite can be seen crawling over a tabulate coral. In the background at the upper right are sponges.



Types of marine life: In Devonian seas, sponges were represented by newly evolved siliceous forms, many of which were similar to the modern Venus flower basket. The association between algae, sponges, and corals that began in the Ordovician continued, with flourishing reefs, such as the one illustrated in the above diorama, thriving in the warm shallow seas. During this time not only the hylaesponges, rugose and tabulate corals (shown above) but also the brachiopods reached their zenith in number and diversity. The spiriferid brachiopods (left) were particularly abundant. Among molluscs, while gastropods, bivalves, and nautiloids continue with little change from the Silurian, the first ammonoids mark the beginning of an important new phase of molluscan evolution. Trilobites were generally on the decline, but a few groups remained abundant, and some giant forms evolved, such as the huge spiny *Terataspis grandis* (30 to 60 cm). The increase in swimming predators (such as new forms of fish and cephalopods) may have contributed to the trilobite decline.



The Devonian saw the rapid evolution diversification of fish, especially the Placodermi, primitive sharks, Sarcopterygii (lobe-finned fish and lungfish) and Actinopterygii (conventional bony fish or ray-finned fish). So pronounced is this evolutionary radiation that the Devonian has been called "the age of Fish".

Terrestrial life: Many arthropods, including eurypterids, arachnids (spiders and their kin) and primitive wingless insects invaded the land. Towards the end of the period the first fish-like tetrapods move ashore. Seed-bearing plants (Gymnosperms) also appeared during the latest Devonian. Seeds mean a freedom from dependence on moist habitats for reproduction, and allowed plants to expand into drier areas.

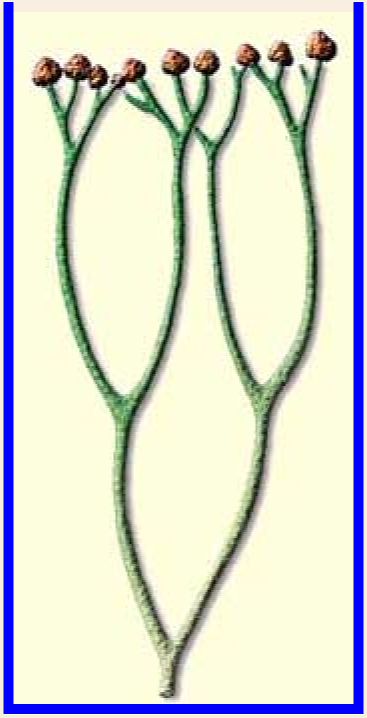
There is a major mass extinction during the Late Devonian (the so-called Frasnian-Famennian event). The tabulate-stromatoporoid reefs disappear completely, with corals so seriously decimated that extensive reef building did not happen until the Triassic with the evolution of a new group of reef-building corals, the scleractinians. Brachiopods, trilobites and primitive fish groups either were either diminished or completely killed off, as were many planktonic and nektonic (floating and swimming) animals. The planktonic graptolites and enigmatic tentaculites die out and trilobites are much reduced. Tropical taxa were the most severely affected. The effect on terrestrial ecosystems was not as marked.

Various causes have been suggested. Global cooling tied to Gondwanan glaciation has been proposed as the cause of the Devonian extinction, as it was also suspected of in the case of the terminal Ordovician extinction. Support for this hypothesis comes from the fact that the forms of marine life most affected by the extinction were the warm water to tropical ones. Another hypothesis is that environmental sea-level and climatic change in conjunction with an extraterrestrial impact (comet/asteroid) caused a global cooling. There are several impact sites known to be of the right potential age to have been involved in this extinction. But neither the glaciation or the impact hypothesis is unequivocally supported by the available data.

Cross-reference:  **Coccosteus site**.

Plants

The subject of Devonian plants is one that has occupied numerous scholars for their entire professional lives. Obviously, we are not going to be able to do it justice here. We have discussed various aspects of the matter in connection with the Rhynie Chert. At Paleozoic Plants, we include a few paragraphs specifically on Devonian plants, with links to more extensive treatment of individual taxa.. Finally, we include links to several of the many good web sites on this topic below. Consequently, there is no obvious need for yet another summary of this topic here – assuming we cared whether or not there was a need. As the astute reader will already have perceived, that sort of utilitarian calculus is rarely involved in decision-making at Palaeos – assuming an astute reader would be reading Palaeos at all, instead of some more authoritative source. But enough of this dizzying ontological circuity. Let us attend



to the subject at hand.

The Devonian Period was, for plants, a sort of Cambrian explosion. Plants began the Devonian, just as animals began the Cambrian, with a small amount of important, but largely cryptic diversity. That is, some of the important groups had already diverged, but we have not yet found much of that divergence in the fossil record. Just as almost all kinds of animals looked more or less like flatworms in the earliest Cambrian, almost all land plants looked more or less like *Cooksonia* at the end of the Silurian. Important specializations had already occurred, but they are hidden by a poor fossil record of small plants which all look more or less the same. However, by the end of the Devonian, plants had adapted to land in many different forms. They had evolved structures capable of raising dense forests up to 30 meters against the force of gravity (*e.g.*, *Archaeopteris*); and were making far more effective use of the resources available to them. However, the "explosion" of forms consisted largely in developing and refining the key evolutionary innovations already present at the beginning of the Period.

The structure of this revolution is revealed by comparing *Cooksonia* with Late Devonian plants. *Cooksonia* itself was already a vascular plant with the key features of the true vascular land plants **[1]**. That is, it had a specialized vascular system (*tracheids*) composed of the cell walls of dead cells (*xylem*) to transport water and nutrients upward. The walls of the tracheids were somewhat thickened to support the stem against gravity. However, the amount of reinforcing material was small and it may not have been the *lignin* (woody tissue) of later tracheophytes. *Cooksonia* also had tiny, adjustable vents (*stoma*) for gas exchange, and well-developed *sporangia* (spore-bearing reproductive structures). Although it lacked a massively reticulated root system, it did have a sort of taproot and ground-level side branches (*rhizomes*), both bearing root hairs. What it lacked were leaves, the massive lignin supports of more derived plants, and seeds. These were acquired in approximately that phylogenetic order.

Cooksonia itself is a member of the rhyniophytes, the basal radiation of vascular plants (Tracheophyta). In broad outline, the Devonian progress of the group looks like this:

```
TRACHEOPHYTA
|--rhyniophytes = "Rhyniopsida": paraphyletic, includes
Cooksonia
`--+--Lycophyta: lycopods (club moss) and zosterophylls
   `--+--Monilophyta: horsetails & ferns
      `--+--Trimerophytopsida: Trimerophyton, Psilophyton & Pertica
         `--Progymnospermopsida: seed plants and a few others
```

Some of the rhyniophytes had already developed "spikes" and various other excuses for increasing surface area to catch more sunlight. The problem is that more surface area also means faster water loss by evaporation. It took a bit longer to evolve the waxy covering that allows plants to form broad leaves. Leaves are present in all of the more derived groups, and seem to have developed at first by growing "webbing" of photosynthetic tissues between small twigs.

Wood is also a Devonian innovation. Wood means axial strength, which means the ability to grow taller to reach open sunlight and to carry a greater weight of branches and leafy, photosynthetic surface per meter of height. Thus it is no surprise that we go from the rather flaccid stems of *Cooksonia* to the true wood of progymnosperms by the Middle Devonian. As soon as the environment of land plants came to be dominated by other land plants, the race would be on to join one of the four great plant guilds: (a) **trees** (tall-growing plants that shade out the competition), (b) **shrubs** (low, shade tolerant, densely growing plants that crowd out competition), (c) **weeds** (fast-growing, opportunistic, adventitious plants that outrun competition by spreading quickly through temporarily open spaces) and (d) **survivalists** (hardy plants that colonize marginal environments where no competitors can live). Wood is plainly an essential for members of the tree guild.

monilophytes and trimerophytes developed refinements of the vascular system, particularly secondary xylem and, in progymnosperms, *phloem*, the specialized vascular tissue that moves the products of photosynthesis down from the leaves to other regions of the plant. This suggests that these plants first developed as shrubs, selected for dense, efficient growth.

It was left to the Carboniferous to develop the seed, a device which, like the amniotic egg of vertebrates, allowed plants to spread far from open water. However, by the end of Devonian, both plants and vertebrates were solidly established on the terrestrial margins and poised to colonize the interior highlands.

Links: The Earliest Land Plants; Devonian Times; Introduction to the Progymnosperms; Lab VII - The Origin of Seed Plants (2).

Image: the image of *Archaeopteris* was adapted from the incomparable materials at **Biodidac.** ATW040711.

Links

The Devonian - the best over-all introduction.

The Devonian Page - nice basic intro - easy to understand - actually a class project

Devonian Times - all about the first tetrapods (four-legged animals). Gives an excellent coverage of the new paradigm that the first tetrapods amphibians were not so much crossopterygian fish crawling on land to a new pond to escape drought (and only evolving legs afterwards), but rather **fish with legs** (i.e. legs evolved *before* moving on land).

The Devonian 'Great Barrier Reef' in what is now West Australia

Browse the Fossil Gallery - Devonian Period - a small selection of Devonian fossils from Nova Scotia

Devonian Age of Kentucky - the fossils of this time and two illustrations

The Devonian Period in Victoria - some photos of fossils from Victoria (South-East Gondwana)

The Great Devonian Controversy : The Shaping of Scientific Knowledge Among Gentlemanly Specialists by Martin J. S. Rudwick - the history of science, relating to the 19th century discovery of Devonian-age rocks

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[1] Phylogenetic taxonomy has not caught on completely among paleobotanists, with the result that there is still a certain amount of pointless debate about exactly what characters should be used to define the Tracheophyta. We respectfully submit that characters should never be used to define taxa at all. Tracheophyta ought to be defined as all organisms more closely related to mangroves than to moss (or some equivalent). Then we could move on to the real job of figuring out what they have in common and who belongs to the group. *See* discussion at Cladograms.

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The Early Devonian

The Early Devonian Epoch of the Devonian Period: 416 to 398 million years ago

Early Devonian land plants
from *Prehistoric Animals*, J. Augusta, illust. by Z. Burian, (Paul Hamilyn, London, 1960), pl.5, and *Life Before Man* by Zdenek V. Spinar, illustrated by Zdenek Burian

Plate Tectonics

During the Early Devonian, the microcontinent of Avalonia collided with the northeastern part of the Laurentia (by now part of the Euramerican continent). This collision produced the Acadian Mountains, which rose in present-day New England and the Canadian Maritime Provinces. This was a large mountain belt with topography perhaps like the present-day Rocky Mountains of western Canada. The eroded roots of the Appalachian Mountains still extend from the southeastern United States to Newfoundland, and form the highland areas of Atlantic Canada. On the opposite side of Euramerica, collisional tectonics took place at the western margins of the Russian Platform, and orogeny took in the Urals and Scythian region. The East-European Platform suffered uplift and inversion tectonics; transtensional basins originated inside the Pechora basin.

Early Devonian Life

Marine Life

Marine Biogeography

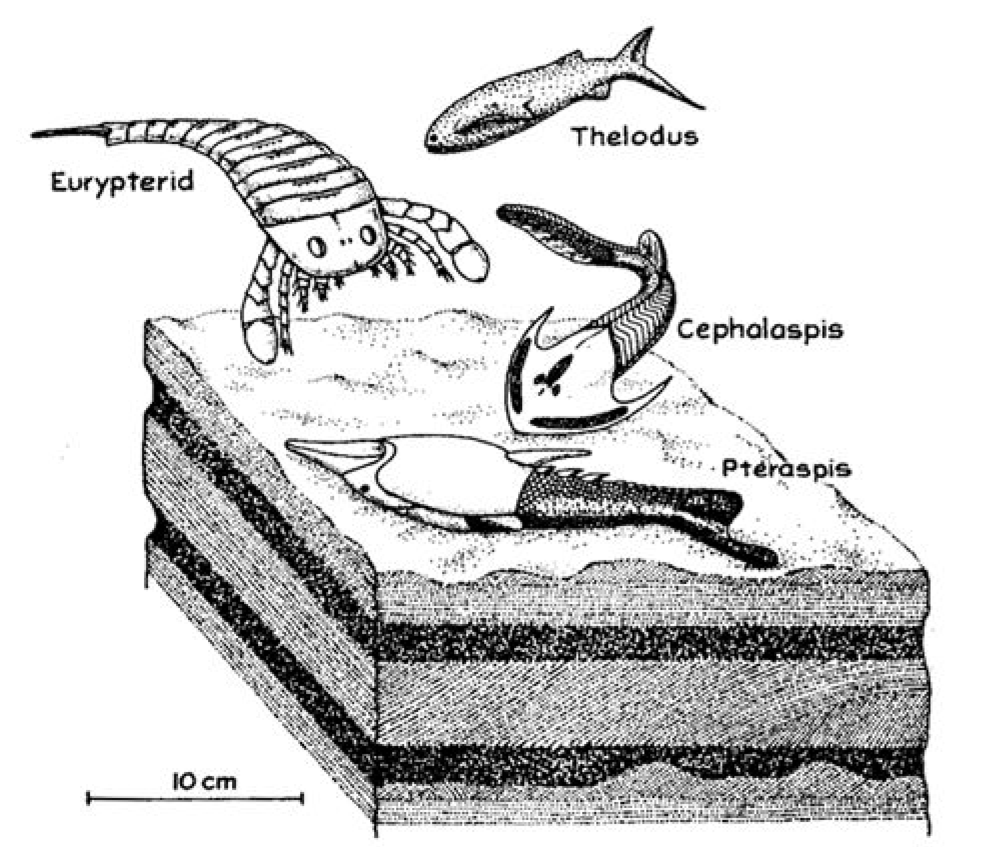
Study of Devonian brachiopod distribution by A. J. Boucat during the 1960s first revealed the existence of three major faunal provinces: (1) Old World province; (2) Appalachian province; and (3) Malvinokaffric province. Distribution of gastropods and other marine invertebrates confirm these conclusions.

The Old World and Appalachian provinces were already in existence at the beginning of the Devonian, although their endemism (the degree to which the biota of that region are unique and found nowhere else) was not very pronounced. It increased as the Devonian wore on, reaching a peak during the later Early Devonian and Middle Devonian time.

Brachiopod faunas

The Malvinokaffric province is characterized by a restricted fauna in which some important groups of brachiopods, such as Atrypida and Gypidalids, are absent. Typical Malvinokaffic genera are *Australospirifer*, *Scaphiocoelia*, *Pleurothyrella* (with unbranched ribs), *Notiochonetes*, *Tanerhynchia*, and *Australocoelia*. These are accompanied by a number of typical Appalachian forms such as *Protoleptostrophia* and *Plicoplasia*. The bulk of the Malvinokaffric brachiopod fauna would seem to owe its origin to Appalachian province forms [ref. Johnson and Boucot].

Marginal Marine Bays and Deltas, and Brackish water environments



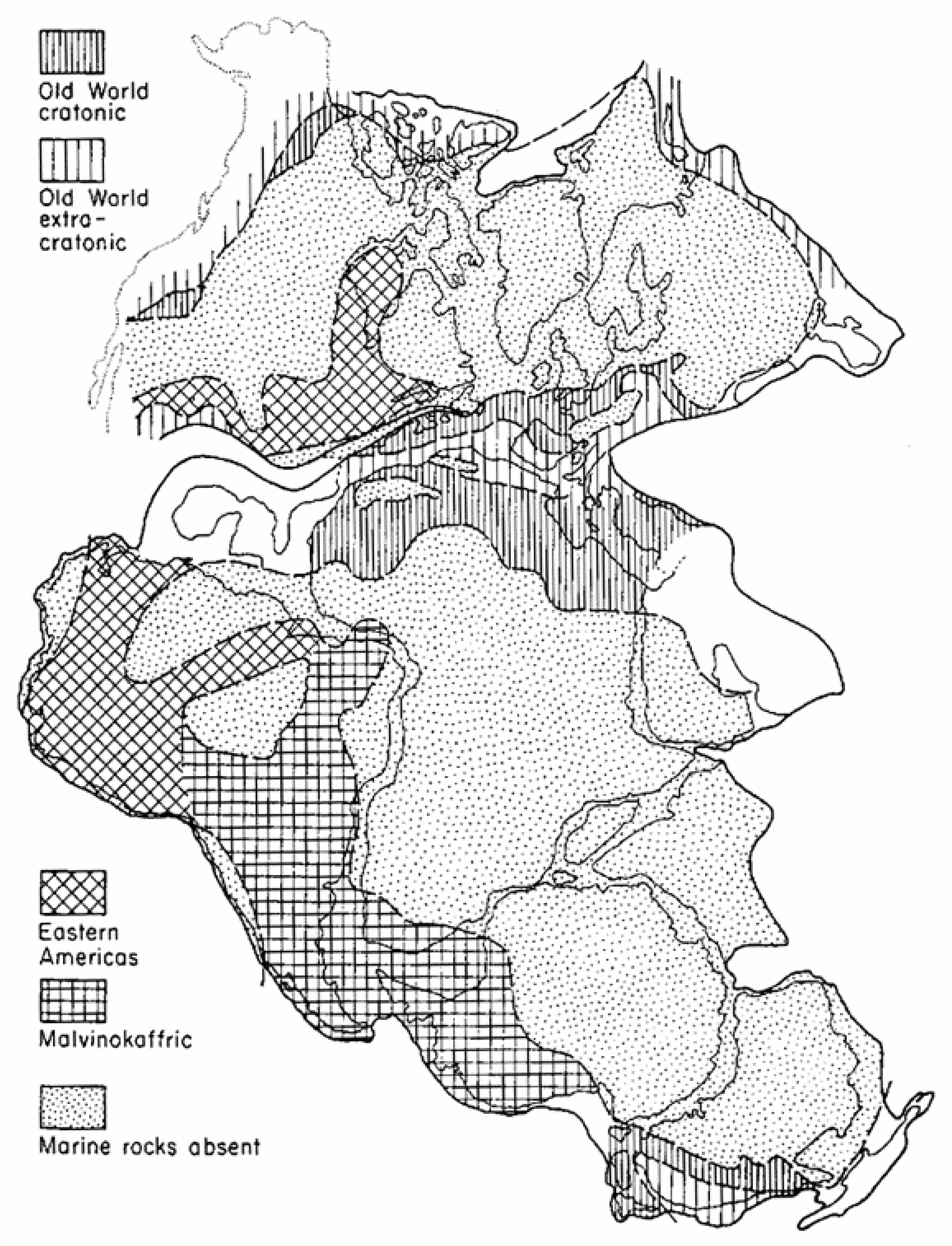
The alluvial environments of the Early Devonian of Euramerica were inhabited by many species of jawless fishes (e.g. *Cephalaspis* and *Pteraspis*) and eurypterids. Placoderm and osteichthyan (bony) fishes are rare in these environments: all, however. may have had recourse to the sea during their life-cycles. The thelodonts especially seem to have been geographically widespread at all stages of their existence.

from D. L. Dineley, *Aspects of a Stratigraphic System: the Devonian*, 1984, Macmillan, p.74

The variety and abundance of marginal marine, estuarine, brackish and freshwater animal life continued to increase throughout the Early Devonian period. Most representative were the diverse types of jawless fish, shown above, including many bizarre armoured forms.

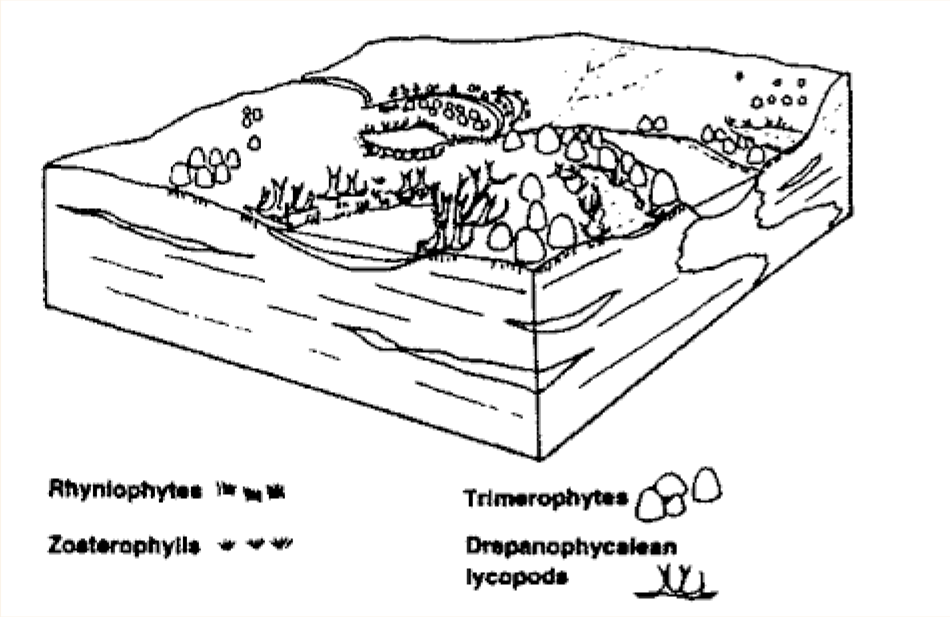
Invertebrates included lingulid brachiopods, bivalves, ostracods, eurypterids, limulids, scorpions, and trilobites.

Vertebrates included a diverse selection of jawless fish (especially the armoured ostracoderms, see above illustration), which are at their height, and rare acanthodians, arthrodiran placoderms, sharks, and lobe-finned fish. The sort of vertebrates that prospered in these marginal marine environments were quite geographically limited. Apart from the thelodonts, they were unable to swim out into the open ocean (perhaps weighed down by their heavy armour), and moreover especially in the case of the jawless fish they could only feed on small organic particles washed down by streams, or on tiny organisms that lived in the mud near shore. Because the early Devonian world was divided into a number of separate island continents, the ostracoderms and placoderms evolved in complete isolation for tens of millions of years, so that completely distinct types of vertebrates inhabited each continent. There is no real counterpart to this in the post-Devonian world. It is as if there only birds in Africa, mammals in Europe, fish in Asia, amphibians in North America, reptiles in South America, etc. (A less extreme but similar situation occurred during the early Tertiary, with different mammalian groups evolving in isolation).



Streams and freshwater environments were not as well inhabited. However, branchiopods, crustaceans (clam shrimps, fairly shrimps and their relatives), ostracods, limulids, eurypterids were probably present, along with various fish types.

Life on Land - Plants and Invertebrates



Plants: Terrestrial vascular plants are still generally small and restricted to the water's edge during the Early Devonian. These forms include the rhyniophytes, zosterophyllophytes, Drepanophycalean lycopsids, and (at the end of early Devonian) Trimerophytes, all of which were true vascular plants with conducting vascular tissue, stomata, and a cuticle to protect against drying. But they were still small forms, lacking proper roots and woody tissue, and hence were unable to grow beyond the height of small bushes. Reproducing by spores, they were confined, like the Silurian *Cooksonia*, to moist, lowland habitats.

Aschelminthes: although such tiny organisms rarely or never leave fossils, it is quite certain that various primitive microscopic organisms as Nematodes and Rotifers had also established themselves on land.

Arthropods: By the Early Devonian the terrestrial invertebrates (arthropods), were well established. The emerging terrestrial plants provided comfortable micro-habitats, food and shelter, for a variety of invertebrates, including fully terrestrial arthropleurids, arachnids (trigonotarbids, spiders, and mites), myriapods (predatory centipedes and herbivorous millipedes), and flightless insects. Several semi-aquatic groups, such as the xiphosurans (horseshoe-crabs), eurypterids, and scorpions, also would venture onto land.

Links

Links

The History of Palaeozoic forests - the earliest land plants

Devonian Times - Going Upstream

The Biota of Early Terrestrial Ecosystems: The Rhynie Chert

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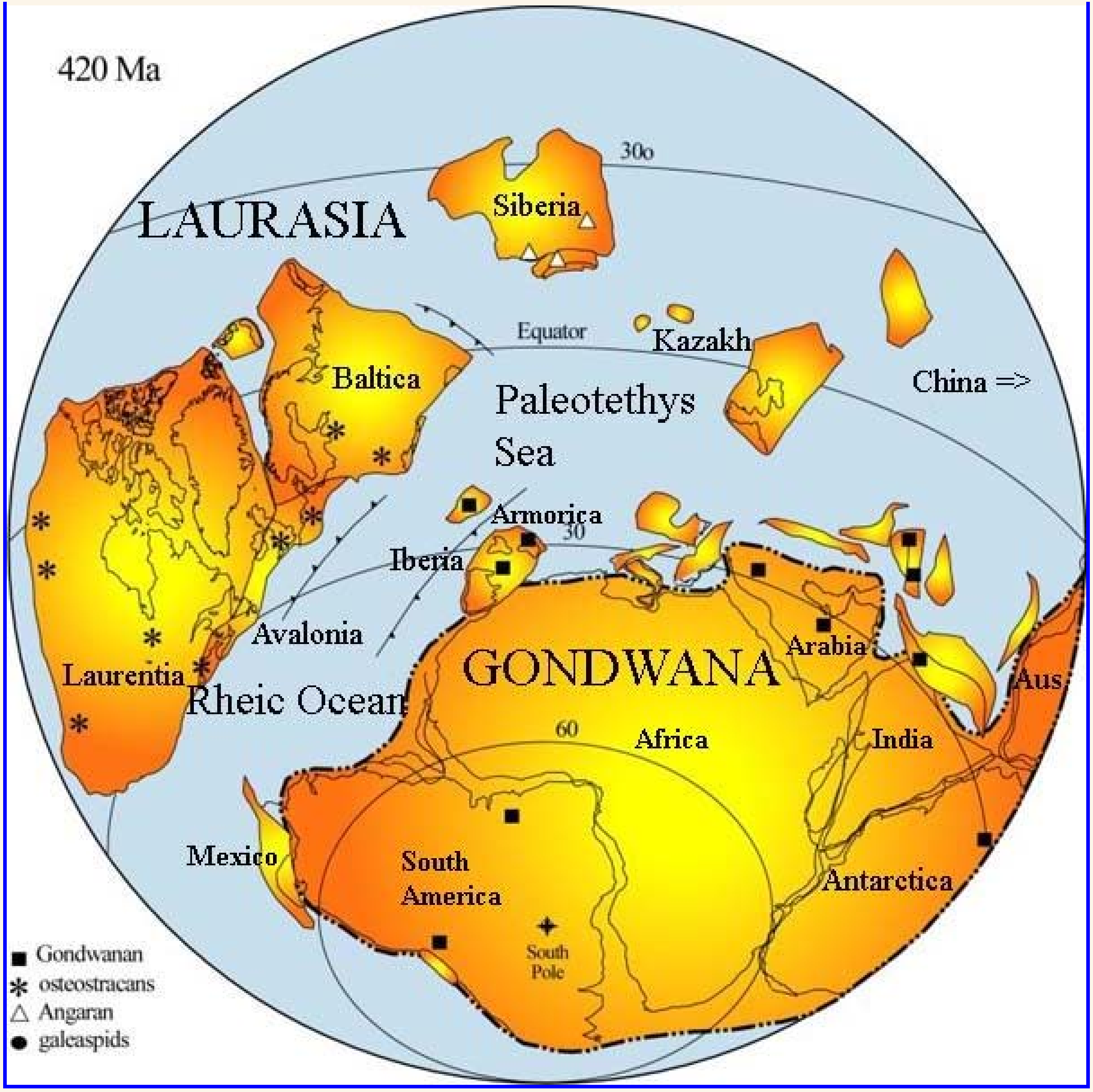
The Lochkovian

The Lochkovian Age of the Early Devonian Epoch: 416 to 411 million years ago

The Geography of the Lochkovian Age

Because of uncertainties about the timing of plate convergences, this particular globe looks much like the globe of the Ludlow Epoch of the Silurian. However a number of differences are well-documented. For example, by this time, the coalescence of Avalonia and



Baltica with North America was complete and no trace remained of the Iapetus Ocean between Avalonia and Laurentia (North America). This did not mean that the geological effects of this collision were over. The Acadian Orogeny continued throughout the Devonian, making the Appalachian area a volcanically active region, and the Scandian Orogeny likewise affected Baltica in the early part of the Devonian.

Furthermore, the entire Laurasian landmass was beginning to move closer to Gondwana, a process which would later result in the formation of the world- continent of Pangea. However, during the Lochkovian, there was still some significant degree of separation -- not only between Laurasia and Gondwana, but also between Laurasia and Siberia, which was still north of the Equator.

The map shows how we know this. The Devonian is called the "Age of Fishes," and with good reason. The Devonian, and the Lochkovian in particular, is the first time when vertebrates become quite common in the fossil record. However *which* fishes we find in this Age depends on where we look. The Angaran faunal province of Siberia was characterized by amphiaspids and other profoundly derived Heterostraci. Laurasian waters were dominated by the Osteostraci, a very different group of jawless fishes. The Gondwanan fishes were different, yet again, and included galeaspids and gnathostomes.

Gnathostomes, fishes with jaws, are first found in numbers in the Ludlow or Pridoli of China, located on the long Sino-Australian peninsula on the other side of Gondwana. By Lochkovian times, gnathostomes were making an important contribution to the fish populations of South China, and were rapidly expanding southward through Australia and Antarctica into the cooler waters of the Gondwanan mainland.

The point of all this is that the different fish communities were *endemic*. That is, they were restricted to particular geographical regions. The most logical explanation is that significant ocean barriers to movement remained between Siberia, Laurasia and Gondwana. The fishes of this age were able enough coastwise swimmers. But few, if any, were equipped to survive in the open ocean.

While Laurasia was drifting southward towards Gondwana, it was also turning counterclockwise, bringing the broad Southern peninsula of Laurentia (the southeastern United States) very rapidly toward South America and Mexico. Some believe that these terranes actually came in contact as early as the Lochkovian. On the North end of Laurasia, Siberia was continuing to drift toward Baltica and was rotating clockwise. This also accelerated the approach of these two terranes. Thus, at least by late Lochkovian or Emsian times, the faunal endemism of the various continents was beginning to break down.

The position of the Chinese plates is quite uncertain during the Lochkovian. South China, at least was probably close to Australia, if we may judge from the increasing pace at which Chinese fishes were emigrating southward. However, North China was apparently rather isolated at this point, and its location is unclear. Another point of contention is the state of Iberia and Armorica, *i.e.* Spain and France. According to some sources these miniterranes had split off Gondwana and were creating a sort of bridge from North Africa to Southern Baltica, separating the Rheic from the Paleotethys. Other authorities believe that the southern European plates were still attached to North African Gondwana at this time. However, there is general agreement that Greece, Italy and Turkey were still part of Gondwana and were located near the coast of Arabia. ATW030219

The Climate of the Lochkovian Age

Sea levels plunged at the end of the Pridoli and remained moderately low throughout the Lochkovian. Continental seas remained, but they were extremely shallow. After a hiatus in the Ludlow and Pridoli, carbon dioxide levels again began to drop, as oxygen rose. Thus, even very shallow waters tended to be reasonably well aerated, but the climate was generally cooler than it had been in earlier ages. ATW030219.

Life in the Lochkovian Age

At this time the Appalachian province of marine invertebrates is limited to the relatively narrow and elongate marine seaway in eastern and south-eastern Laurentia (North America). Other marine areas belong to the extremely widespread Old World province. This fauna is for the most part quite distinct from that of Euramerica. Janvier (1996) reconstructs an Early Devonian fish fauna in the 'Chinese realm': the 400-million year-old fauna or the Bac Bun Formation of Vietnam (Lochkovian-Pragian) as including: (1) the dipnomorph *Youngolepis* ; (2) the acanthodian *Nostolepis*. (3) lungfish; (4) antiarchs (including *Yunnanolepis*, *Chuchinolepis*, and *Vanchienolepis*); and (5) galeaspids, (including *Polybranchiaspis* and *Bannhuanaspis*). These fishes lived in coastal lagoons or shallow marine waters. in association with various marine invertebrates (e.g. brachiopods).

On land, along with the continuation of *Cooksonia* and Rhyniaphytes, the Lochkovian saw the appearance worldwide of two other types of simple pteridophyte. *Zosterophyllum*, like *Cooksonia*, had smooth axes containing a simple central bundle of tracheids, but its sporangia were attached to the sides of the axis (lateral rather than terminal) and were aggregated into a compact spike. The best-known examples of *Zosterophyllum* come from Euramerica, where it is thought that they lived, together with some rhyniophytes, on the dry shores of mountain lakes or on the banks of rivers running through plains nearer the sea. A period of diversification based on the *Cooksonia* and *Zosterophyllum* types of organization then followed, together with the first occurrences of *Psilophyton*. The finding of fossils preserved in various different ways has allowed the description of the internal anatomy of these plants, and this is used, together with the position of their sporangia, in the classification of these early, simple vascular plants (excluding the lycopsids) into three major groups, the rhyniophytes, the Zosterophyllophyta, and the Trimerophyta. Friday & Ingram (1985).

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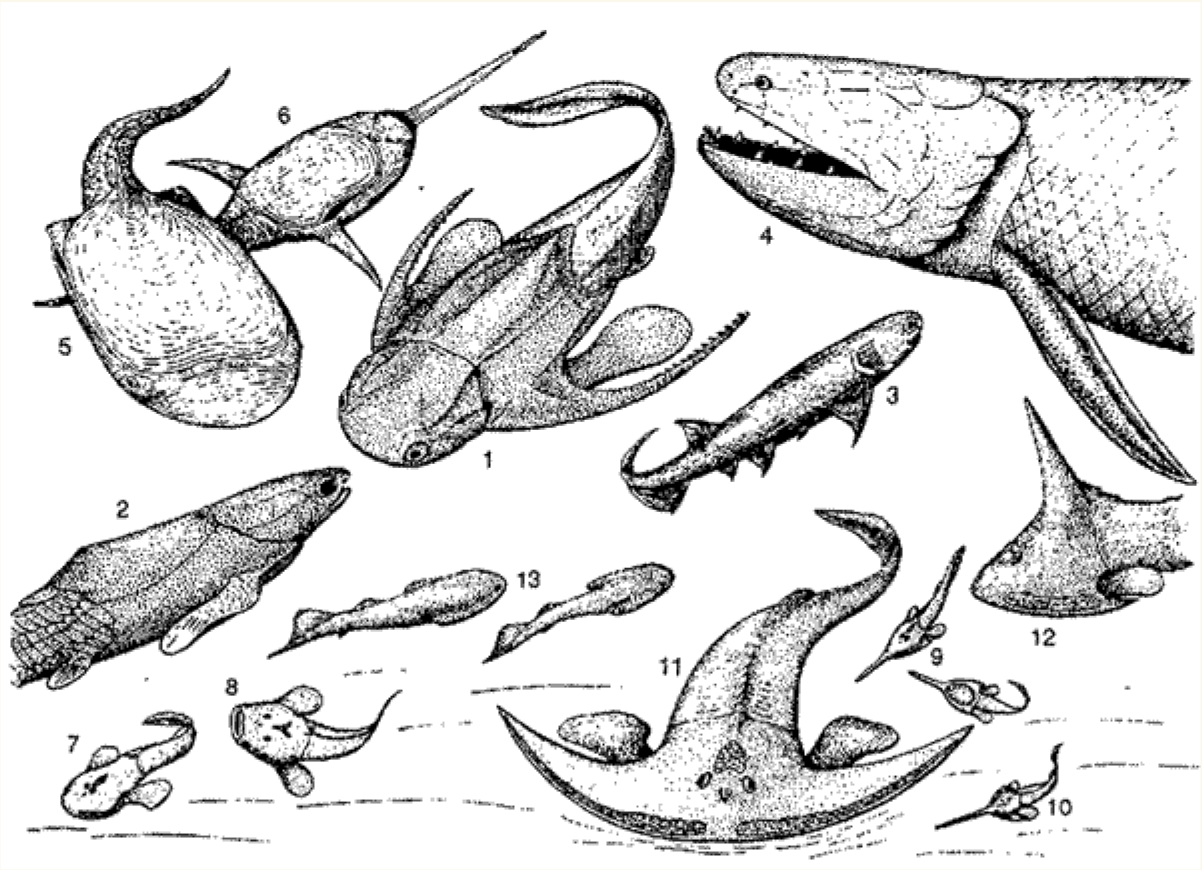
The Pragian (Siegennian)

The Pragian Age of the Early Devonian Epoch: 411 to 407 million years ago

Marginal Marine Biota



Early Devonian fishes from the Old Red Sandstone of Spitzbergen (Wood Ray Formation). This fauna displays a remarkable number of jawed fishes, such as placoderms (1. *Dicksonosteus*, 2 *Sigaspis*), acanthodians (3. *Mesacanthus*), and porolepiformes (4. *Porolepis*). Jawless fishes nevertheless remain fairly abundant and diverse, with the same major taxa as in the Silurian, i.e. heterostracans (5. *Zascinaspis* 6. *Doryaspis*), osteostracans (7. *Norselaspis*, 8, *Gustavaspis*; 9, *Belonaspis*; 10 *Boreaspis*; 11. *Parametererorаspis* 12 *Machiaraspis*) and thelodonts (13 *Turinia*). As a whole, this fauna differs from the previous Silurian ones by the large size of some species (1, 4, 11) which could reach about a metre in length. These fish inhabited marginal marine (bay, estuarine, delta, etc) environments

Reconstruction from Philippe Janvier, *Early Vertebrates*, (1996, Clarendon Press, Oxford) p, 6

Early Terrestrial Communities - the Rhynie Chert

The excellent preservation of the Rhynie Chert allows a window into the past, preserving a diversity of very primitive terrestrial plants and minute arthropods. Some of these tiny creatures fed on decaying plant material, some were carnivores and their is even some suggestive evidence of animal attack on living plants (which would be the first known instance of a terrestrial herbivore). A fungus, *Paleomyces*, is also found infecting the soft tissues of the Rhynie Chert plants. It is still unclear whether *Paleomyces* was a decomposing organism, feeding on dead plant material, a parasite or a mycorrhizal symbiont. If it was a symbiote it may have helped early land plants solve the problems associated terrestrial life.

Some of the Rhynie flora present considerable taxonomic problems, in that several show intermediate characteristics and do not fit easily into existing groups. *Aglaophyton*, for example, lacks conventionally thickened tracheids in the central tissue which nevertheless presumably served to conduct water, so it is technically not at the grade of a true vascular plant, while *Asteroxylon* appears to be an intermediate between the rhyniophytes and the lycopsids, since a vascular supply does not extend to the tips of the leaves, as occurs in modern lycopsids.

Links

The GSSP for the Pragian is described at **Lochkovian - Pragian Boundary**. The geography of the Pragian is illustrated and described **here**. Some Pragian trilobites are discussed at **Rhenohercynian trilobites**, ophiuroids at **Hotchkiss, FHC- Cheiropterasteridae**, a giant brachiopod at **Mergl & Massa (2005)**, some Rugosa at **Wrzolek**

(2002), and crinoids at **Lecanocrinus and Taxocrinus in the Czech Republic**. In fact, any number of Pragian-related articles by Prof. Rudolf Prokop and others can be found at **Index of free articles**.

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The Emsian

The Emsian Age of the Early Devonian Epoch: 407 to 398 million years ago

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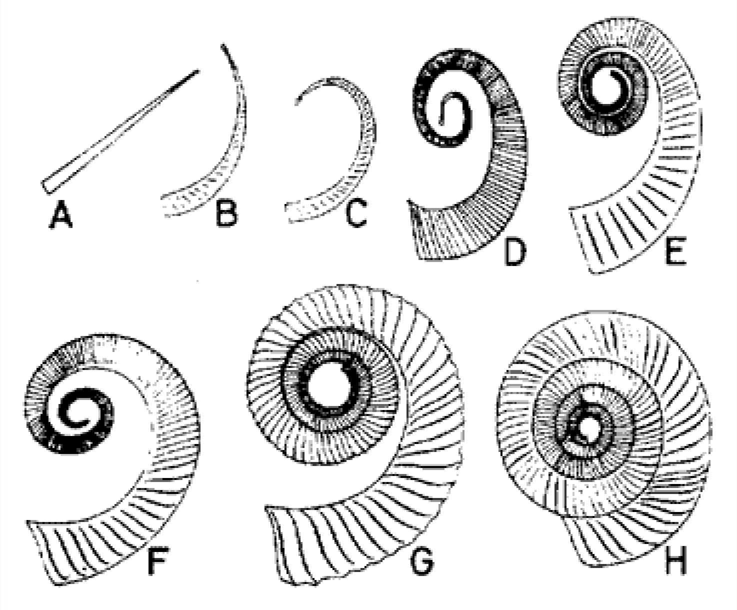
Birth of the Ammonoids



evolution of the ammonoids - A morphological succession of shells
A. *Lobobactrites* , B-C, *Cyrtobactrites*
D-F Anetoceras (Anetoceras), G-H Anetoceras (Erbenoceras)

The Emsain age saw the evolution of a new and important cephalopod group, the Ammanoids. They appear suddenly at the start of the epoch, evolving from straight-shelled Bactritids in the space of no more than a million years or so (and quite probably a lot less. By the end of the epoch, a period of no more than four or five million years, they were world-wide in their distribution and diverse in form. Here we have a classic illustration of an evolutionary radiation, such as occurs frequently in the history of life when a new life-form appears and moves into a vacant or quasi-vacant ecological niche.

Early Emsian ammonoids include *Anetoceras*, *Teicherticeras*, *Convoluticeras*, *Talenticeras*, *Mimagoniatites*, and the bactrid proto-ammonoids *Lobobactrites* and *Cyrtobactrites*. It is even possible to trace a morphological succession between these forms, from the tiny straight shelled bactritids to the larger coiled types. This is shown in the diagram at the top of the page.

Apart from the Bactritids, which are ammonoid - nautiloid transitional forms, all these early ammonoids belong to the suborder Anarcestina of the order Anarcestida. All have extremely simple suture lines.

These cephalopods were nectonic, ocean-going forms, and even at this very early date had a world-wide distribution, being known not only on the western side of the Armorican micro-continent (Germany and Spain, with a possible Euramerican record from England), but also from Antarctic southeast Gondwana (southeast Australia). This same *Anetoceras-Erbenoceras-Teicherticeras* ammonoid faunas is also known (whether from earliest or later Emsian) from west Armorica (Czechoslovakia) south to northern and central Gondwana coast (Morocco and Turkey), east to the Chinese terraine, as well as north to the north-easternmost part of Euramerica (northern part of the Ural geosyncline), and north-western (Canadian Arctic) and western (Nevada) part of the continent.

By the Late Emsian genera include *Taskanites*, *Sellanarcestes*, *Mimosphinctes*, *Palaeogoniatites* and *Cyrtoceratites*, and the bizarre *Augurites* and *Celaeceras*. By this time the division of the early ammonoids into the Anarcestina and Agoniatitina had been achieved.

Despite their early widespread distribution, the ammonoids remained a minor group throughout the Emsian. Known faunas are relatively few and at most localities specimens are rare.

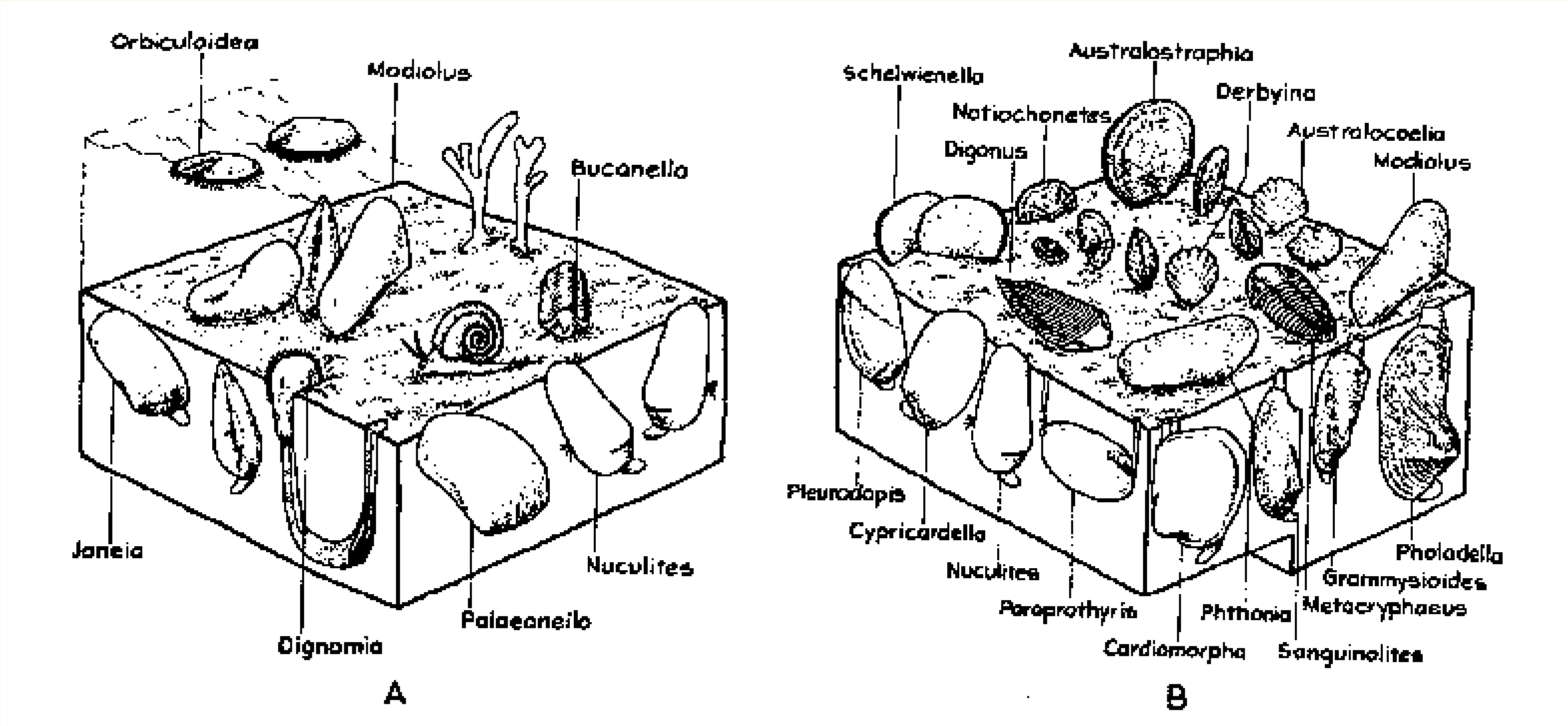
Biostratigraphic zones

Division	Zone - conodont	Zone - pollen (A)	Zone - pollen (B)	Zone - ammonoid
Later	patulus	douglastownense/eurypterota	apiculatus/proteus	Sellanarcestes wenkenbachi
	serotinus	annulatus/sextanti	foveolatus/dubia	
	inversus/laticostatus			Mimagoniates zorgensis
Earlier	perbonus/gronbergi		annulatus/belatus	
	dehiscens			Anetoceras hunsrueckianum

conodont and pollen info from G.C. Young, "Middle Palaeozoic Macrovertebrate Biostratigraphy of Eastern Gondwana," in John A. Long ed., *Palaeozoic Vertebrate Biostratigraphy and Biogeography*, (1993; John Hopkins University Press, Baltimore, 1994 ed.) p.212, fig.9.2

ammonoid info from (a book that unfortunately has a different series of conodont zones for the same time period!)
the correlation of ammonoid zones with the other zones is guess work, so hopefully some kind straigrapher will one day come across this page and point out the actual correlation.

marine communities



Reconstructions of temperate shallow water marine communities from the Parana Basin of Brazil (Jaguariava Shale).- part of the Malvinokaffric bio-province
A: the *Dignomia* (lingulid) community - intertidal to shallow marine
B. the *Australocoelia* community - shallow marine (to 50 metres depth)
diagram from D.L. Dineley, *Aspects of a Stratigraphic System: the Devonian* (Macmillan, 1984) p.134

During Emsian time faunas are widely recognized throughout Gondwana (southern South America, South Africa, and Antarctica) as constituting a distinct and well-represented Malvinokaffric province. An Appalachian source is likely for the bulk of the Malvinokaffric fauna; an Old World source has been ruled out for most of the Malvinokaifric brachiopod assemblage.

Meanwhile, the Old World province has become divisible into a number of subprovinces, i.e., the Rhenish-Bohemian, Uralian, Tasman, New Zealand, and Cordilleran. But with the disappearance of the Malvinokaffric from central and south Gondwana (South Africa and Antarctica) before the end of the Emsian, bioregionalism then became limited to the Appalachian and Old World provinces.

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The Middle Devonian

The Middle Devonian Epoch: 398 to 385 million years ago

> "Silurian-Devonian marine biogeography is dominated through the Eifelian by a global subdivision into a widespread cool to cold climate realm that contrasts with warm conditions elsewhere. Following the Eifelian the global climatic gradient decreased markedly, resulting in the elimination of the cool to cold realm. Laurentian marine faunas display a marked level of endemism through the Givetian, following which there is an overall cosmopolitanism."

Silurian-Devonian Biogeography - A.J. Boucot & Robert B. Blodgett - The Fourth, Millennium, International Brachiopod Congress

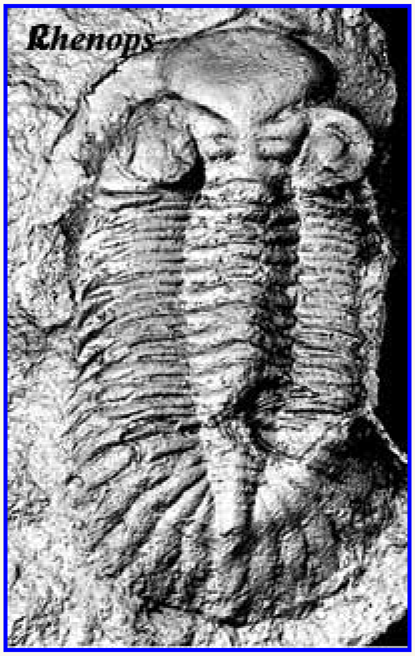
Middle Devonian Sites

The Middle Devonian is a rather short epoch, and has no really outstanding fossil sites. However, there are a large number of lesser-known sites, particularly in the traditional Old Red Continent. This region is now scattered among a number of continental masses. In the Middle Devonian, one could have included many of the more important Northern Hemisphere sites in a broad strip passing roughly southwest to northeast starting in the state of Ohio, USA, passing through Pennsylvania and New York, through Scotland and along the coast of Northern Europe to the Baltics. Another group of sites would lie in a shorter, almost parallel line to the northwest, from Western Canada, through the Canadian Arctic to Siberia. Chinese and Gondwanan Middle Devonian sites are quite rare. Some, like the Aztec Siltstone in Victorialand, Antarctica, may be quite rich, but are poorly known.

North America: In Middle Devonian times, the interior of the North American craton was covered by shallow seas on an irregular basis. The ebb and flow of the seas may have been relatively quick, and large bone beds of fish stranded in drying lowland areas are found in the Columbus and Delaware Limestones of Ohio, along with other, more conventional exposures. To the east (the paleo-southeast) vast reefs were buried as Avalonia closed in and merged with North America. These left many fossils in the states of West Virginia (*e.g.* the Mahantango Formation) and points north. The two fossiliferous zones intersect in Pennsylvania and New York which have, in fact, the best, or at least best known, Middle Devonian exposures in the world. These regions include several spots on the south shore of Lake Erie, the Onondaga Limestone, the Hamilton Group in upper New York State, and various other sites in New York. One of the most unique sites of Middle Devonian age is the "Gilboa Forest" in Gilboa, New York. This is possibly the oldest known forest anywhere. It consists -- not even of *Archaeopteris* -- but of giant progymnosperm ferns.

Far off in the Canadian Arctic are probably measureless Middle Devonian treasures to be found, but the region is poorly explored, from a paleontological point of view. *See* Marss *et al*. (2002) for an example of what may be there to find.

Europe: The best known Middle Devonian site of all is probably Lethen Bar in Scotland, in the heart of the Old Red Continent, which has been known since the time of Agassiz in the 1840's. This site has yielded numerous vertebrate fossils, particularly placoderms and early osteichthyans, such as the *Cheirolepis* shown here. It is one of a number of Scottish sites known only from the now-abandoned sandstone quarries which led to the discovery of the Old Red Continent. Lethen Bar was part of the Orcadian Basin, a huge lake and/or bay which occupied much of northern Britain in the Middle Devonian.



The fishing continues to be good across parts of central Germany and France. This area includes what was, at the time, both the southern margin of Europe (actually, Baltica) and the various bits and pieces of the microcontinent of Armorica which were suturing to the main landmass of Baltica. These are reef and marine exposures, rich in trilobites, echinoderms, and other invertebrates. For vertebrates, we go to the Holy Cross Mountains of Poland and to the Baltics. These were the northwestern extremes of Baltica, home to a number of less common Middle Devonian fishes, such as the psammosteids described by Tarlo (1964). Further east (or paleo-north), there are a few sites known for other heterostracans and for thelodonts. However, most of this fauna belongs to the Early Devonian.

Gondwana: Of all the Gondwanan continents, we are not able to say much. The Xichong Formation of Yunnan Province and the Do Son Formation of Vietnam both have Middle Devonian fossils, but the sites are either poorly known or poorly developed. In any event we have little information. Australia, which is well-supplied with Early and Late Devonian sites, has rather little in the way of Middle Devonian exposures. The Bunga Beds and Mulga Downs localities in New South Wales are exceptions. The Aztec Siltstone of Antarctica has been fruitful yielding, in particular, placoderms and sharks. However, the dating is not well constrained and it is, obviously, not the easiest place to explore. The Atlas Mountains of Morocco are the source of many commercially available trilobite fossils, although political disturbances, as well as climate, have also made this region periodically difficult to access in recent years.

One new Gondwanan site with considerable promise is the Canõ del Oeste Formation, which lies on the border between Venezuela and Columbia in the Perijá Mountains. In recent years, this has yielded interesting new terrestrial plant material, as well as near-shore marine invertebrates, such as the *Rhenops* shown here. *See*, deCarvalho &

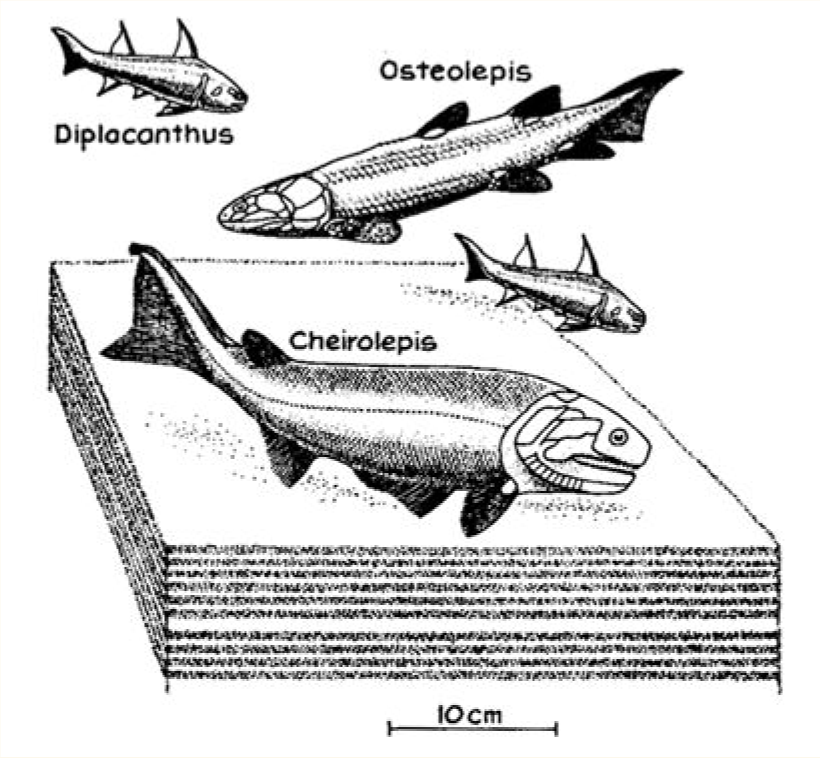
Moody (2000). ATW040711.

Life in the Middle Devonian

By the Middle Devonian the armoured jawless ostracoderms were in decline, and instead the jawed fish were undergoing a great evolutionary radiation in both the sea and in freshwater. The warm, shallow, oxygen-depleted waters of Devonian inland lakes, surrounded by early plants, may have provided an environment in which certain fish developed many of the essential features (e.g. well developed lungs, ability to crawl out of the water and onto the mud for short periods of time, possibly in search of invertebrate food) which would developed by some of their descendants as tetrapods.

The newly emerging jawed fishes become more diverse and some become dominant predators.

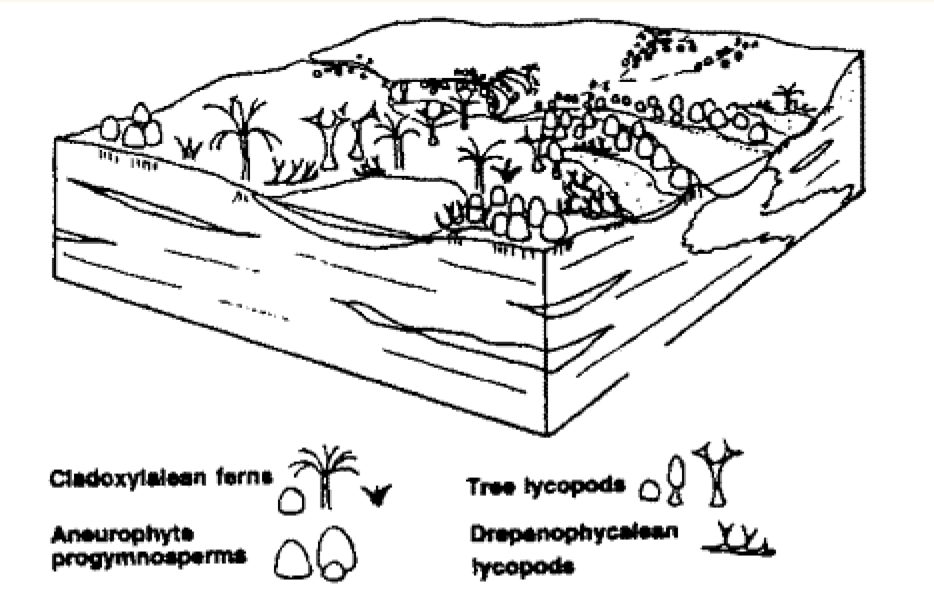
Marginal Marine Bays and Deltas, and Brackish and Freshwater



A Middle Devonian lacustrine community in the Orcadian Basin may have included, apart from the showing acanthodian (*Diplacanthus*), actinopterygian (*Cheirolepis*), and crossopterygian (*Osteolepis*) fish shown above, antiarch and arthrodire Placoderm and lungfish. From time to time mortality was locally very high and perhaps because of desiccation, water bloom or other causes. The absence of traces of invertebrate animal life is puzzling

from D. L. Dineley, *Aspects of a Stratigraphic System: the Devonian*, 1984, MacMillan, p.74

Life on Land - Plants and Arthropods



The Middle Devonian was a time of progressive innovation, with lycopsids, sphenopsids (horsetails), early ferns, and a group called the progymnosperms (ancestral to higher or seed plants) all appearing. The most readily recognizable plants were the lycopsids with their small leaves spiraling along each stem. One of the most completely preserved was the herbaceous Leclercqia from Middle Devonian sediments. Its branched leaves were five-pointed and bore a ligule (a small scale-like outgrowth), while the xylem resembled that of the primary xylem of the huge Carboniferous tree-lycopsids called *Lepidodendron*, of which it seemed to be an ancestor. Reproducing by spores, all these plants were confined, to moist, lowland habitats.

Living among these early land plants were a diverse selection of arthropods, including spiders, mites, myriapods and collembolids

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The Eifelian

The Eifelian Age of the Middle Devonian Epoch: 398 to 392 million years ago

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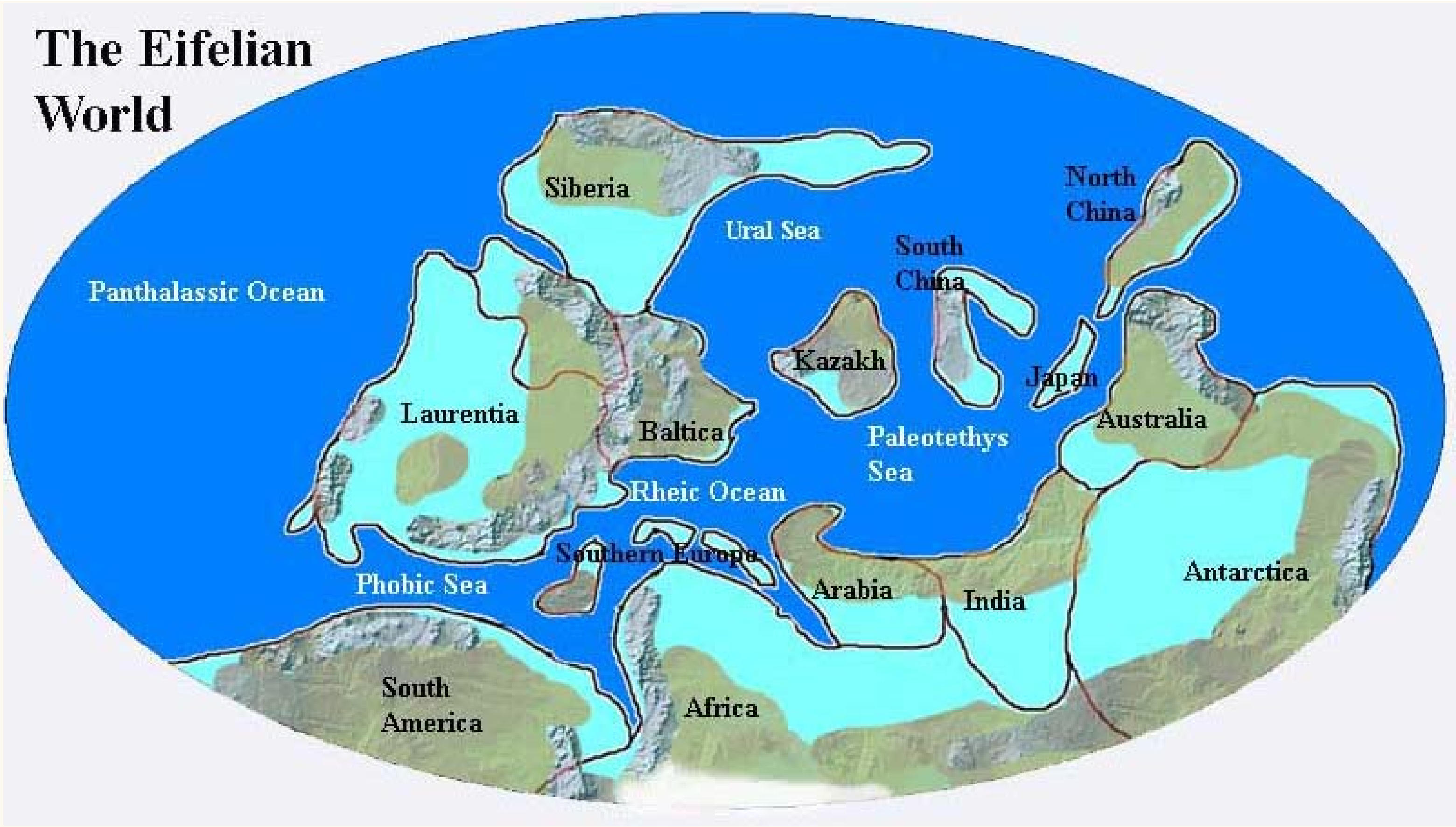
Geography



As always, when we are forced to use home-made graphics, the reader may correctly assume that there is something terribly wrong with the state of real knowledge in the area. There is no lack of Middle Devonian maps, but the degree of correspondence between them is extraordinarily poor. The basic facts of North American (Laurentian) and North European (Baltican) geography are well known. However, the position of the other continents, and the degree to which they lay above sea level, seems to be the subject of considerable dispute. We have therefore drawn a sort of compromise map. We strongly discourage anyone from taking it very seriously.

In North America, the Acadian Orogeny **[1]** was at or near its end. The mountains in the east and south probably stood as tall as they ever would -- perhaps as tall as the Andes today -- but volcanic activity was almost at an end. In the west, volcanic island arcs continued to form and accrete to the North American craton, although this process, too was nearing its end. North of Laurentia, a series of relatively small land masses were created between Laurentia and Siberia, including parts of the Canadian Arctic and Alaska's North Slope.

The European side of Laurasia (Laurentia plus Baltica) was more active, and the Caledonian belt, running between Greenland and Scotland was periodically quite active. Nevertheless, much of this activity was due to the gradual counterclockwise rotation of Laurentia *away* from Baltica, so this was an extensional, not collisional, process. With the gradual subsidence of mountain- building and marginal subduction in northern and eastern Laurasia, erosion created vast new beds of sediment -- the famous "Old Red Continent" sediments of this area which have done so much for Late Paleozoic paleontology.

In the vast southern continent of Gondwana, South America continued its slow clockwise rotation, gradually closing the Phobic Sea. There is some evidence for a medium- sized bolide strike in the area of the Rheic Ocean towards the end of the Eifelian. However, if this occurred, the effects were relatively short-lived. Eastern Gondwana was relatively flat, and the Paleotethys was shallow as well, to judge by the extensive carbonate sediments of this age. This feature may well have created a broad migrational highway for East Gondwanan marine and freshwater species to spread westward. Certainly the endemism of Early Devonian vertebrate life begins to break down during the Eifelian.

Notes: **[1]** A recent valiant, but probably futile attempt to standardize the nomenclature of this series of mountain-building events has been made by McKerrow *et al*. (2000). ATW030405.

Stratigraphy

The most recent ICS date for the beginning of the Eifelian is 397.5 ±2.7

Mya. As with all of the Devonian stages, the error margins are rather high. The base of the Eifelian is defined by its Global Stratotype Section and Point (GSSP): the first appearance of the conodont subspecies *Polygnathus costatus partitus* in the Wetteldorf Richtschnitt, near the town of Schönecken-Wetteldorf, in the Eifel Hills of Germany, a bit southwest of Bonn. At the time, this was near the south coast of the continent of Baltica -- but not for long. The islands of Armorica were finishing their fast passage of the Rheic Ocean from Gondwana and were about to collide with Baltica, eventually forming parts of present-day central and southern Europe. The base of the Eifelian is associated with a major faunal turnover in many sections, for reasons which are not known.

Polygnathus costatus partitus
From the Geological Museum of Peking Univ.

A parastratotype section is located in a quarry near Prague, Czech Republic. The Eifelian is the same as the Couvinian Age of older European nomenclature. The base of the Eifelian (but not its end) also coincides with the Chinese Yingtangian Age, which is also defined by reference to*P.c. partitus*.

Conodonts: Conodonts are the mainstay of Eifelian stratigraphy. Commonly used conodonts (with zone indicator species noted) include the distinctive conodont*Icriodus corniger retrodepressus* which follows *P.c. partitus* (*partitus* Zone) closely in time. Another early arrival is *P. ziegleranus*. The middle of the Eifelian is marked by *P.c. costatus* (*costatus* Zone) and *P. australis* (*australis* Zone). Toward the end of the Age, elements of *Tortodus kockelianus kockelianus* (*kockelianus* Zone), *P. ensensis* (*ensensis* Zone), and *P. xylus* are found in that order. Pyle *et al*. (2003).

Ammonoids: One web source summarizes an ammonoid (goniatite) zonation scheme for North Africa as follows: *Foordites veniens* to *Pinacites jugleri* Unit (*partitus* to earliest *costatus* Zones; *Pinacites jugleri* (early *costatus* Zone); *Subanarcestes macrocephalus* and *Cabrieroceras crispiforme* Unit (early to middle *costatus* Zone) *Cabrieroceras housei* Unit (middle to late *costatus* Zone); *Agoniatites vanuxemi*, *Parodiceras magnosellaris*, and *A. obliquus* Unit (latest *costatus* to ?*eiflius* Zone); *Holzapfeloceras circumflexiferum* Unit (*ensensis* to the Givetian *timorensis* Zones). Klug, Christian- Quantitative stratigraphy and taxonomy of late ... *See also*, the section on ammonoids below.

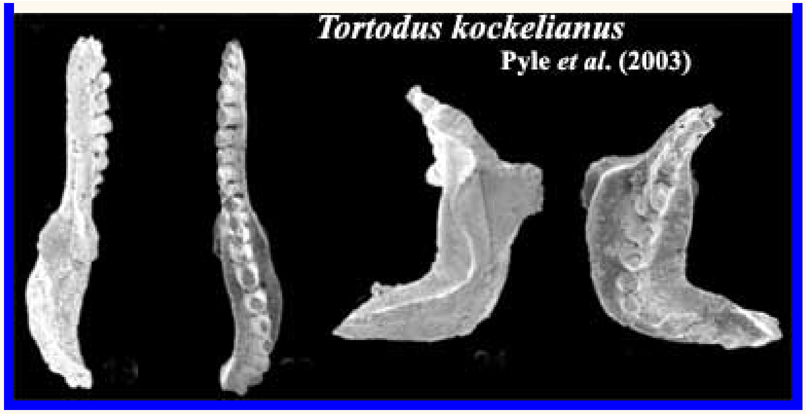
Pinacites jugleri

Corals: Tabulate corals do not appear to give much stratigraphic resolution. However, they have been used in Eastern Europe for some purposes. So, for example, *Cyathophyllum dianthus* and *Thamnophyllum caespitosum* are said to be indicative of the Eifelian and lowermost Givetian of Slovakia. Biostratigraphy and rugose corals of Moravian Devonian ... But this does not seem to correlate even with the Eifelian corals next door in the Czech Republic. Spacek *et al*. (2002).

Trilobites: Undoubtedly, someone has a good trilobite zonation scheme for the Eifelian. However, we were only able to uncover general agreement that *Phacops latifrons* is associated with the Early Eifelian.

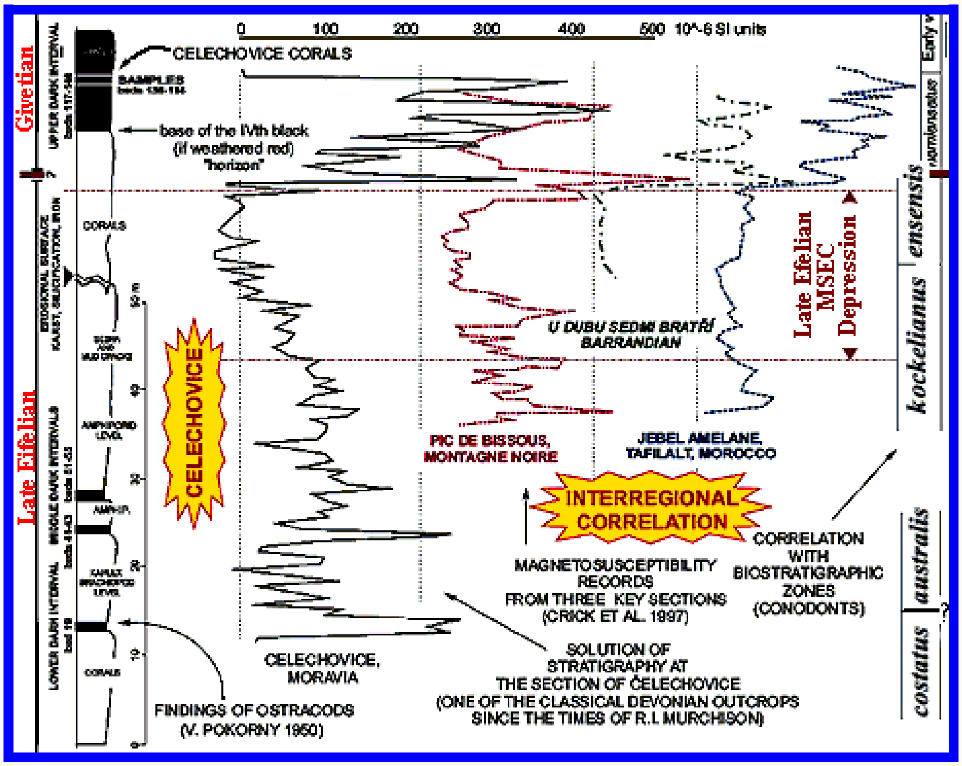
Vertebrates: *Asterolepis* appears all over the world during the Eifelian, and is a good indicator to that extent. However, it apparently has no greater resolution. Other placoderms have notoriously endemic distribution and appearance. Stratigraphic occurrence of some placoderm fishes in the Middle .... It has been reported, based on as-yet unpublished data, that the acanthodian *Diplacanthus solidus* is indicative of Eifelian age. Mannik *et al*. (2002).

Strata: As is typical of Devonian sediments, it is possible to make some reasonably good correlations of strata across the Atlantic, for the obvious reason that there was no Atlantic in Devonian times. In the



Late Emsian, crinoid-bearing carbonates indicative of shallower waters are found in "normally" deeper water areas, suggesting that the Eifelian began with unusually low sea levels. Sea levels apparently increased to a highstand in the upper *kockelianus* Zone which was associated with black shales, organic-rich sediments, and other indications of ocean anoxia.

Gamma Rays and Man-in-the-Moon Marigolds: In recent years there has been a serious attempt to use gamma ray spectroscopy, magnetosusceptibility (MSEC), and zircon fission track analysis, among other very high tech approaches to Paleozoic stratigraphy. The idea is not quite as crack-pot as is sounds, and some results have been amazingly good, or at least highly reproducible (unlike electron thermoluminescence, which had a brief, but disastrous, influence on some Neogene dating schemes).



The utility of MSEC and these other methods is based on the fact that carbonate sediments have effectively zero ability to be magnetized by strong external magnetic fields and contain no radioactive nucleides with high-energy emissions. For reasons unknown, this is particularly true of Paleozoic carbonates. However, at times of surface exposure or low sediment accumulation, or as a result of volcanic activity, extraterrestrial impacts, or unusual cosmic ray activity, carbonates may accumulate atmospheric dust particles containing minute amounts of iron, uranium and thorium. These can be used to create surprisingly consistent stratigraphic sequences if one can perform the incredibly finicky analysis needed to measure magnetic susceptibility, very low level gamma ray spectroscopy, and microscopic analysis of fission tracks. In recent years, commercially available, industrial grade equipment has come on the market which allows this sort of work to be done outside multi-billion dollar research facilities.

Its a little early yet to take these studies *too* seriously. However, studies from both Gondwana and Baltica confirm that something rather drastic happened just before the end of the Eifelian. This may have been a prolonged something, since the aberration builds up beginning in the upper *kockelianus* Zone and peaks in the upper *ensensis* Zone. This correlates roughly with the high sea levels deduced from stratigraphy. MSEC buffs tend to see this as a demonstration of the ability of these techniques to recover unexplained new paleogeophysical events. It may be that the widespread anoxia of the time simply reduced the rate of biogenic carbonate accumulation, thus causing the sediments to appear enriched in atmospheric dust. However, a really sharp peak of magnetosusceptibility just at the Eifelian-Givetian boundary is harder to dismiss as trivial. *See*, the data in the image, adapted from Hladil & Pruner (2001). These are known, among the magnetosusceptible, as the Kacak Events.

The second Kacak (or *otomari*) Event is, as it turns out, associate by the now-familiar litany of shocked quartz, metal isotope anomalies, a large negative carbon isotope shift, and microspherules suggesting an extraterrestrial impact at the end of the Eifelian, associated with extinctions in at least some parts of the world. Ellwood *et al*. (2003). It seems increasingly clear, if still completely inexplicable, that many inferred extraterrestrial visitations are preceded by some rather marked earthly portents of doom -- such as the first Kacak Event here. Sooner or later, one hopes, someone will make sense of this bizarre pattern. ATW040717.

Climate

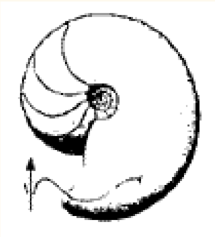
The Eifelian was a period of low, but gradually rising seas. The climate was generally cool and arid, and a small ice cap probably existed at the South Pole in southern Africa. However, the gradual northward drift of many Gondwanan lands increased the temperatures experienced by Gondwanan biota. This effect was enhanced by increased climate stratification. That is, the temperature differences between polar and equatorial regions increased.

Although most of the world was dry, climate stratification allowed a narrow equatorial tropical belt to develop. Here, land plants spread inland for the first time. The earliest coal forests are from about this age, and are found across northern Laurentia, Baltica, southern Kazakhstan and South China. ATW030405

Life in the Eifelian Age

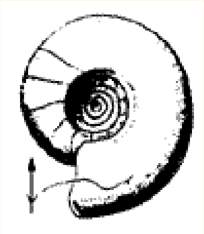
Ammonoidea

Pinacites
(late Eifelian)



Agoniatites

(Early Eifelian)



Anarcestes

(late Emsian to early Eifelian)

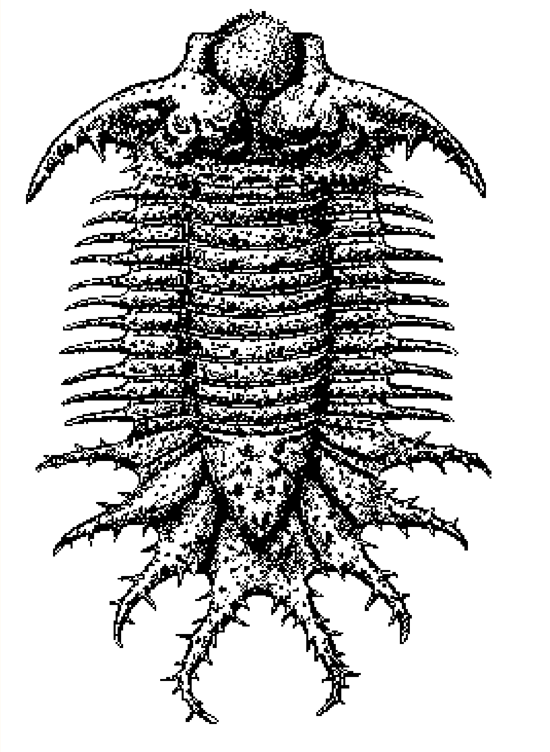
Ammonoid evolution in the earliest Middle Devonian produced the genera *Agoniatites*, *Laganites*, *Werneroceras* and *Subanarcestes* and by the Late Eifelian *Pinacites*, *Sobolewia*, *Paraphyllites*, and *Foordites*, with earlier genera such as *Gyrocemtites*, *Mimagoniatites* and *Anarcestes* continuing from the Emsian. All these genera were first described from Europe which, throughout the Devonian, has the fullest record of Devonian Ammonoidea.

During this epoch, the Ammonoidea remain rare. Faunas of Armorica (western Europe) are very similar to those of Gondwana (North Africa), even to the extent of showing the same pathological features. In fact throughout the entire middle Devonian ammonoids remained rare, showing little morphological diversification.

left ammonoid evolution during the Eifelian epoch. Note the shell becoming increasingly more tightly coiled. Drawings from M. R. House, "Devonian Goniatites", in A. Hallam, ed. *Atlas of Paleogeography*, p.100

MAK990322

Trilobites



the magnificent giant trilobite *Terataspis grandis* (Hall)
50 cm long
Onondagan stage,
New York
MAK990322

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The Givetian

The Givetian Age of the Middle Devonian Period: 386 to 392 million years ago

Marine Invertebrates

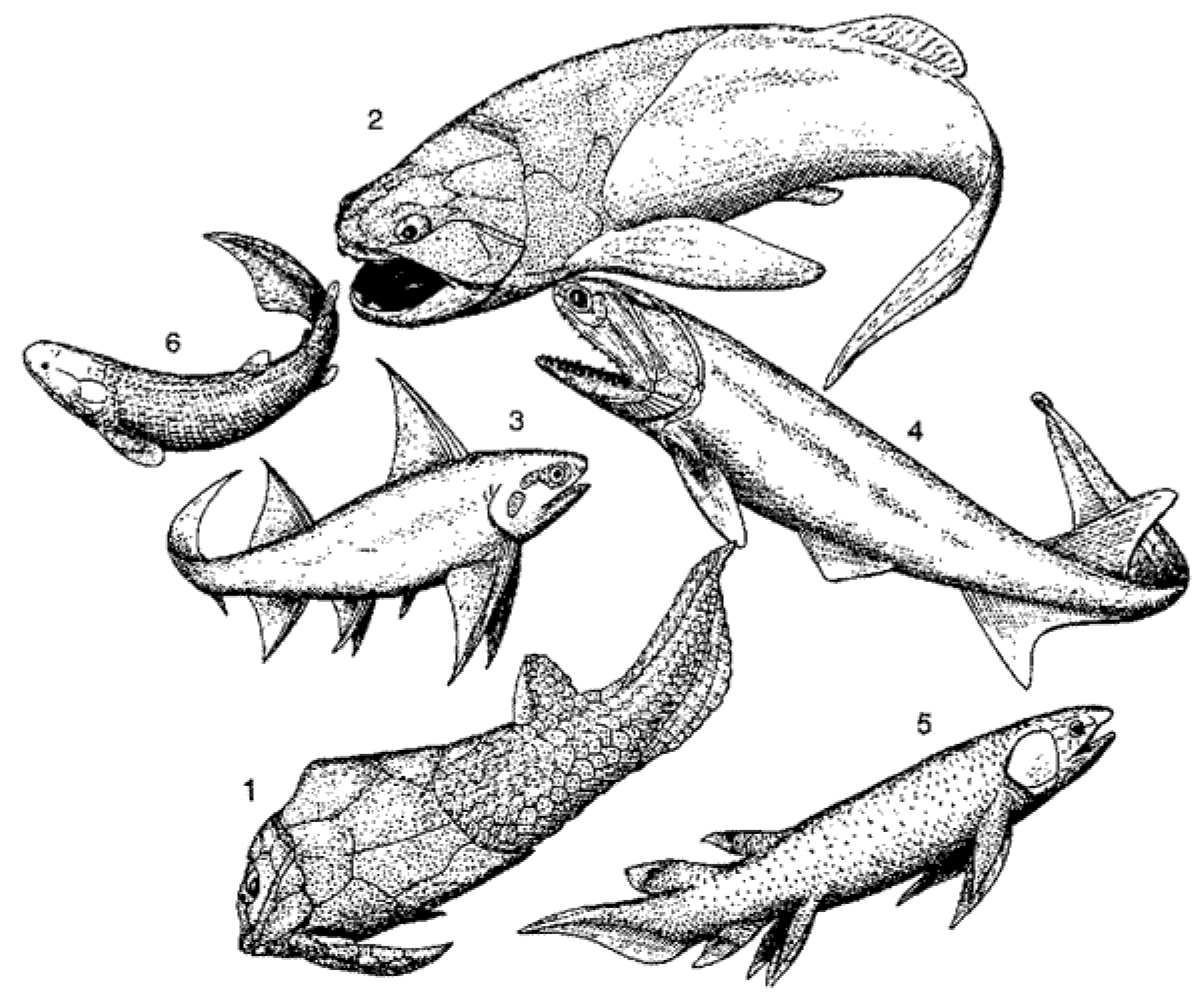
Stratigraphic distribution patterns for Givetian and Frasnian gastropods of the Polish segment of southern shelf of Euramerica (Holy Cross Mountains and Krakow areas) indicates that the late Givetian was marked by radical impoverishment in gastropods, connected with Taghanic and Manticoceras events. [ref Gastropods from Givetian and Frasnian of southern Poland and the global biotic crises - Number 04 (April) 1999, Volume 47 of Przegl?d Geologiczny (Geological Review, Polish Geological Institute)

Trilobites

Dechenella macrocephalus
Hamilton Group, New York. Dorsal view
(Kevin's Trilobite Homepage)

Greenops boothi
Widder Shale, Hamilton Group,
Arkona, Ontario, Canada
(Kevin's Trilobite Homepage)

Marginal Marine Biota



Fishes of the Middle Devonian locality of Lethen Bar, in Scotland (Givetian, about 377 Ma). They include antiarchs (1 *Pterichthyodes)*; and arthrodire (2. *Coccosteus*) placoderms, acanthodians (3. *Diplacanthus*), ray-finned fish (4, *Cheirolepis*), lungfish (5, *Dipterus*), and osteolepiform lobe-finned fish (6. *Osteolepis*), representing the lineage that gave rise to land animals.

Reconstruction from Philippe Janvier's book *Early Vertebrates*, (Clarendon Press, Oxford) p, 9

The First Forests

the lycopsid *Archaeosigillaria* (center) together with the progymnosperm *Aneurophton* (left, the fern-tree like plant), representatives of the flora from the Gilboa Forest (Catskill Mountains, New York). None of these plants grew very tall. Note the mushroom-like bases (absence of true root system)
from *The Fossil Book* - Fenton & Fenton, 1958, Doubleday & Co., p.284

see also **The First Forests**

By the Givetian epoch trees had grown large enough to form forests. These trees belonged to ancient groups of plants like progymnosperms and lycopsids, and reproduced by spores, as ferns still do today. These trees still lacked proper roots, and the base of the trunk swelled out like the bottom of a mushroom, another primitive land dweller. These trees also provided very little shade or shelter, having a crown of open branches or large fronds instead of proper leaves.

Differences in composition of two assemblages from the Middle Devonian of New York State, USA, one dominated by progymnosperms and ferns, the other by sphenopsids and lycopsids, have tentatively been related to differences in habitats, with the second of these assemblages perhaps occupying a similar niche to the late Carboniferous swamp floras. It is possible, however, to generalize a little on the structure of communities. The acquisition of a lateral meristem, for ex- ample, allowed an increase in girth and hence greater height. This would have led to the development of a forest with many different layers of foliage and an increase in the types of habitat available for colonization by animals. Some of these habitats would have been deeply shaded, and here the heterosporous condition and possession of seeds would have been advantageous, as the food reserves of the female gametophyte tissues in the seed would have allowed the young sporophyte to develop without the need for immediate photosynthesis. The seed habitat would also have allowed the colonization of much drier environments

The recently discovered Middle Devonian Gilboa fauna contains flattened fragments of trigonotarbids, centipede fangs, a spider, a mite and a bristletail, another wingless insect.

Evolutionary Ecology and Coordinated Stasis of Devonian Benthic Faunas in the Appalachian Basin (link http://ucaswww.mcm.uc.edu/geology/brett/deptwebpage/coordin.htm no longer valid)

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The Late Devonian

The Late Devonian Epoch of the Devonian Period: 385 to 359 million years ago

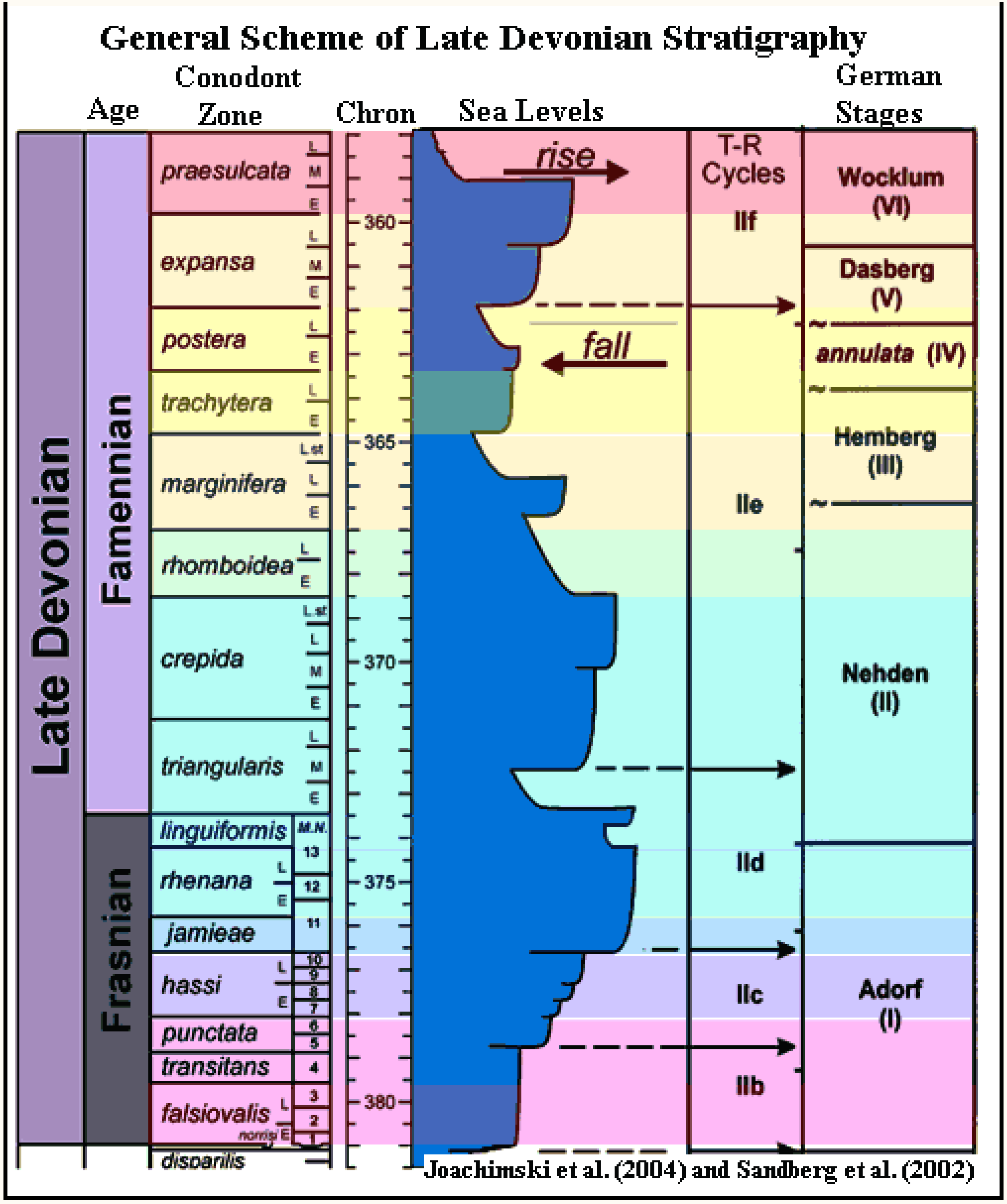
Introduction

Archaeopteris forests generated shelter, shade, and nutrients (in the form of small animals and invertebrates) that provided an ideal environment for the early tetrapodomorphs, thus leading to the vertebrate conquest of land and the evolution of land animals (including, eventually, us).

Painting copyright Doug Henderson, reproduced with permission.

Stratigraphy

Late Devonian stratigraphy has been intensively studied; and there seems to be considerable agreement on basics, particularly for the Euramerican world. The disagreement there is on what it means. The attached scheme is taken from Joachimski *et al*. (2004) and Sandberg *et al*. (2002). We have not tracked down each of the conodonts for which the conodont zones are named. However, they are almost all species of *Palmatolepis*. The exceptions are the *Mesotaxis falsiovalis* Zone (earliest Frasnian) and the *Siphonodella praesulcata* Zone (latest Famennian). Some variations in the conodont nomenclature are also found. Thus, the *postera* Zone is sometimes



referred to as the *styriacus* Zone. The "*costatus* Zone" is also frequently mentioned. This corresponds (probably) with the upper half of the *expansa* Zone. Kaiser *et al*. (2004).

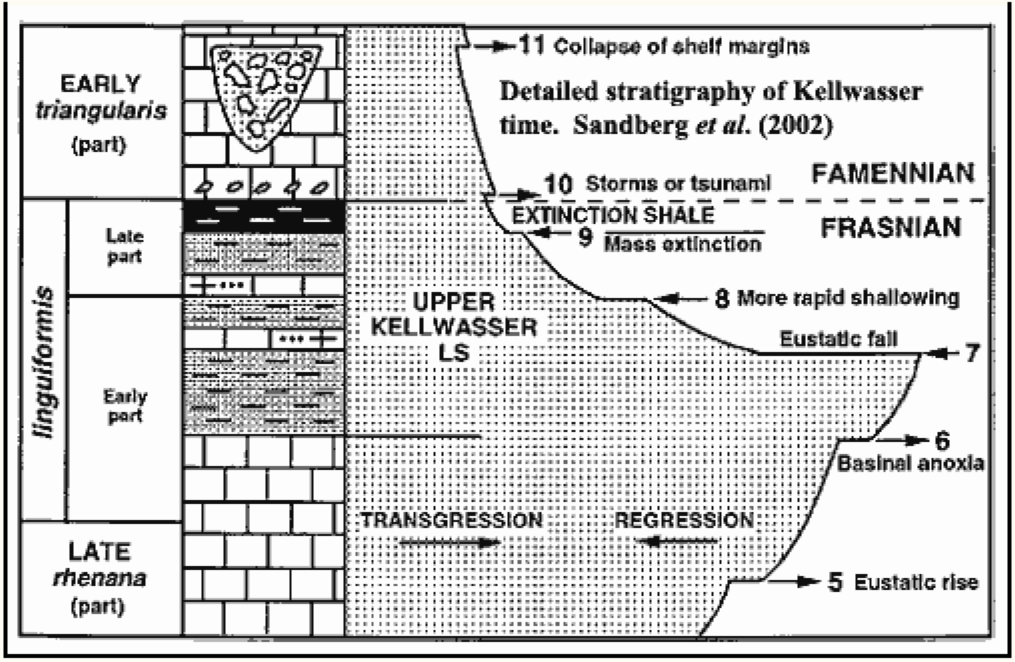
This arrangement has been correlated with strata from northern Europe and the Western United States. However, it is not clear whether it can be successfully applied to Gondwana lands. Critical points, such as the Frasnian - Famennian boundary and the base of the Carboniferous, have proven very hard to identify in (for example) Eastern Australia, Antarctica, and Africa. Kaiser *et al*. (2004). So, the Late Devonian may not be quite so neatly laid out as the figure might suggest.

Note also that the chronological portion of the chart is no longer consistent with ICS dating. You can get a reasonable approximation of the current ICS dates in the Famennian simply by adding 1 My to the ages on the chart. Things may not be so simple for the Frasnian.

The precision and world-wide correlation of this arrangement are of some interest because Sandberg and others have aggressively argued for a strong extraterrestrial influence over events in this epoch, as well as for an Ice Age, or actually several ice ages, covering all of the Famennian. This dramatic reading of the Late Devonian is almost entirely based on a close reading of strata and faunal lists from northern Baltica and western Laurentia, without so much as a dropstone or tektite (at a relevant time) to back it up.

Whatever value their hypotheses may have, these workers have given us a very close and detailed look at the sequence of events in two, well- separated regions of Euramerica, and that is something very much worth knowing. Briefly summarized, the story goes like this.

The Frasnian was a time of rising seas. This is normally a good thing for life. However, as in parts of the Mesozoic, sometimes the sea rises so rapidly that the reefs are unable to keep up. When this happens, near-shore communities may "drown" for various reasons: because benthic autotrophs find themselves below the level where they can receive enough sunlight to survive, or because of unsuitable substrate, sedimentation, or grade. With the



productive base of the food chain gone, the entire community may collapse. Such an event may have occurred in the *rhenana* Zone, or perhaps the *jamiae* (at the beginning of transgression cycle IId), as evidenced by the invasion of the normally pelagic conodont, *Palmatolepis semichatovae*, into near-shore waters and perhaps the appearance of anoxic bottom muds.

In the succeeding *linguiformis* Zone, the sea fell, recovered, and then fell precipitously and for an extended period. This is the time of the Frasnian-Famennian extinction or Kellwasser Event. The Kellwasser was devastating to marine life on a specific or generic level, but had little effect on higher taxa. In short, it was less a mass extinction than a mass turnover. The Kellwasser Event appears to be spread over occur a significant length of time, terminating in a black "extinction" layer followed, in some locations, by evidence of severe disturbances which seem to indicate storm or tsunami effects.

Particularly in view of the lack of more global sampling, it is hard to put a definite interpretation on this this data, and we will not attempt to do so. The Kellwasser Event was followed by generally falling sea levels in the Famennian, punctuated by reversals, particularly towards the end of the Age. Sandberg *et al*. (2002) ascribe this pattern to polar glaciation interrupted by interglacials. Again, absent more direct evidence of a Late Devonian ice age, we are reluctant to go so far.

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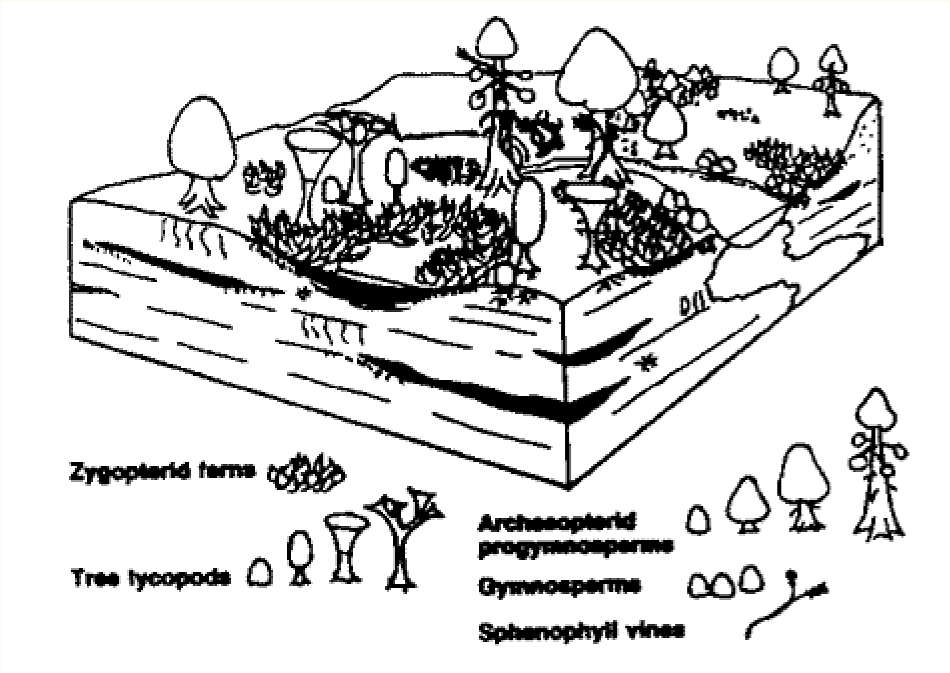
Late Devonian Life

Extinction of coral reefs

About the middle of the Late Devonian epoch, towards the end of the Frasnian epoch, worldwide environmental changes, including anoxia (lack of oxygen in the oceans, perhaps the result of algal blooms) and a sudden drop in sea level (drying up the shallow seas where life thrived, and the replacement of a mild maritime climate with a harsh continental one), caused one of the greatest mass extinctions in the history of life. The victims included many important marine organisms, and especially reef biota. The previously flourishing reefs were decimated. The long association between algae, sponges, stromatoporoids, and corals that began in Ordovician times and had continued for some 130 million years without significant disturbance came to a sudden end.

Land Plants

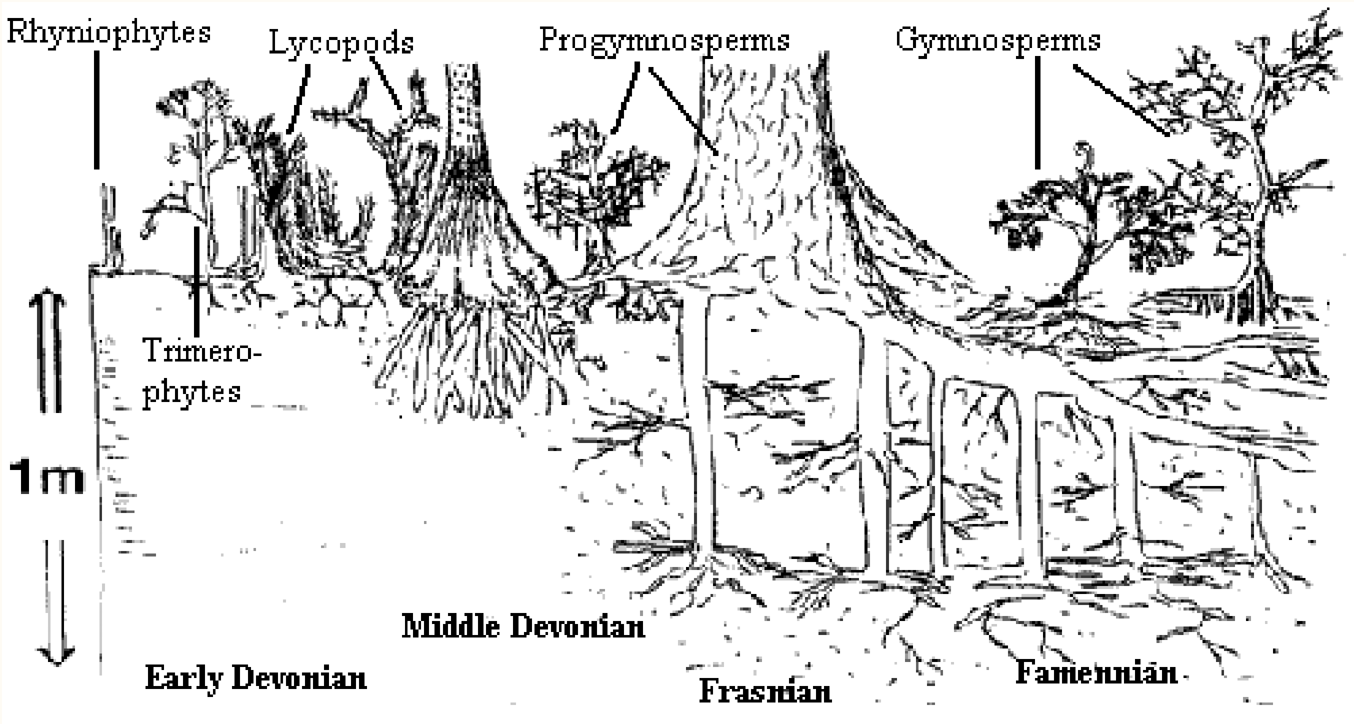


Plants: Lycopsids included some of the stems were of diameter and their bark superficially resembled that of Carboniferous tree-lycopsids, implying that some, such *Protolepidodendropsis*, were a few metres high, and by the end of the period the group included substantial forms such as *Cyclostigma*.

Links between the evolution of land plants, weathering processes, and marine anoxic events

"The Devonian Period was characterized by major changes in both the terrestrial biosphere e g the evolution of trees and seed plants and the appearance of multi-storied forests, and in the marine biosphere an extended biotic crisis that decimated tropical marine benthos, especially the stromatoporoid tabulate coral reef community. The connections between these terrestrial and marine events are poorly understood but a key may lie in the role of soils as a geochemical interface between the lithosphere and atmosphere/hydrosphere, and the role of land plants in mediating weathering processes at this interface. The effectiveness of terrestrial floras in weathering was significantly enhanced as a consequence of increases in the size and geographic extent of vascular land plants during the Devonian. In this regard, the most important palaeobotanical innovations were (1) arborescence tree stature), which increased maximum depths of root penetration and rhizoturbation [see diagram below], and (2) the seed habit, which freed land plants from reproductive dependence on moist lowland habitats and allowed colonization of drier upland and primary successional areas. These developments resulted in a transient intensification of pedogenesis (soil formation) and to large increases in the thickness and areal extent of soils. Enhanced chemical weathering may have led to increased riverine nutrient fluxes that promoted development of eutrophic conditions in epicontinental seaways, resulting in algal blooms, widespread bottom water anoxia, and high sedimentary organic carbon fluxes. Long-term effects included drawdown of atmospheric pCO_2 and global cooling leading to a brief Late Devonian glaciation, which set the stage for icehouse conditions during the Permo-Carboniferous. This model provides a framework for understanding links between early land plant evolution and coeval marine anoxic and biotic events, but further testing of Devonian terrestrial-marine teleconnections is needed."

Thomas J. Algeo and Stephen E. Scheckler, "Terrestrial-marine teleconnections in the Devonian: links between the evolution of land plants, weathering processes, and marine anoxic events", Phil. Trans. R. Soc. Lond. B (1998) 353 113-130



earlier<------------------------->later

increasing terrestrial plant root depth penetration with time during the Devonian, leading to increasing soil depth and weathering. rhy=rhyniophytes such as *Aglaophyton* or *Horneophyton*; tri=trimerophytes such as *Psilophyton*; lyc-he = early herbaceous lycopsids such as *Asteroxylon* or *Drepanophycus*; lyc.tr=early tree lycopsids such as *Lepidosigillaria* or *Cyclostigma*; prog-ao=aneurophyte Progymnosperms such as *Tetraxylopteris*; prog-arc=*Archaeopteris* progymnosperms; gym=early gymnosperms such as *Elkinsia* or *Moresnetia*; and Zyg=zygopierid ferns such as *Rhacophyton*. Scale bar, 1 meter.

Appearance of tetrapods

The Late Devonian period marked the time when the first tetrapods animals evolved from their sarcopterygian ancestors. There were at least two successive and distinct waves of tetrapodomorph evolution, the Frasnian Elpistostegalians, which seem to have been exterminated by the Frasnian-Famennian extinction event, and the Famennian tetrapods (such as *Acanthostega* and *Ichthyostega*) which were to become the ancestors of the Carboniferous labyrinthodonts. These tetrapods were almost entirely aquatic, although they were clearly able to crawl up on the mud and move about out of water. The first tetrapod skeletons are known from the Late Devonian of Greenland, but other traces of Devonian fossil evidence, such as some tetrapod footprints and fragmentary remains from Australia, hint at a much greater distribution of Devonian tetrapods than is currently revealed in the fossil record.

Links

Murderous Trees

Developing a Sequence Stratigraphic Framework for the Late Devonian Chattanooga Shale of the southeastern US - "The Late Devonian Chattanooga Shale of Tennessee and Kentucky is in most areas a thin black shale deposit of less than 10 meters thickness. It is a distal equivalent to the almost 3000m thick Catskill sequence, and encompasses most of the Frasnian and Famennian, approximately 14 million years of earth history."

Devonian times - going upstream

"Brachiopod faunal extinction and recovery during the Frasnian-Famennian biotic crisis" Number 04 (April) 1999, Volume 47 of Przegl?d Geologiczny (Geological Review) Polish Geological Institute

The Late Devonian Mass Extinction (The Critical Moments and Perspectives in Paleobiology and Earth History Series) by George R. McGhee, Jr. - a book about the Frasnian-Famennian extinction

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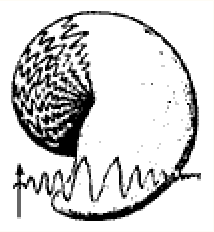
The Frasnian

The Frasnian Age of the Late Devonian Period: 385 to 375 Million years ago

Ammonoidea

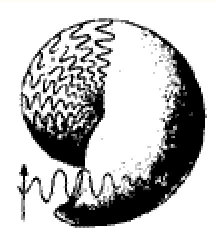
Manticoceras
(Middle Frasnian to earliest Famennian)



Beloceras
(Middle to Late Frasnian)

The Frasnian epoch saw the evolution of quite distinct, and short-lived, goniatite groups belonging to the Gephuroceratacea, and Pharciceratacеae, which are united by the distinctive proliferation of umbilicsl lobes. Some of these genera are illustrated at the left. A cosmopolitan distribution for the Devonian was achieved in the Frasnian by *Manticoceras* and its relatives, the fossil shells of which are known from North America, Asia and Australia, as well as the rich record in Europe and North Africa.

left Frasnian ammonoids, illustrating shell form and suture lines: Body chamber length not necessarily correctly indicated. Drawings from M. R. House, "Devonian Goniatites", in A. Hallam, ed. *Atlas of Paleogeography*, p.100



Synpharciceras

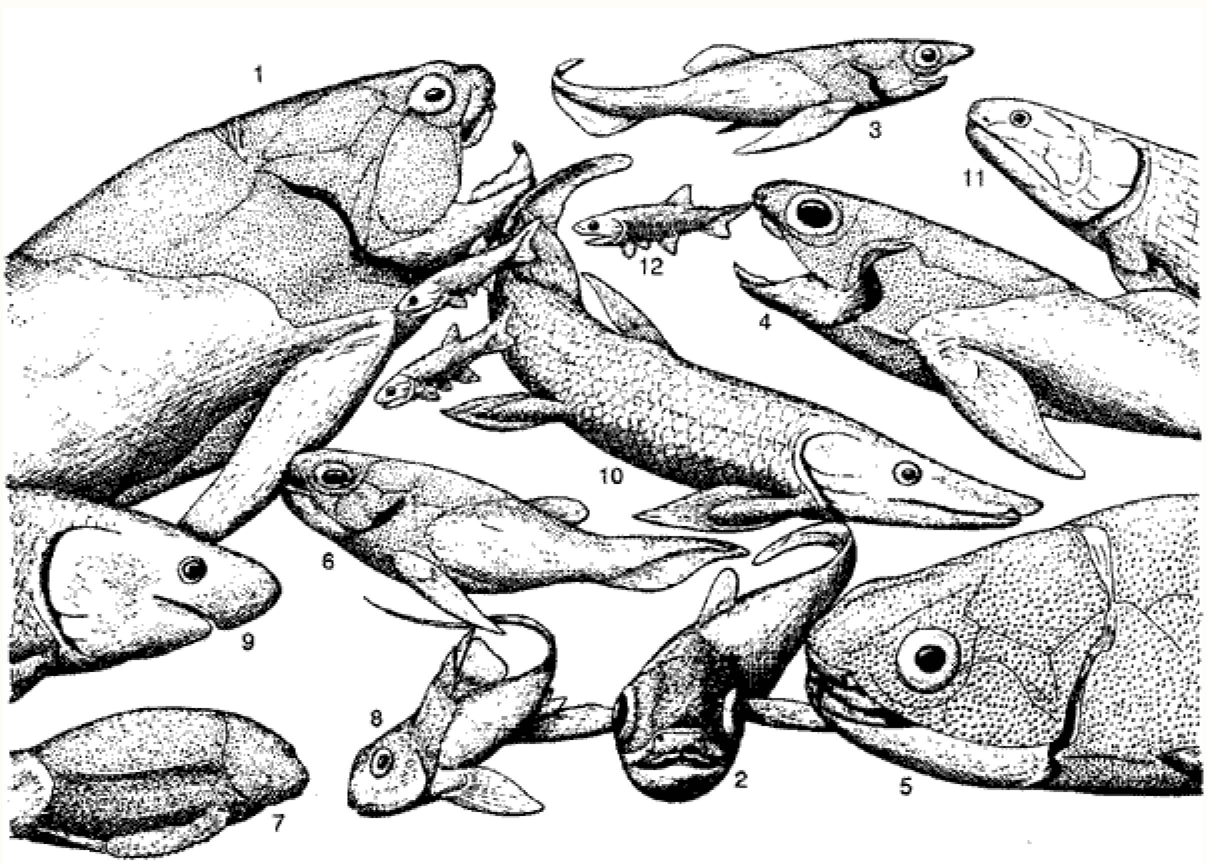
(early Frasnian)

The Early Frasnian

Ammonoids

The earliest Frasnian *Lunulicosta* zone is characterized by genera such at Pharciceras, Synpharciceras, Timanites, Epitornoceras. Koenenites and distinctive species of Ponticeras and Tornoceras. Europe and North Africa have the fullest record

Marine Fishes



The marine fish fauna (found in association with coral reefs) from the famous Late Devonian locality of Gogo, north-western Australia (Early Frasnian), displays an amazing diversity of placoderms. Most of these are arthrodires (1, *Eastmanosteus*; 2, *Latocamurus*; 3. *Tubonasus*; 4, *Incisoscutum*; 5. *Harrytoombsia*; 6, *Torosteus*). Other placoderm groups are represented by the antiarch (7, *Bothriolepis*) and ptyctodontids (8, *Campbellodus*). The lobe-finned fishes are lungfishes (9, *Holodipterus*; 10, *Griphognathus*) and Osteolepiformes (11, *Gogonasas*). Small ray-finned fishes (12, *Mimia*) were also fairly abundant.

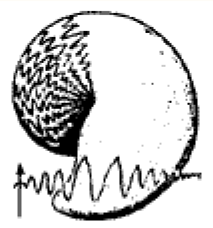
Reconstruction from Philippe Janvier's book *Early Vertebrates*, (1996, Clarendon Press, Oxford) p, 13

The Middle Frasnian

Ammonoidea

Manticoceras

(Middle Frasnian to earliest Famennian)



Beloceras

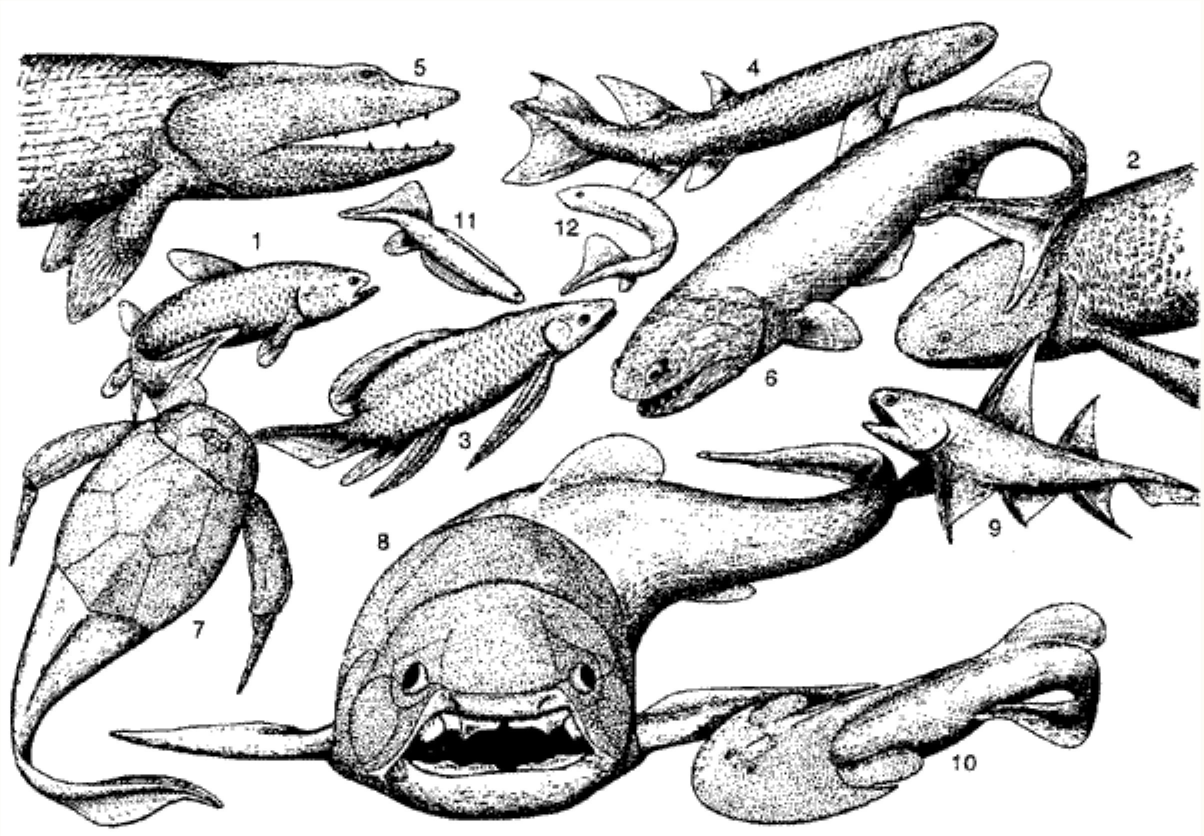
(Middle to Late Frasnian)

Middle Frasnian ammonoid faunas, that is those of the Cordatum zone, are characterized especially by the genus Mantioceras and Beloceras, although both continue later, the former with distinctive late species. *Mantioceras* especially is characterized by a cosmopolitan distribution, being known from every continent except South America (and the absence there would be due to lack of fossilferous localities rather than actual biogography). *Beloceras* has a more restricted range, but is still known from the Chinese (Southern Kwangsi), Euramerica (New York) and Gondwana (Western Australia) terranes. This incidentally was also a time of cosmopolitan brachiopod and fish distribution. It would seem that the land masses had come into closer proximity, allowing migration between previously separate continental shelves.

left Middle Frasnian ammonoids, illustrating shell form and suture lines:: Body chamber length not necessarily correctly indicated. Drawings from M. R. House, "Devonian Goniatites", in A. Hallam, ed. *Atlas of Paleogeography*, p.100

Fish

Estuarine Vertebrate Faunas



The Miguasha fish fauna (Escumenic fish fauna of Quebec (north central Euramerica) presents a remarkable diversity of early vertebrates, although chondrichthyans (sharks), which are largely represented in other localities of similar age, are absent. There is a variety of lobe finned fishes (sarcopterygia), belonging to five major taxa: the actinistians (1. *Miguashuia*). porolepiforms (2, *Holoptychius*), lungfishes (3, *Scuamenacia*), Osteolepiformes (4, *Eusthenopteron*), and elpistostegalians (5, *Elpistostege*), which are the immediate ancestors of the tetrapods. Ray-finned fishes (Actinopterygii) are rare with only one large form (6 *Cheirolepis*). In addition, there are archaic elements, such as the antiarch (7, *Bothriolepis*) and arthrodire (*Plourdosteus*) placoderms as well as acanthodians (9, *Diplacanthus*). and the youngest known osteostracan jawless fishes (10, *Escuminaspis*) Two anaspid-like naked jawless fishes (11. *Endeiolepis*, 12. *Euphanerops*) may be close relatives of the extant lampreys. These fishes lived in an estuary surrounded by ferns.

Reconstruction from Philippe Janvier's book *Early Vertebrates*, (1996, Clarendon Press, Oxford) p, 11

Land Plants

> "(studies of plant assemblages from New York state show that) During the middle of the Frasnian, significant floristic changes appear to have occurred, but the extent to which these changes reflect differences in the depositional settings is unclear. Aneurophytalean progymnosperms declined precipitously in abundance, and diversity drops from six to two genera in the New York section. Archaeopterid progymnosperms increased in abundance and diversity. Herbaceous "ferns" and lycophytes became rare to absent, although lycopsid trees remained. The landscape was altered drastically by the subsequent rise of Archaeopteris forests. These dominance-diversity changes have been attributed to the same factors that ultimately caused the Frasnian- Famennian marine extinctions (Scheckler 1986a), possibly climatic change associated with the onset of Gondwanan glaciation (Veevers and Powell 1987; Crowley and North 1988). The decline in diversity and major shifts in dominance patterns continued into the late Frasnian."

Behrensmeyer *et al* (ed.) Paleozoic Terrestrial Ecosystems pp.222-223

The Late Frasnian

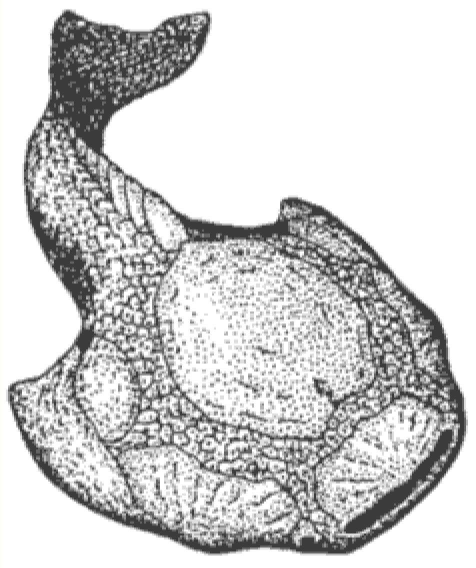
Brachiopods

During the later Frasnian the diversification gradually declines and reaches its minimum at the F-F boundary (the extinction event). Two entire orders, the Atrypida and Pentamerida, die out completely, as do many Orthid and Stropheodontid families.

Ammonoids

Knowledge of Late Frasnian goniatite faunas is rather sparse. The *Holzapfeli* zone faunas were first described from Germany and have been recognized in Devon, England, and in eastern North America. Their occurrence in Gondwana (North Africa) has been doubted (Petter, 1959). Bogoslovski (1969) recognizes Late Frasnian faunas in the Rudnyi Altai and the Urals. The species which characterize this level belong to *Archoceras, Aulatornocetas, Crickites* and *Manticoceras*, that is, genera with a longer range than the *Holzapfeli* zone. Nonetheless, it would seem that there is a restriction in the distribution of Late Frasnian ammonites, although this is a subject that needs a more detailed study.

Marginal Marine



Psammolepis, the last and largest of the ostracoderms (Jawless fish). This harmless bottom-dweller reached two meters in length.

Reconstruction from Philippe Janvier's book *Early Vertebrates*, (1996, Clarendon Press, Oxford)

Land Plants

"Late Frasnian plant communities also are known from localities in New York (Scheckler 1986a). The most characteristic plants are Archaeopteris species, some of which produced growth rings indicating some kind of seasonality (Creber and Chaloner 1984). Because nearly all species had small laminar leaves arrayed on large, flattened branch systems, a shaded forest was likely. These trees appear to have produced many deciduous branches with attached laminate foliage, which resulted in a much greater yield of litter than that produced by earlier plants; the branches may have been shed seasonally, perhaps at the beginning of the dry season (Scheckler 1978). Increased amounts of litter may have accentuated the role of fire in these communities as a factor in disturbance and succession (Cope and Chaloner 1980; Chaloner and Cope 1982; but see also Beck et al. 1982). Archaeopteris trees formed low-diversity gallery forests in waterlogged soils along streamsides or on wet floodplains, as suggested by abundant Archaeopteris remains in channel and organic-rich sediments (Beck 1964; Retallack 1985a,b). Late Frasnian calcareous paleosols have been interpreted as well-drained areas that may have supported shrubby and herbaceous vegetation (Retallaek 1985a). Such landscapes probably had considerable spatial heterogeneity, which is more detectable with paleosols than with the limited spectrum of environments that preserve megafossils. Forested areas had become common by the late Frasnian and there were clear habitat distinctions among the plants. Structural and taxonomic diversity, although low, were increased relative to earlier Devonian plant communities. However, guild depths of trees in many of these environments were low, with limited overlap in any one assemblage. This should have predisposed these ecosystems to extensive structural change in the face of extinctions."

Behrensmeyer *et al* (ed.) Paleozoic Terrestrial Ecosystems pp.222-223

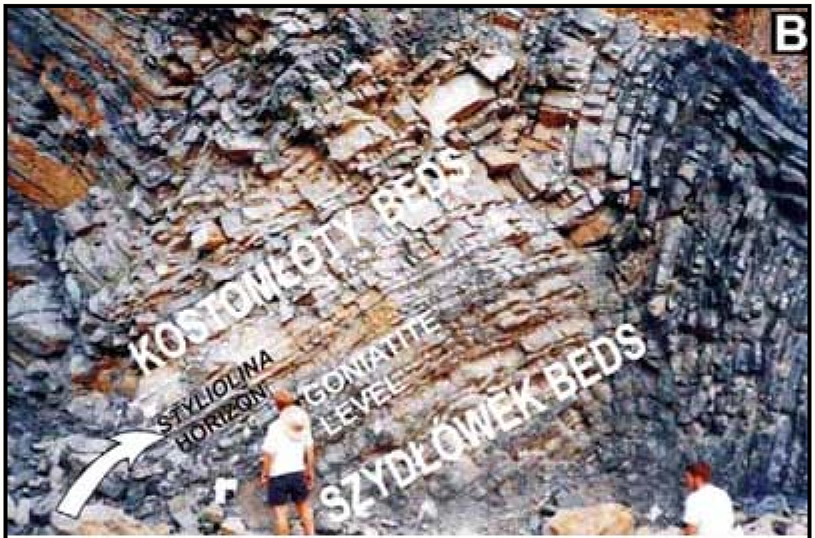
Frasnian-Fammanian Mass-Extinction

The end of the Frasnian is marked by a large mass-extinction event. Although mass extinctions are usually at the end of a geological period, marking a radical shift in fossil remains (which was what inspired the 19th century geologists to place the demarcations for these periods at these particular levels), the Devonian extinction occurred in the middle of the Late Devonian, at the boundary between the Frasnian and Famennian ages. Those dramatic events drastically affected the marine community, but had little impact on terrestrial flora. The main victims were the major reef-building organisms: the stromatoporoid sponges, and rugose and tabulate corals. Among other marine biota, seventy percent of the taxa did not survive into the Carboniferous, with brachiopods, trilobites, conodonts, and acritarchs the most severely affected groups. Jawless fishes and placoderms were also affected, although many placoderm lineages survived quite happily until the end Devonian.

Explanations for this mass extinction include an episode of global cooling, and associated lowering of sea-level, and Meteorite impacts.

Links

The Devonian Mass Extinction



Geologists examine a Frasnian exposure for the subtle signs of sedimentary transitions ...

Chemo-biostratigraphic Study on the Devonian Frasnian-Famennian Event BAI Shunliang

As usual, a good first stop on the web is **GeoWhen Database - Frasnian** for latest dating and orientation in time, regional equivalents, etc.

Most serious web pages related to the Frasnian are concerned with the Frasnian-Famennian extinction -- the so-called Kellwasser Event(s). Among these are a completely unreasonable number of articles from **Acta Paleontologica Polonica**, including: **Trilobites from the latest Frasnian Kellwasser Crisis in North ...**, **Chondrichthyan fauna of the Frasnian–Famennian boundary beds in Poland**, and **Frasnian–Famennian brachiopod extinction and recovery in southern ...**. Other journals are also sometimes represented: **Geochemistry of the Frasnian-Famennian boundary in Belgium- Mass ...**, **White Rose Consortium ePrints Repository - Geochemical and ...**.

This is definitely not one of those periods for which one cannot find journal articles on the web. In fact, the problem is finding anything else. **Rhenohercynian trilobites** has some nice images of Frasnian trilobites. The Devonian Times site has a little on the tetrapods of the Frasnian (**Devonian Times - New Directions**). **Dr. Jared Morrow** (Univ. Northern Colo.) has a page with a great many useful abstract and journal links, as well as basic stratigraphic information and the like. **Professor Grzegorz Racki** is probably one of the best-known names in Frasnian research, and his website has even more links to work through. ATW050829.

(uploaded on Kheper Site on 31 May 1999)
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The Famennian

The Famennian Age of the Late Devonian Epoch: 375 to 359 million years ago

Introduction: new opportunities - new animals inherit the world

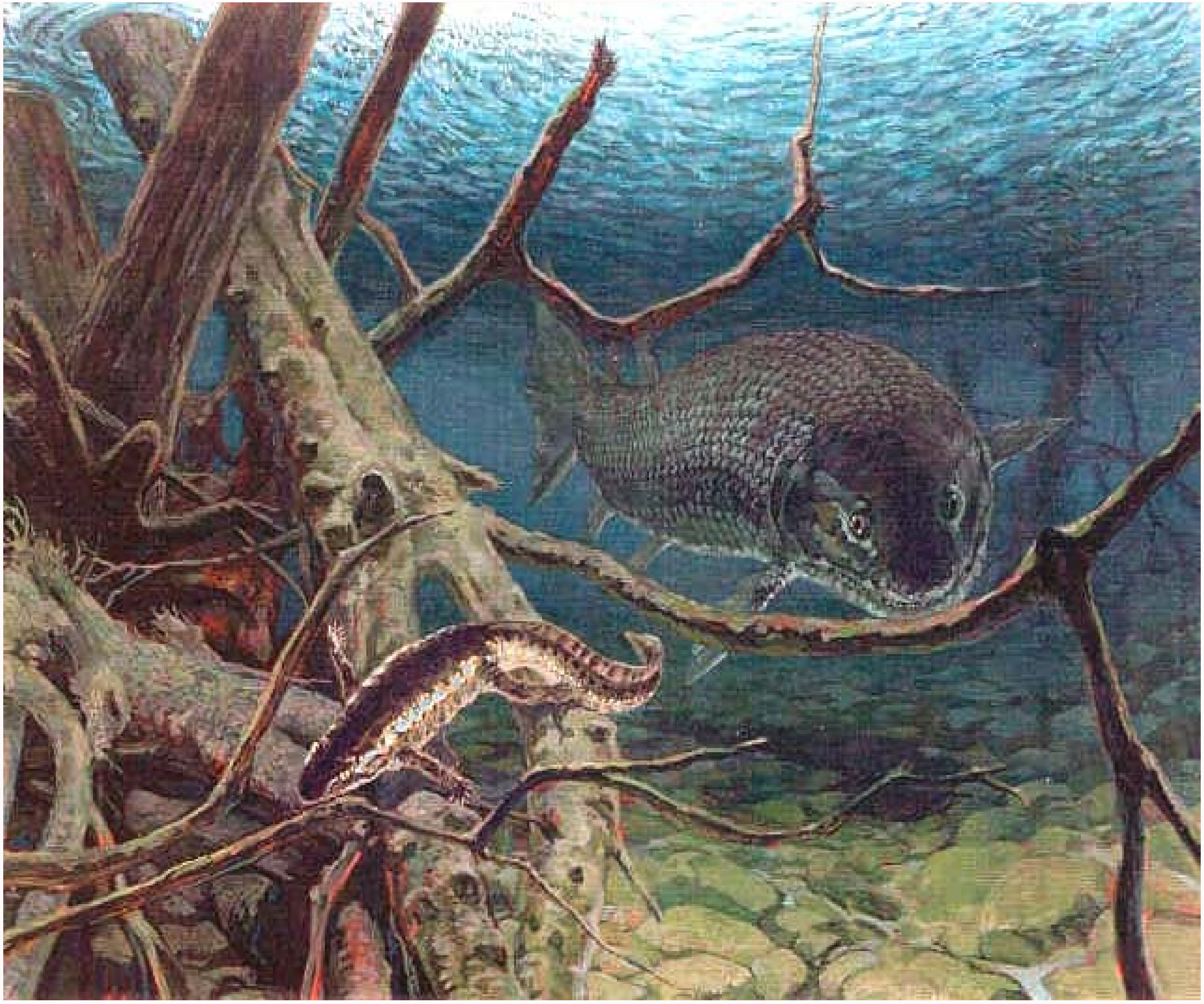
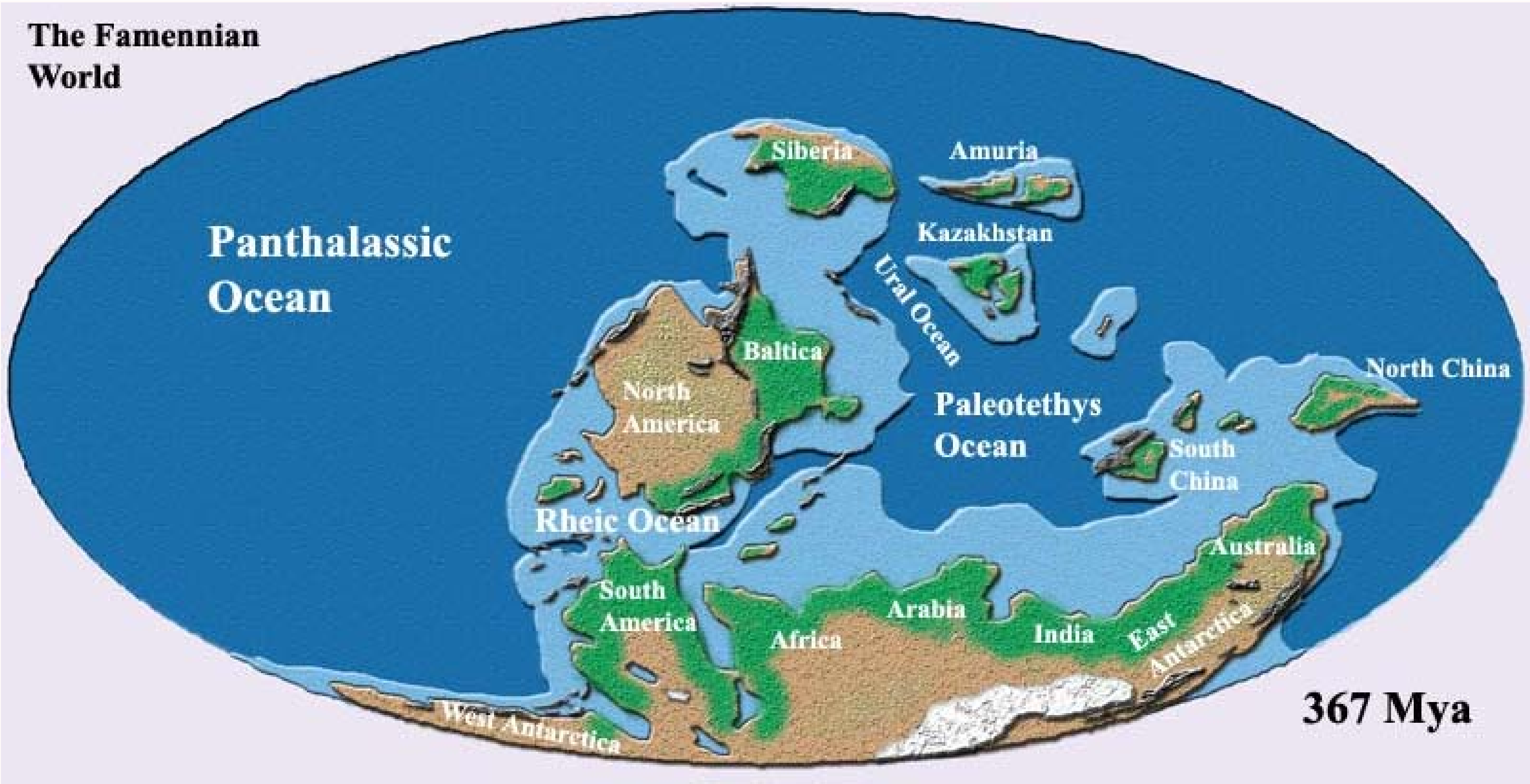


image © D. W. Miller, used with permission

The organisms that survived the Frasnian-Famennian extinction were the ones that were to rule the Earth for the next sixty or so million years. Included were new types of coral, brachiopods, ammonoids, and a number of lineages of fish and tetrapods, as shown in the above illustration.

Famennian Geography



ATW050114. Map public domain. No rights reserved. An enormous, 2400 x 1200 pixel,unlabelled version of this map is available (free) in all the usual formats, including a Photoshop® .psd file with each topographical type on a different layer. That one is 9 MB. Email augwhite@sbcglobal.net.

Famennian Life

Reef Communities

Following the annihilation of the reef organisms with the Frasnian-Famennian mass extinction, only scarce and greatly impoverished reef communities, consisting in the main of algal stromatolites, survived. It was not until well after the beginning of the Carboniferous period, some 10 or 15 million years later, that there was a resurgence in the reef biome.

Land Plants

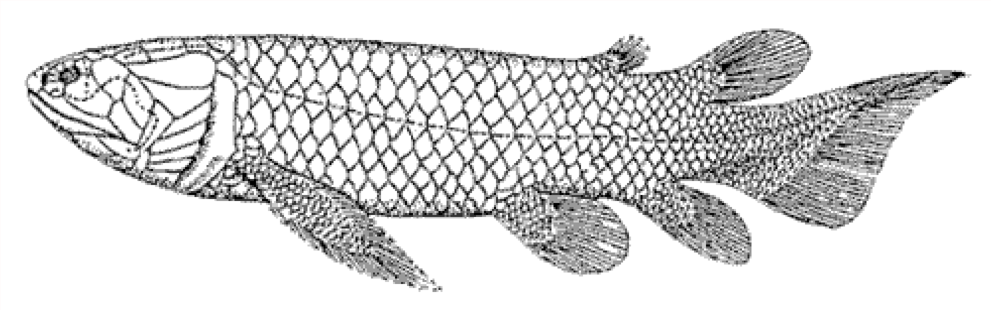
During the Late Famennian the seed habit evolved. The appearance of gymnosperms occurred when seeds within cup-shaped structures are recorded in an assemblage of 'ferns', lycophytes and progymnosperms in the Famennian deposits from the USA.

"Origin and Development of Land Flora and Fauna", in Adrian Friday and David S. Ingram (*ed.*) The Cambridge Encyclopaedia of Life Sciences, 1985, p.329

Brachiopods

With the end of the Frasnian and the advent of Famennian time, brachiopod faunas are known to have undergone mass extinction of many important groups. Two entire orders, the Atrypida and Pentamerida, as well as many Orthid and Stropheodontid families, died out. Of a list of 71 Frasnian genera, only 10 survived into the Famennian. These are *Atribonium, Aulacella, Crurithyris, Cupularostrum, Cytina, Cyrtospirifer, Productella, Retichonetes, Schizophora*, and *Steinhagella*. The Early Famennian brachiopod post-extinction assemblage is dominated mainly by only two dwarf species which represent rhynchonellids and spiriferids. There is an intensive process of brachiopod rediversification. and the Frasnian survivors are joined by a new evolutionary radiation, including a great many new rhynchonellid, productid, athyrid, and spiriferid genera, some widely distributed. Thus the Carboniferous fauna actually began during the early Devonian (the productida became so common during the Carboniferous that one could actually call that period the "Age of Productids."

Fish



Holoptychius
The characteristic scales of this lobe-finned fish have been found worldwide
length 75 cm
Order Porolepiformes

Links

Links

Devonian Times - a detailed yet very readable account of the important Late Devonian Red Hill fossil locality in Clinton County, north-central Pennsylvania.

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Notes

[1] We might expect to see rather significant, but opposite, grade effects in both Northern Europe and the American Southwest. Late Devonian paleogeography is a little unclear, but it is likely that northern Europe was pressing hard against the flank of Laurentia.

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Carboniferous period

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Carboniferous Period

The Carboniferous

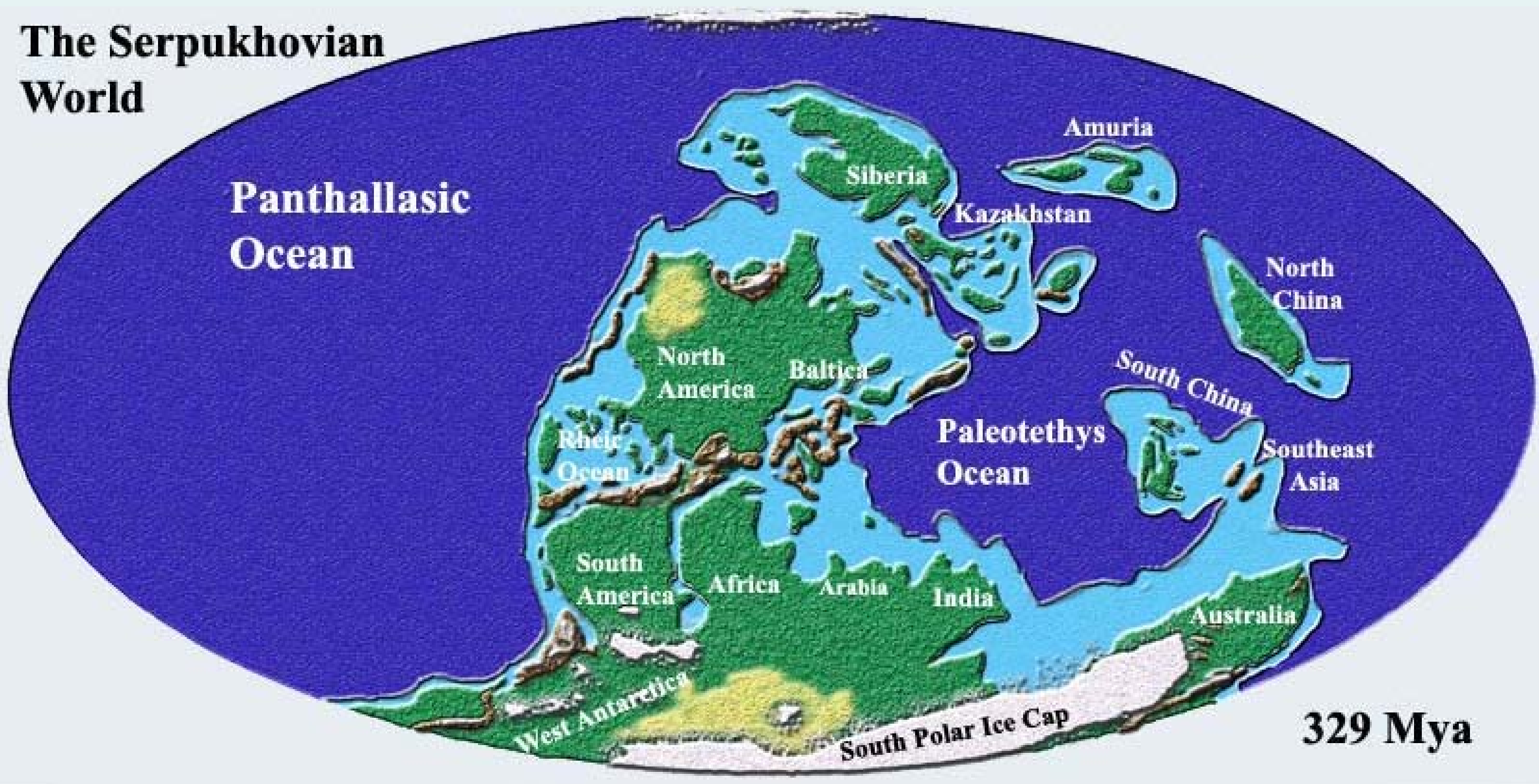
The Carboniferous Period of the Paleozoic Era: 299 to 359 million years ago

image from Earth History Resources

Introduction

The name Coal Measures was proposed by Farey in 1807 and 1811. term Carboniferous - coal bearing - was proposed by the English geologist William Conybeare and William Phillips in a paper published in 1822 to designate coal-bearing strata in north-central England. Conybeare and Phillips's Medial or Carboniferous Order included the Mountain or Carboniferous Limestone, Millstone Grit, and Coal Measures as it's three divisions. It was the first geological period to be established.. Subsequently in Continental Europe and Britain the system was divided into a Lower and an Upper Carboniferous. Meanwhile the American geologist Alexander Winchell proposed the name Mississippian in 1869 for Lower Carboniferous strata along the Mississippi River drainage region, and later, in 1891 Henry S. Williams suggested Pennsylvanian for the Upper Carboniferous. The terms Mississippian and Pennsylvanian Periods were then used by American geologists and palaeontologists instead of the one Carboniferous Period. Some recent fiddling with stratigraphic boundaries has allowed the American system to be matched with the Lower/early and Upper/later Carboniferous, giving a single international standard for the period.

Geography of the Carboniferous



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During the late Early Carboniferous, East Gondwanaland, for the first time since Early Paleozoic, began to drift toward the South Pole. By early Late Carboniferous, the South American-North African margin of Gondwanaland had collided with the northern Devonian supercontinent of Euramerica becomes Laurasia by the late Carboniferous. There is regional subsidence of the East-European Platform (east Laurussia/Euramerica) due to compressional stresses at the platform's margins. The northward drifting Gondwanaland then collides with Laurasia, resulting in a fold belt and mountain building from Poland through central Europe to the Appalachians. Through the collision of these two supercontinents arises Pangaea. At this time Pangaea was shaped like a huge "pack man", with a huge mouth facing eastward across the equator. The large open mouth becomes the Tethys Ocean. While East Gondwanaland drifted toward the South Pole, most of the East and Southeast Asian terranes were left in equatorial positions, forming a chain of continental terranes at the eastern edge of the Tethys Ocean.

Carboniferous Stratigraphy

Period	Subperiod	Epoch	When began	Duration
Permian	Cisuralian	Asselian	299.0 mya	4.4
Carboniferous (you are here!)	Pennsylvanian (late Carboniferous)	Gzhelian	303.4	4.4
		Kasimovian	307.2	3.8
		Moscovian	311.7	4.5
		Bashkirian	318.1	6.4
	Mississippian (early Carboniferous)	Serpukhovian	328.3	10.2
		Viséan	345.3	17.0
		Tournaisian	359.2	13.9
Devonian	Late Devonian	Famennian	374.5	15.3

The Tournaisian Epoch

Dawn of the Carboniferous. Plants mostly small (the late Devonian forests gone), first terrestrial tetrapods appear. Marine and freshwater life furnishes. Sharks diversify to take up ecological niches vacated by the placoderms

The Viséan

Carboniferous flora flourishes. Giant amphibious eurypterids. Tetrapods become common and diverse, including both terrestrial and aquatic forms. The first pre- or proto-amniotes appear on land

The Serpukhovian

Euramerica tropical and dominated by huge forests - the "coal swamp" biome. Dramatic evolutionary radiation of insects; flight appears (flying insects). The giant arthropleurids appear. Tetrapods flourish, with primitive forms co-existing alongside more advanced ones.

The Bashkirian

Terrestrial arthropods very common and diverse. Many types of tetrapods. Reptiles present but small and insignificant.

The Moscovian

While Euramerica is covered in tropical forests, Gondwana suffers glaciation and ice ages. Life abundant and diverse. Reptiles begin to diversify, but still overshadowed by amphibians

The Kasimovian

Drought decimates the great Euramerican lycopods ("scale trees"), resulting in a tree-fern dominated flora. Tetrapods and terrestrial arthropods remain abundant and diverse. The arthropleurids die out before the beginning of the Gzhelian

The Gzhelian

Dramatic radiation of reptiles (in response to drier conditions?), especially the pelycosaurs, who replace the stem tetrapods as the dominant life-form on land and in the swamps

Carboniferous Climate

The early part of the period is mostly warm, but there is a pronounced cooling and glaciation during the second half, triggered by Gondwanaland's southward migration. Although the equatorial regions remain warm and wet and tropical, the poles are gripped in a massive ice age, one that lasts for many millions of years. Vast sheets of ice cover Gondwanaland.

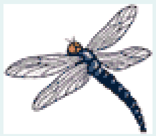
Life in the Carboniferous

In the oceans coral reefs and invertebrate life flourish, with groups such as brachiopods, echinoderms, ammonites, bryozoa, and corals diversify and are common. Among brachiopods, Productids, Spiriferids and Rhynchonellids are abundant. Terebratulids are also very common. Nautiloid cephalopods are represented by tightly coiled nautilids, with straight shelled and curved shelled forms becoming increasingly rare. Ammonoids are common; almost all types being the Goniatites, with suture lines a little more complex than those of the Devonian. Trilobites are rare, represented only by the proetids. Among echinoderms, blastoids and crinoids are extremely common, especially in the Early Carboniferous (Mississippian)

Among fish, the armoured placoderm and ostracoderm and marine lobe-finned fish (apart from the odd coelacanths) that so dominated the Devonian seas are all gone, to be replaced by an amazing diversity of sharks (Chondrichthyes).

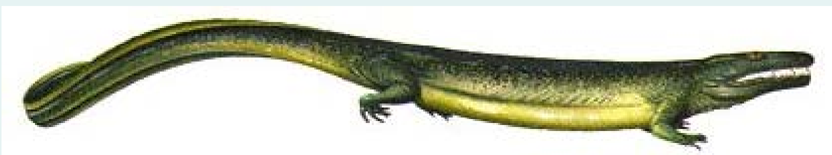
On land, especially in the Euramerican part of Pangea, the equatorial regions are covered by forests. The moist tropical climate produces a lush plant growth, which eventually becomes the great Coal Deposits (hence the name Carboniferous - "coal bearing"). The fern-like but seed-bearing pteridosperms, the huge green-stemmed Lepidodendrale lycopods (*Lepidodendron*, *Sigillaria*, etc, 35 meters tall), the giant sphenopsid *Calamites* (20 meters in height), and the strap-leaved mangrove-rooted Cordaitales (*Cordaites*, up to 45 meters) are all abundant, and tied closely to water. The drier uplands were much more sparsely covered. Meanwhile, Gondwanaland, with its colder Antarctic climate, has its own very distinct flora, dominated by glossopterid pteridosperms.

So vigorous is the growth of these ancient trees that they seemed to have sucked much of the carbon dioxide out of the atmosphere, producing a surfeit of oxygen. Oxygen levels were higher during this time than at any other time in the history of the Earth



Inhabiting the great forests were many types of insects, spiders, and other types of arthropods evolve. Encouraged by the oxygen-rich atmosphere, the abundance of food in the decaying forest leaf-litter, and the absence of large terrestrial vertebrates, many reach huge sizes. The dragonfly-like Meganeura, an aerial predator, had a wingspan of 60 to 75 cm. The inoffensive stocky-bodied and armoured millipede-like Arthropleura was 1.8 meters long, and the semi-terrestrial Hibbertopterid eurypterids were perhaps as large, while some scorpions reached 50 or 70cm. Alongside these giants were more conventionally sized invertebrates.

In the water and water margins the tetrapods flourish, are the dominant life form, and many different types inhabit the rivers, ponds, and swamps of the Carboniferous tropics, including many crocodile, eel, and salamander-like forms. But the largest hunters of the time were the gigantic rhizodont fish, reaching 7 meters in length. Meanwhile, the first reptiles appear, adapted to life lived totally on land, but remain insignificant until at least the very end of the Carboniferous.



Greererpeton - a large carnivorous tetrapod that lived an eel-like existence in rivers and swamps length to 2 metres. Equatorial swamps; late Viséan to early Serpukhovian *Collins Illustrated Encyclopaedia of Dinosaurs and Prehistoric Animals*, pp.50, 52,

Links

LINKS

Carboniferous Forests - Ralph E. Taggart - good non-technical intro to Carboniferous terrestrial life. Covers main groups of Carboniferous plants, also brief mention of insects, tetrapods, and reptiles

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The Mississippian

The Mississippian Epoch of the Carboniferous Period: 359 to 318 Mya

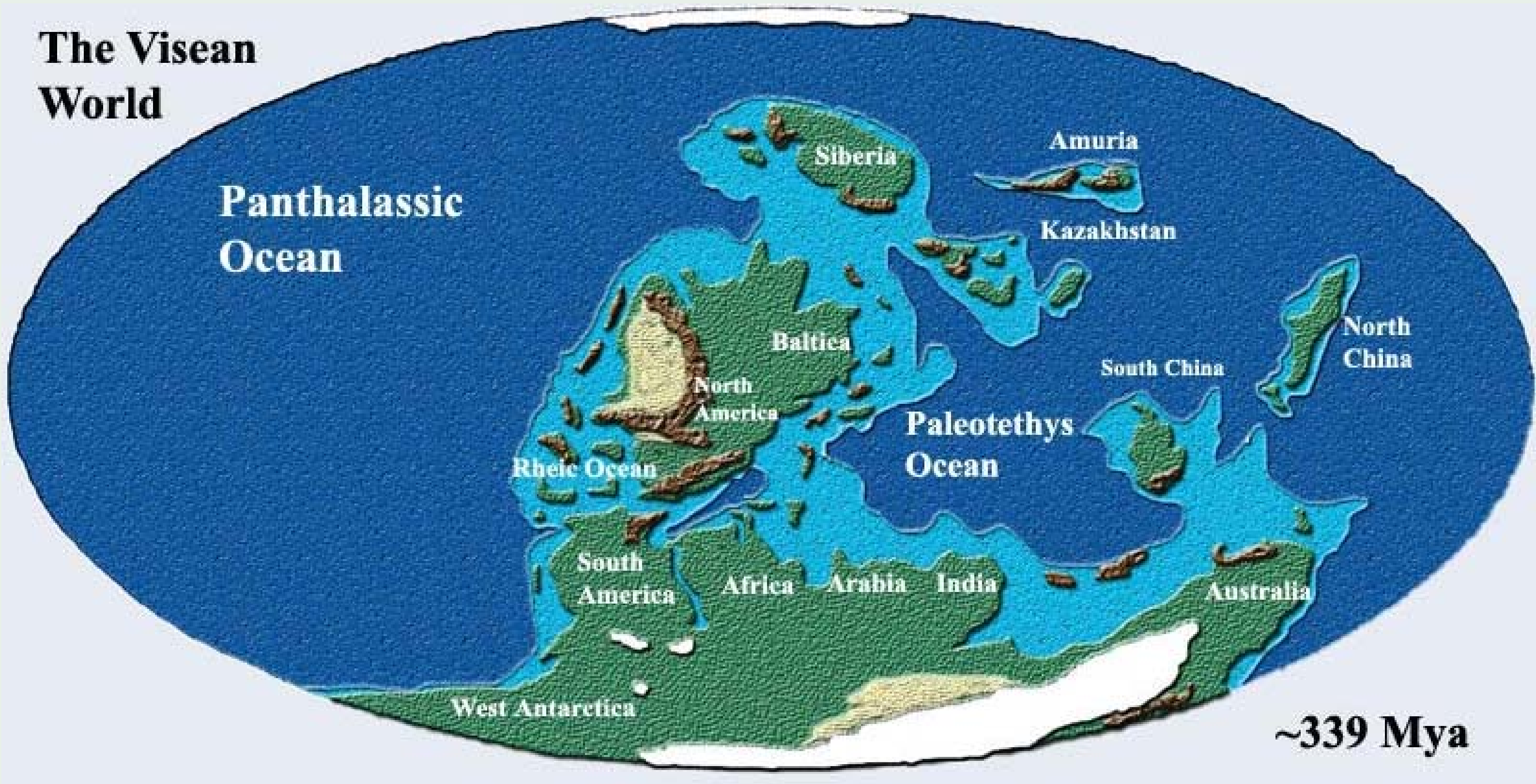
Introduction

The Early Carboniferous or Mississippian sub-period lasted for about 40 million years. During that time animal life, both vertebrate and invertebrate, consolidated its position on land the way plant life did during the Devonian. Euramerica and western Gondwana drifted northwards and moved closer together. This movement caused a lot of mountain building - the Varisca-Hercynian Orogeny - in Europe.

The American geologist Alexander Winchell formally proposed the name Mississippian in 1869 for the Lower Carboniferous strata (mostly limestones from limy mud laid down in a shallow sea) that are extensively exposed along the Upper Mississippi River drainage region. In 1891 H. S. Williams divided the "Carboniferous or Pennine" System into Pennsylvanian and Mississippian. In 1911 Ulrich divided the Mississippian into Waverleyan and Tennesseean systems.

The term Mississippian is used by American geologists and paleontologist but did not catch on in Europe or elsewhere, where Carboniferous was retained. The Mississippian and the "Lower Carboniferous" are not actually equivalent. Nevertheless some recent fiddling with boundaries has allowed the two to be matched and the Mississippian became a formal international term for the Early (Lower) Carboniferous, encompassing the Tournaisian, Viséan, and Serpukhovian Ages.

Geography of the Mississippian



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The Mississippian saw mountain building in what is now western North America. A glaciated Gondwana nears southern Euramerica and continues to collide with ancestral Europe, resulting in the Hercynian Orogeny and great mountains in southern Europe.

Mississippian Stratigraphy

Period/Epoch	Age	Faunal Stages	When began	Duration
Pennsylvanian (late Carboniferous)	Bashkirian	Kinderscoutian	322.8	
Mississippian (early Carboniferous) you are here!	Serpukhovian	Alportian Chokierian Arnsbergian Pendleian	325.6 328.3 332.9	2.8 2.7 4.5
	Viséan	Brigantian Asbian Holkerian Arundian Chadian	336 339.4 342.8 345 349.5	17
	Tournaisian	Ivorian Hastarian	353.8 362.5	13
Devonian	D3	Famennian		

Mississippian Life

Marine Biota

Arthropods, corals, bryozoa, crinoids, and mollusks flourished in warm shallow seas. Echinoderms - especially Crinoids were extremely numerous. Trilobites were much reduced in numbers, and confined to a single superfamily, the Proetoidea (also spelled Proeteacea). The last of the dendrite graptiloids died out. The first of the giant fusulinid foramnifers (marine amoebas) appear, but these are still tiny and insignificant

Cephalopoda

Of the nautiloid (palcephalopoda) cephalopods only the nautilida flourished. The giant straight-shelled *Rayonnoceras*, up to perhaps 6 meters in length, was the last of the Actinocerida. The bulbous-shelled Oncocerida also died out at this time. Many types of Ammonoid cephalopods evolved, mostly of the simple goniatiatic suture pattern. Especially in northwest Europe, their fossils are of great stratigraphic importance. The first ceratic ammonoids appear, with a more complex suture pattern.

Vertebrates

Sharks, actinopterygian, and sarcopterygian fish were all numerous and diverse. The Actinopterygii were mostly of the "paleonisciforms."

Freshwater and Terrestrial Biota

There are major differences between Late Devonian and early Mississippian vegetation. Areas that were previously forest were now dominated by shrubby r-selected plants, mostly pteridosperms less than 2 meters in height. In other words weeds. Only later did lycopsid and calamite trees reappear, paving the way for the giant forests of the late Carboniferous (Pennsylvanian) period.

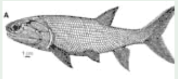
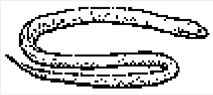
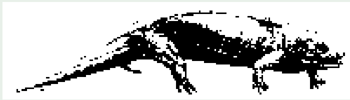
The climate, originally hot and dry, became cooler and wet later in the Mississippian period. Plants became important ground cover in this lush new environment, producing shelter for invertebrates which in turn provided food for early tetrapods.

Terrestrial invertebrates are poorly known, but it is likely that they consisted of mites, scorpions and other arachnids, millipedes, arthropleurids, collembolans (springtails), and an increasing diversity of litter-reducing insects (e.g. blattoids). Some Eurypterids of this time may have been partially terrestrial.

This was the period of greatest tetrapod evolutionary radiation. The early generations of aquatic Ichhyostegids were replaced by various parallel lineages of labyrinthodont and Lepospondyl amphibians. All the major ancient tetrapod groups seem to have appeared at this time. the majority were probably semi-aquatic, but early terrestrial forms and proto-reptiles appeared as well. The fresh-water Rhizodontiform fish - tetrapod "uncles" that like lungfish were capable of breathing air on occasion - were the super predators of the swamps, streams and lakes, with *Rhizodus* attaining 5 to 6 meters in length.

The Mississippian terrestrial food chain seems to have been much more primitive and less efficient then that of today. The major link between plant productivity and animal consumers seems to have been, as in the Devonian, through detritivorous arthropods. Insect herbivory was only just beginning at the end of the Mississippian sub-period, and tetrapod herbivory unknown. Most insects and arachnids scrounged for food in leaf litter, and served as the primary food source for the early terrestrial tetrapods.

ref: Anna K. Behrensmeyer, John D. Damuth, William A. Dimichele, and Hans-Dieter Sues, *Terrestrial Ecosystems Through Time : Evolutionary Paleoecology of Terrestrial Plants and Animals*

habitat	river, pond and swamp (semi or fully aquatic)	water margins (mixed terrestrial & amphibious)	lowlands and flood plain (fully terrestrial)
type of creature	 		

Tetrapod Bioprovinces

During this period there seems to have been only a single tetrapod province, although that may be because all known tetrapod fossils of this age are from tropical Euramerica; there are none known further than 5 degrees north or 20 degrees south of Viséan paleoequator. It is not known whether this is because the rest of the world was uninhabitable to animal life at the time (due to the increasing polar ice age conditions) or simply because no other localities have yet been discovered.

Crassigyrinus
a very primitive eel-like aquatic ?tetrapod
Viséan to Serpukhovian of Europe
length 2 metres

Links

LINKS

Browse the Fossil Gallery - Lower Carboniferous (Mississippian) Period - a nice selection of fossils from Nova Scotia

Mississippian - includes paleogeographic maps

During the Early Carboniferous Pangea Begins to Form.

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The Tournaisian Age (=Lower Mississippian Epoch)

The Tournasian Age of the Mississippian Epoch: 359 to 345 million years ago

The Tournaisian is in the ICS geologic timescale the lowest stage or oldest age of the Mississippian, the oldest subsystem of the Carboniferous. The Tournaisian age lasted from 359.2 ± 2.5 Ma to 345.3 ± 2.1 Ma. It is preceded by the Famennian (the uppermost stage of the Devonian) and is followed by the Viséan.

The Tournaisian was named after the Belgian city of Tournai. It was introduced in scientific literature by Belgian geologist André Hubert Dumont in 1832. Like many Devonian and lower Carboniferous stages, the Tournaisian is a unit from West European regional stratigraphy that is now used in the official international time scale.

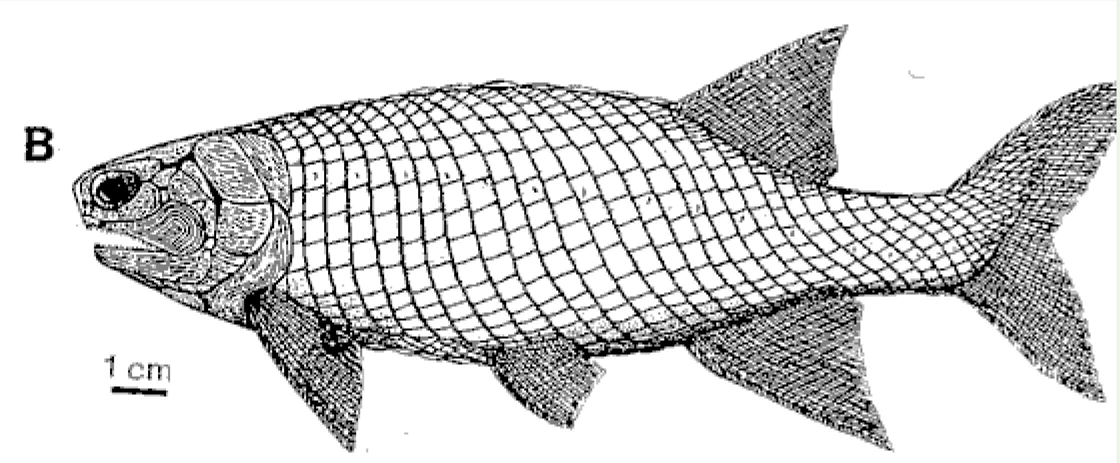
The Tournaisian coincides with Romer's gap, a period of remarkably little terrestrial fossils, thus constituting a discontinuity between the Devonian and the more modern terrestrial ecosystems of the Carboniferous.

Life

In this age plants were generally small consisting mostly of Lycopods & ferns. The first terrestrial tetrapods appear. Sharks radiate due to the extinction of the Placoderms. Bony and lobed finned fishes also radiate, as well as Crinoids, Blastoids & Bryozoans.

Climate & Geography Euramerica at the beginning of the Tournaisian.

The Climate was generally warm with high Sea levels. Minimal glaciatians occured at this time. The continents were arranged much the same as they were at the end of the Devonian. Gondwana straddled the southern hemisphere while Euramerica, located on the equator, continued to move towards Gondwana. Siberia occupied the nothern hemisphere. Yogi111207



Novogonatodus kasantsevae
Early actinopterygian fish - family Gonatotidae
(fresh water)
Mansfield, Victoria, Australia
(south-east Gondwanaland)

Location (present geography)	Stage		Nova Scotia
Tournaisian	**Ivorian**	350 352 354	Horton Bluff (undescribed tetrapod remains)
	Hastarian	356 358 360 362	

Links

	Links	

FOSSILS of NOVA SCOTIA Horton Bluff - The Discovery- about a trackway made by a very large tetrapodomorph - each footprint was 30 cm long and they were spaced 30 cm apart. The tracks are deep with raised edges, suggesting that the animal was heavy and the mud very soft. The type of creature that made the trackway is not known.

Blue Beach Fossils - a new privately run museum that just opened up featuring the flora and fauna of Horton Bluff, Nova Scotia, Tournasian fossils. It contains information about the site as well as some images of fossils that they have found and are currently working on.

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The Viséan Age
(=Middle Mississippian Epoch)

Mississippian (Early Carboniferous Period): 327 to 342 Mya

Introduction

The Viséan is an age in the ICS geologic timescale or a stage in the stratigraphic column. It is the second stage of the Mississippian, the lower subsystem of the Carboniferous. The Visean lasted from 345.3 ± 2.1 to 328.3 ±1.6 Ma. It follows the Tournaisian age/stage and is followed by the Serpukhovian age/stage. This period, representing the later Early Carboniferous was a time of great innovation on land, with a great radiation of stem tetrapods and the first proto-amniotes.

Major Events

Typical Carboniferous tetrapods appear for the first time.

Stratigraphy

		approx time	Nor t h	A m e r	i c a	Western Europe
Location						Scotland

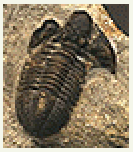
(present geography)	Age		Iowa	West Virginia	Nova Scotia	Midland Valley
	Brigantian	334 336	St Louis Formation	Bickett Shale Bluefield formation		East Kirkton
	Asbian	338				
Viséan	**Holkerian**	340 342				Wardie Shales
	Arundian	344				
	Chadian	346 348				

The climate of the Visean was similar to the Tournaisian at the beginning of the age but became increasingly warmer as it progressed. This is evidenced by migration patterns of marine invertibrates and land plants towards the polar regions. (Raymond 1985, 1990. Kelley and Raymond 1991).

Plants

The Visean forests were similar to the Tournaisian, however they consisted of different species and were more diverse and adapted to different habitats. Unlike modern plant groups where different species live in diverse habitats, those of the Visean were much more specific and preferred certain habitats, meaning the plant groups that inhabited wetlands will have no species that inhabit uplands and vice versa. Vegetation includes the lycopsid tree *Archaeosigillaria*, sphenopsids like *Archaeocalamites*/*Calamites* and *Sphenophyllum*, filicalean ferns, and small pteridosperms such as *Heterangium*. MAK020624, Yogi121212

Invertebrates



Class Trilobita
Order **Ptychopariida**
Suborder: **Illaenina**
Superfamily: **Proetacea**
Family: **Phillipsiidae**

Phillipsia sp.

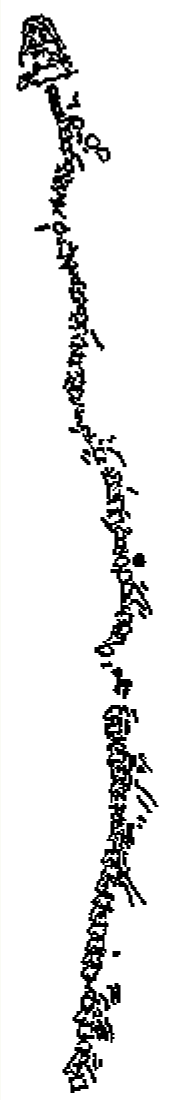
Horizon: Middle Mississippian, Warsaw Formation
Locality: Sunset Hills, Missouri

Vertebrates

In the Visean age the early tetrapods had radiated into at least three main branches. Recognizable basal-group tetrapods are representative of the temnospondyls (*Balanerpeton*) lepospondyls and anthracosaurs (*Silvanerpeton*, *Eoherpeton*), which were the relatives and ancestors of the Amniota. Aistopods snake like lepospondyl amphibians appeared in the Visean (e.g. *Lethiscus*) as well as Adelogyrinids similar to Aistopods except they retained a shoulder girdle. Despite their very early date they were aklready highly specilaised animals. The first possible amniotes or stem amniotes appeared, such as *Casineria*, resembling small lizards that evolved from amphibian reptiliomorphs.

Alongside these more advanced forms were a wide range of stem tetrapods (*Crassigyrinus*, *Loxomma*, *Eucritta*, etc). Recently "Gondwanan" tetrapods of middle Visean age were discovered in Australia (Thulborn 1996). The latest Visean East Kirkton quarry near Bathgate in Midlothian, Scotland is a virtual snapshot of late Visean life made up of tetrapods, scorpions, millipedes, eurypterids and a wide variety of plants. Yogi121212 MAK120102

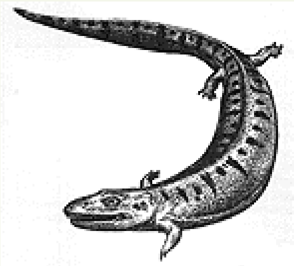
A Visean bestiary



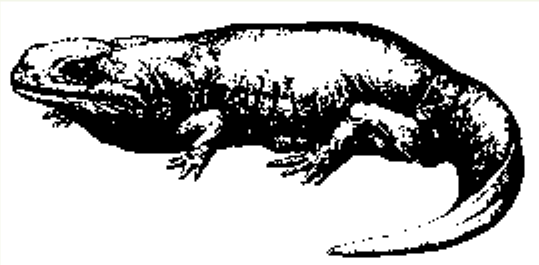
Class: **Tetrapoda**
Subclass "Lepospondyli" (polyphyletic?)
Order: **Aistopoda**
Family: **Lethisciidae**

Lethiscus stocki *Wellstead 1982*

Horizon: Holkerian Stage
Locality:
Comments: This small eel-like amphibian is one of the earliest known non-Devonian tetrapods. The body is already very specialized, with no trace of limbs or limb girdles



Class: **Tetrapoda**



Class: **Tetrapoda**
Order: **Temnospondyli**
Superfamily: incertae sedis

Order: **Embolomeri**

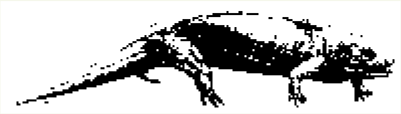
Pholidogaster

Horizon:
Locality:
Comments:

Family: **Dendrerpetontidae**

Dendrerpeton

Horizon: Brigantian Age
Locality:
Comments: a genus of temnospondyl found at East Kirkton (early Serpukhovian) and elsewhere drawing by Mike Coates



Class: **Tetrapoda**
Order: **Anthracosauria**
Suborder: **Embolomeri**
Family: **Eoherpetontidae**

Eoherpeton

Horizon:
Locality:
Comments: drawing by Mike Coates Depending on your preferred chronology, the famous East Kirkton site is either late Visean or Early Serpukhovian . We have followed Carroll 2009 p.63 in giving the date as late Brigantian of the latest Visean

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The Serpukhovian Age
(=Upper Mississippian Epoch)

The Serpukhovian Age of the Mississippian Epoch: 328 to 318 million years ago

Introduction

The Serpukhovian is the last of the three ages that make up the Mississippian Epoch. This is the Age from which come the remarkable tetrapods of East Kirkton and the Dora Bone Beds, as well as the wonderful chondrichthyan fauna of Bear Creek. This Age saw the appearance and rapid diversification of of winged insects, "typical" Paleozoic tetrapods, proto-amniotes, and the great Coal Swamp forests.

Sea levels were moderate throughout the Carboniferous. The seas rose steadily through most of the Sepukhovian, but fell rather sharply at the end of the Age, coincident with the onset of icehouse conditions and the beginnings of the Pennsylvanian Ice Age. Grossman *et al*. (2002); Mii *et al.* (2001). At about this same time, the connection between the Rheic and Paleotethys Oceans closed as Gondwana met and sutured to Laurussia (North America plus Baltica) to form Pangaea. This resulted in partial thermal isolation of the Paleotethys, which became a great semi-tropical bay. The climate, which had been fairly equable throughout most of the Mississippian, became more strongly zonal. Interestingly, these dramatic climate changes in the Late Serpukhovian occurred at just about the same time as the major evolutionary events of the Age: the sudden spread of winged insects, the evolution of protoamniotes (*e.g.*, Embolomeri), and a rapid turnover in brachiopod genera.

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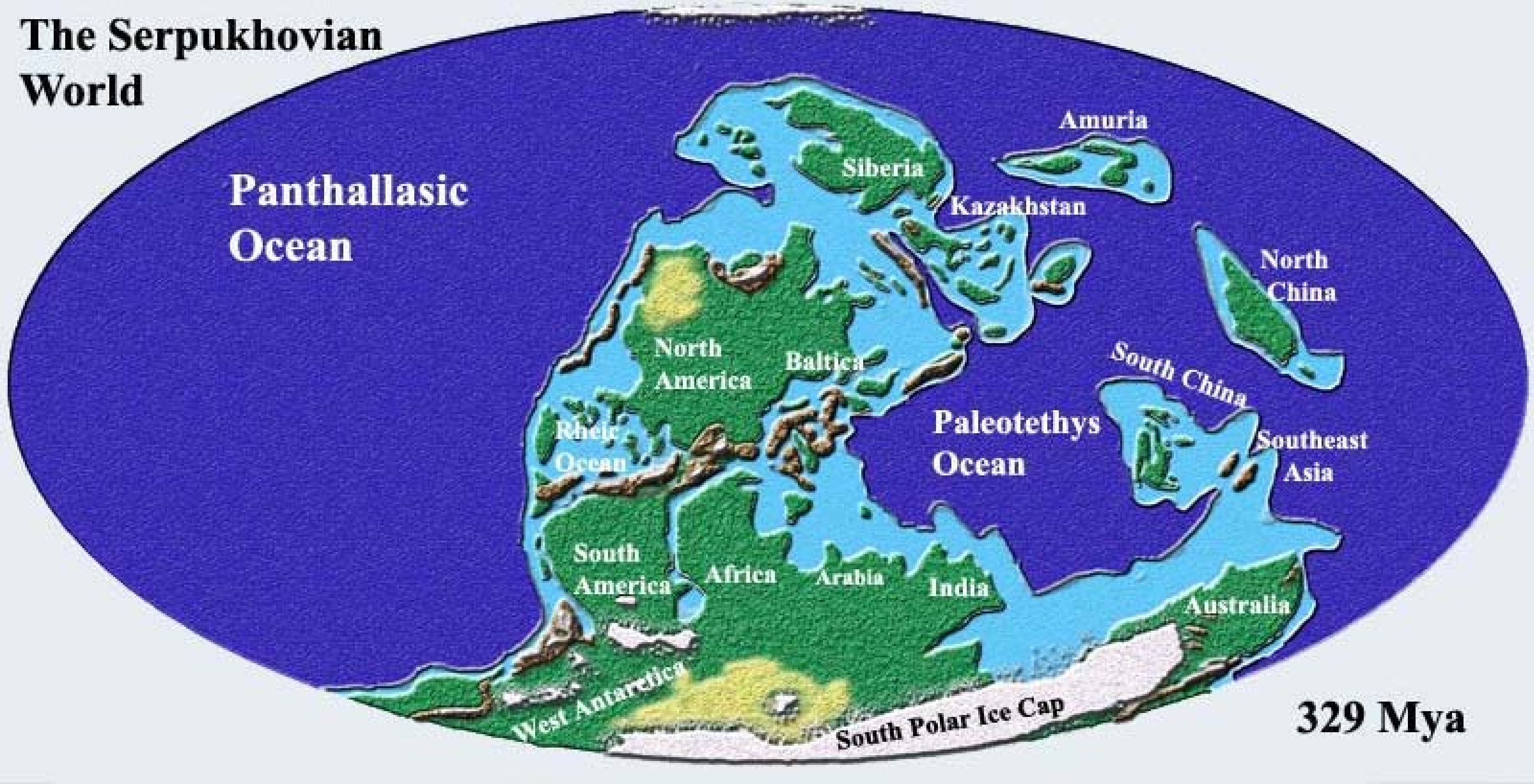
Serpukhovian Geography



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Stratigraphy

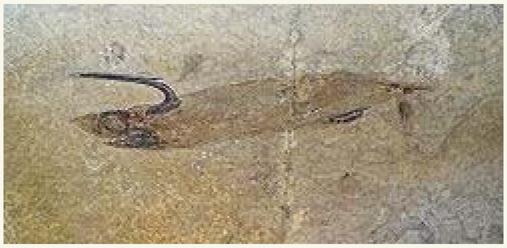
The following table correlates strata with tetrapod fossils (amphibians):

		approx time *	North America				Western Europe
Location (present geography)	Age		Utah	Iowa	West Virginia	Nova Scotia	Scotland Midland Valley
	Alportian	324					
Serpukhovian	**Chokierian**	326 328					
	Arnsbergian	330					
	Pendleian	332	Manning Canyon Shale				Dora Bone Bed, Crowdenbeath, Fife

Notes:

* approximate time in MYA (millions of years ago) - in two million year intervals

Important Fossil Sites



The small shark *Falcatus falcatus*, from the Bear Gulch limestone of Montana.
Photo by H. Zell - Wikipedia

The Dora lagerstätten of East Kirkton, Scotland (late Visean or possibly Earliest Serpukhovian), stands out as a unique glimpse of Middle Carboniferous vertebrates. The somewhat later Bear Gulch locality in Montana (Late Serpukhovian or possibly Bashkirian) provides an important glimpse of Carboniferous fish life.

Invertebrates

Goniatites suffer a mass extinction but a few lineages continue onto the following Bashkirian epoch.

The Blastoid echinoderm *Pentremites godoni*

Vertebrates

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The Pennsylvanian

The Pennsylvanian Epoch of the Carboniferous Period: 318 to 299 Mya


The Pennsylvanian was the time of the great 'Coal Swamp Forests' which dominated the equatorial regions of the planet. Typical Carboniferous forest, late Pennsylvanian. (screenshot from Prehistoric Park TV series)

Lasting some 33 million or so years, the Late Carboniferous or Pennsylvanian age was the high point of stem tetrapod evolution, especially during the Bashkirian and Moscovian epochs. During this time the first reptiles and synapsids evolved and quickly diversified. By the end of the period these new forms, especially the synapsids, had supplanted the stem tetrapods as the dominant life form on land.

Geography

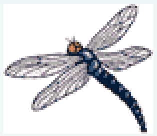
During the late Carboniferous period Laurussia and Siberia collide to form Laurasia; meanwhile Gondwana comes up from the south. The resulting Appalachian, Ouachita, Marathon, Ural, Variscan, and Hercynian orogenies formed some of the largest mountains of all time. As a result of the collision of Gondwana and Laurasia the supercontinent of Pangea comes into being.

Life - the Biosphere

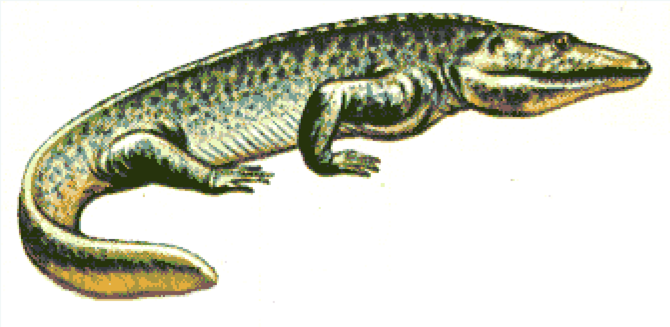
On land, great forest swamps covered extensive equatorial areas. These forests consisted of diverse plants including tree ferns, which grew 15 meters in height, *Calmites*, a giant version of the modern "horsetail" plant, lycopods (e.g. *Lepidodendron*, which attained a height of 30 metres), the extinct group of plants called "seed ferns" (see illustration at left), and primitive Conifer-like plants (*Cordaites*) that reached 40 meters in height

Alethopteris from the Pennsylvanian of West Virginia, USA. From Indiana9 Fossils (which has a whole page of *Alethopteris* images).

The extensive burial of biologically-produced carbon led to a buildup of surplus oxygen in the atmosphere; estimates place the peak oxygen content as high as 35%, compared to 21% today. This oxygen level resulted in insect and amphibian gigantism--creatures whose size is constrained by respiratory systems that are limited in their ability to



diffuse oxygen. In this In the moist oxygen rich atmosphere flying insects were abundant, and some attained huge size, such as *Meganeura*, with a wing span of 70 centimetres



Diplovertebron - a medium-sized semi-aquatic tetrapod
length 1 to 1.5 metres
Moscovian of Europe

Tetrapods were abundant, especially the "labyrinthodonts," so called because of the complex (labyrinthine) pattern of folded enamel in their teeth. They filled every available ecological niche, from fully aquatic eel-like forms, to large semiaquatic crocodile like animals and small forms like modern day newts and salamanders, to terrestrial types similar to reptiles. Some types (the Aïstopoda) lost their legs altogether, superficially resembling snakes.

The earliest Reptiles also evolved at this time, such as *Hylonomus* (left) but remained relatively insignificant until the end of the period. Reptiles have a big advantage over stem tetrapods in that they do not have to return to water to breed; they can lay their eggs on dry land. So it is likely that with the appearance of reptiles the tetrapods* (land animals) were able to colonize the uplands for the first time, where they fed on an abundance of insects.

Coal Measures

The name "Carboniferous" derives from the fact that most of the important coal producing strata are of this age. However, it is specifically in the Late Carboniferous or Pennsylvanian sub-period that this is so. During this time most of the world's coal deposits were laid down, the coal being formed from compressed layers of rotting vegetation. MAK

The large coal deposits of the Carboniferous primarily owe their existence to two factors. The first of these is the appearance of bark-bearing trees (and in particular the evolution of the bark fiber lignin). The second is the lower sea levels that occurred during the Carboniferous as compared to the Devonian period. This allowed for the development of extensive lowland swamps and forests in North America and Europe. Large quantities of wood were buried during this period because animals and decomposing bacteria had not yet evolved that could effectively digest the new lignin. Those early plants made extensive use of lignin. They had bark to wood ratios of 8 to 1, and even as high as 20 to 1. This compares to modern values less than 1 to 4. This bark, which must have been used as support as well as protection, probably had 38% to 58% lignin. Lignin is insoluble, too large to pass through cell walls, too heterogeneous for specific enzymes, and toxic, so that few organisms other than Basidiomycetes fungi can degrade it. It can not be oxidized in an atmosphere of less than 5% oxygen. It can linger in soil for thousands of years and inhibits decay of other substances. Probably the reason for its high percentages is protection from insect herbivory in a world containing very effective insect herbivores, but nothing remotely as effective as modern insectivores and probably many fewer poisons than currently. In any case coal measures could easily have made thick deposits on well drained soils as well as swamps. Yogi111211

Stratigraphic Divisions

Epoch	Age	European epochs	Age	When began	Duration
Cisuralian	Asselian	Autunian	Asselian	299.0	4.4
Pennsylvanian (late Carboniferous) you are here!	Gzhelian	Stephanian_C Stephanian B	Noginskian Klazminskian	303.4	4.4
	Kasimovian	Stephanian A	Dorogomilovskian Chamovnicheskian Krevyakinskian	307.2	3.8
	Moscovian	Westphalian_D Westphalian C	Myachkovskian Podolskian Kashirskian Vereiskian	311.7	4.5
	Bashkirian	Westphalian B Westphalian A Namurian C Namurian B	Melekesskian Chermshanskian Yeadonian Marsdenian Kinderscoutian	318.1	6.4
Mississippian (early Carboniferous)	Serpukhovian	Namurian A		328.3	10.2

Resources

Links

Pennsylvanian map page

PENNSYLVANIAN PERIOD

Browse the Fossil Gallery - Upper Carboniferous (Pennsylvanian) Period - a nice selection of fossils from Nova Scotia

Radiometric Dating Controversy

PENNSYLVANIAN TIME-SCALE PROBLEMS - the usual given for the Pennsylvanian is around 34 million years. A meticulous new study of central European stratigraphy now pegs the Pennsylvanian as spanning only 19 million years; a 44% change! This figure, if it is genuine, casts doubt on the origin of the famous Pennsylvanian cyclothems (repetitive strata) in North America, previously correlated with sea level changes forced by variations in the earth's orbit (the Milankovitch periods). One wonders how reliable radiometric dating is? Consider the discrepancy regarding dating for the base of Cambrian. I have therefore retained the old dating of the Pennsylvanian here, tending confirmation of these new findings.

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The Bashkirian Age
(=Lower Pennsylvanian Epoch)

The Bashkirian Age of the Pennsylvanian Epoch: 318 to 312 million years ago

Introduction

The Bashkirian is in the ICS geologic timescale the lowest stage or oldest age of the Pennsylvanian, the youngest subsystem of the Carboniferous. The Bashkirian age lasted from 318.1 ± 1.3 to 311.7 ± 1.1 Ma, is preceded by the Serpukhovian and is followed by the Moscovian. The Bashkirian could be described as later Middle Carboniferous; the first of the four epochs that make up the Pennsylvanian subperiod.

At this time, the Euramerican tropics come to be dominated by great lowland swamps, characterized by lycophyte, sphenopsid, and medullosan plants, and inhabited by many types of invertebrates, stem tetrapods and the occasional primitive reptile. Meanwhile, Gondwana is covered by spreading ice sheets.

Important Fossil Sites

The Bear Gulch locality in Montana provides an important glimpse of Carboniferous fish life.

Major Events

Polar Gondwana covered in ice. The great Coal Swamps (or mires) become an important biome.

Stratigraphy

Based on the stratotype of the Moscow Basin / Urals. Incorporates the Namurian B and C and Westpahlian A of the Western Europe.

Divided into five ages. The Marsdenian, Kinderscoutian, and Yeadonian are based on Namurian goniatite zones defined in the British Isles, and collectively make up the Early Bashkirian. The Chermshanskian and Melekesskian are part of the standard Russian sequence and are used to define the Late Bashkirian

Geography

Low lying tropical wetlands in Euramerica.

Climate

At this time the southern hemisphere, namely the supercontinent of Gondwana, became significantly glaciated. The paleo north pole also experienced glaciation though not as extensive as the south. This cooling trend started in the Serpukhovian as evidenced by the migration of marine invertibrates away from the paleo south pole (Isbell et al., 2003). As the poles became more frigid the equatorial regions became wetter and possibly warmer. Despite glaciation in Gondwana, the equatorial regions remain tropical.

Life

Plants

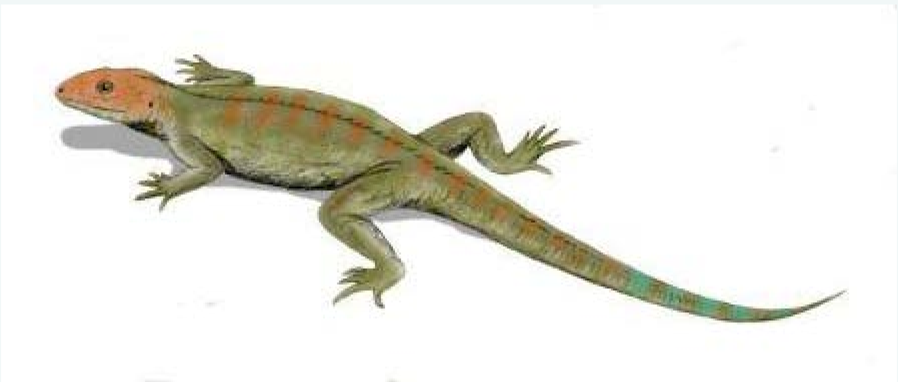
The equatorial wetlands enable the rise of the great Carboniferous Coal Swamps (or mires). Important plants include *Lepidophloios*, *Diaphorodendron*, *Paracyclopodites*, *Sigillaria*, *Calamites*, *Sphenophyllum*, *Psaronius*, and *Medullosa*.

.

Invertebrates

Sudden appearance of winged insects of various kinds

Vertebrates



Hylonomus lyelli, an early reptile from the Late Carboniferous of Nova Scotia, Canada. Life reconstruction by Nobu Tamura

Chondrichthyes are diverse in seas, and current forms are joined by a new lineage, the Eugeneodontida. Osteichthyes are common in fresh water, and include both the Rhizodontiformes and the Osteolepiformes. In the ponds, rivers and swamps and on land stem tetrapods continue to constitute the majority of tetrapods. Amniotes made their appearance, with the oldest unquestionable reptile, *Hylonomus*, approximately 315 million years ago.

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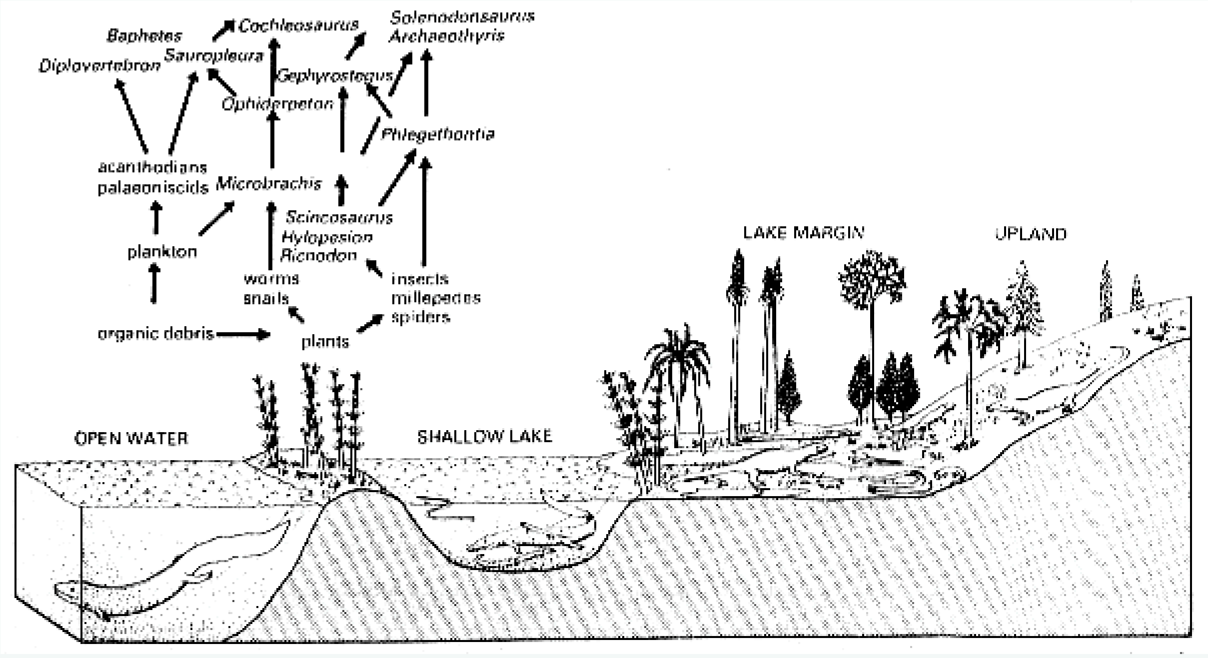
The Moscovian
(=Middle Pennsylvanian Epoch)

The Moscovian Age of the Pennsylvanian Epoch



Nýrany ecosystem (Bohemia - Czech Republic) - late Moscovian (Maychkovskian Age) of Euramerica diagram from Michael J. Benton, *Vertebrate Palaeontology - Biology and Evolution*, (Unwin Hyman, London)

Introduction

The Moscovian is in the ICS geologic timescale a stage or age in the Pennsylvanian, the youngest subsystem of the Carboniferous. The Moscovian age lasted from 311.7 ± 1.1 to 306.5 ± 1.0 Ma,[2] is preceded by the Bashkirian and is followed by the Kasimovian. The Moscovian overlaps with the European regional Westphalian stage. This epoch represented the culmination of the Late Carboniferous biota

The great tropical rainforests of Euramerica supported towering lycopsids and a heterogeneous mix of vegetation. These Lycopsid dominated forests, altered landscapes by creating organic-rich anastomosing river systems with multiple channels and stable alluvial islands.

Animal species distribution was very cosmopolitan at this time with the same species existing everywhere across tropical Pangaea. Invertibrates were abundant and diverse. Terrestrial vertebrates were predominantly amphibians and a few basal amniotes (‘reptiles’). Amphibians were tied to waterside habitats and were primarily piscivores, though a few had evolved insectivory. Almost unnoticed amongst the tetrapods, an important event was taking place. Alongside the Protorothyridid Captorhinids (Eureptilia), and barely distinguishable from them, was the earliest known Pelycosaur (Synapsida), Archaeothyris. The interplay between these two great divisions of amniotes - the Sauropsida (or Eureptilia) and the Theropsida (or Synapsida) will characterize tetrapod evolution up until the present day.

At the end of the Moscovian and continuing into the early Kasimovian, climate change affected the ecology of the rain forests resulting in a tree-fern dominated flora, replacing the lycopsids. The drier climate also affected amphibians resulting in a reduction in species, while the reptiles, better adapted to the drier conditions, diversified into more species. Yogi111212

Major Events

Gondwana glaciation reaches its maximum extent.

Important Fossil Sites

The Mazon Creek is a very important Carboniferous Lagerstätten

Invertebrates

Terrestrial arthropods flourish and insects continue their radiation which began in the Bashkirian.

	 Phylum : **Mollusca** Class: **Cephalopoda**	 Phylum : **Echinoderma**

Phylum : **Mollusca**
Class: **Gastropoda**
Order:
Family:

Worthenia tabulata *(Conrad)*

Horizon: Minturn Formation, Late Atokan Stage (Kashirskian Age)
Locality: McCoy, Eagle County, Colorado, USA
Comments: Collector: Chris Itano

Order: **Pseudorthocerida**
Family: **Pseudorthoceridae**

Pseudorthoceras knoxense

Horizon: Minturn Formation, Late Atokan Stage (Kashirskian Age)
Locality: McCoy, Eagle County, Colorado, USA
Comments:

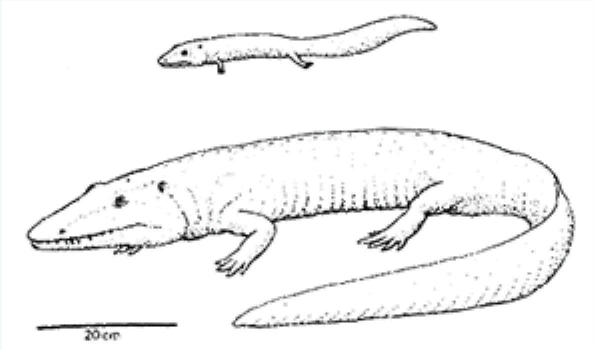
Class: **Crinoidea**

Aglaocrinus keytei *Strimple and Moore 1973*

Horizon: Minturn Formation - Late Atokan Stage (Kashirskian Age)
Locality: McCoy, Eagle County, Colorado, USA
Comments: Collector: Chris Itano

Vertebrates

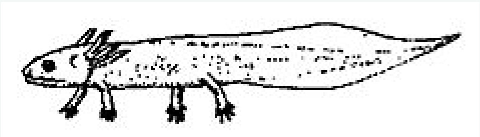
The golden age of amphibians. A selection of diverse types known from a single locality is shown below.



Class: **Tetrapoda**
Order: **Temnospondyli**
Superfamily: Edopoidea
Family: Cochleosauridae

Cochleosaurus bohemicus *(Fric) 1885*

Length: 1.5 metres
Horizon: Westphalian D
Locality: Nýrany, Czech Republic
Comments: *Cochleosaurus* adult and juvenile illustrated above. This large semi-aquatic tetrapod filled an ecological role not unlike that of the modern crocodile. A common animal, at least four dozen specimens are known from this locality.



Class: **Tetrapoda**
Order: **Temnospondyli**
Superfamily: **"Eryopoidea"**
Family: **Branchiosauridae**

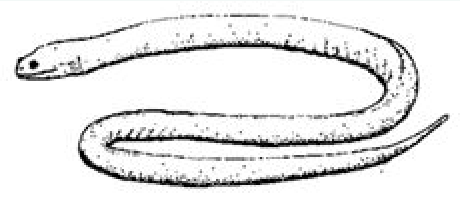
Branchiosaurus salamandriodes *Fric 1876*

Length: 15 cm - snout to pelvis
Horizon: Westphalian D
Locality: Nýrany, Czech Republic
Comments: Shallow-water/swamp-lake aquatic - note the external gills. Like the modern Axotl or Mexican "walking fish", this little creature led a wholly aquatic existence. At least three dozen specimens are known from this locality.

Class: **Tetrapoda**
Order: **Temnospondyli**
Superfamily: **"Eryopoidea"**
Family: **Micromelerpetonidae**

"Limnerpeton" laticeps *Fric 1881*

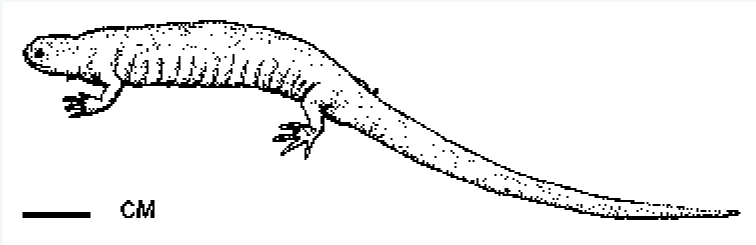
Length: 11 cm - snout to pelvis
Horizon: Westphalian D
Locality: Nýrany, Czech Republic
Comments: A small shallow-water/swamp-lake aquatic form. A common species, at least four dozen specimens are known from this locality.



Class: **Tetrapoda**
Subclass "Lepospondyli" (polyphyletic?)
Order: **Aistopoda**
Family: **Ophiderpetonidae**

Ophiderpeton granulosum *Fric 1880*

Length: 1.5 metres
Horizon: Westphalian D
Locality: Nýrany, Czech Republic
Comments: Shallow-water/swamp-lake aquatic; an eel or snake-like limbless amphibian, about two dozen specimens are known from here.



Class: **Tetrapoda**
Subclass "Lepospondyli" (polyphyletic?)
Order: **Nectridea**
Family: **Scincosauridae**

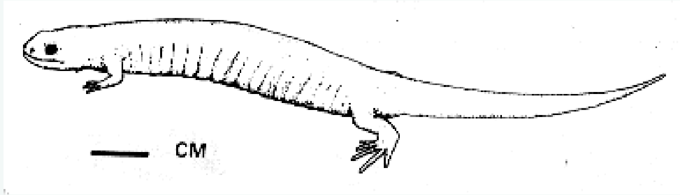
Scincosaurus crassus *Fric 1876*

Length: 5.5 cm - snout to pelvis
Horizon: Westphalian D
Locality: Nýrany, Czech Republic
Comments: terrestrial/pond-margin; ; a very common form, at least 66 specimens have been found at this locality.

Class: **Tetrapoda**
Subclass "Lepospondyli" (polyphyletic?)
Order: **Microsauria**
Family: **Microbrachidae**

Microbrachis pelikani *Fric 1876*

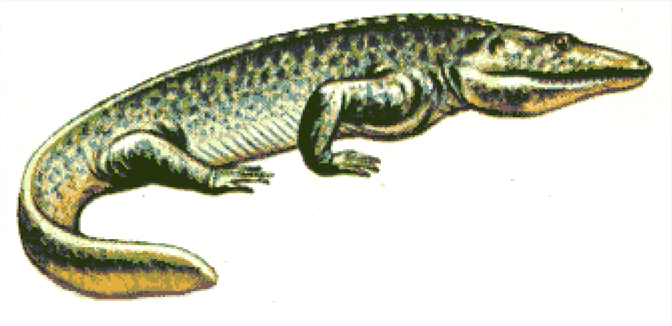
Length: 17 cm - snout to pelvis
Horizon: Westphalian D
Locality: Nýrany, Czech Republic
Comments: Shallow-water/swamp-lake aquatic; a very common form, at least 82 specimens have been recovered from this locality



Class: **Tetrapoda**
Subclass "Lepospondyli" (polyphyletic?)
Order: **Microsauria**
Family: **Hyoplesiontidae**

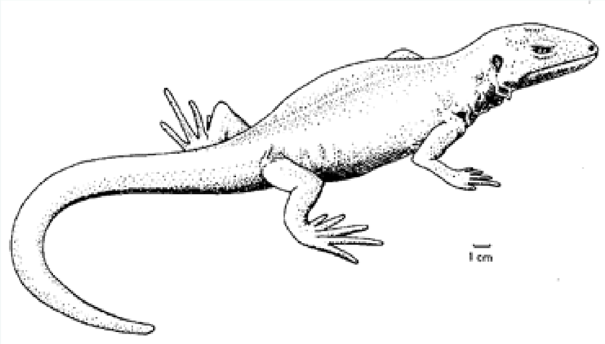
Hyoplesion longicostatum *(Fric) 1883*

Length: 8 cm - snout to pelvis
Horizon: Westphalian D
Locality: Nýrany, Czech Republic
Comments: terrestrial/pond-margin, a dozen specimens are known



Class: **Tetrapoda**
Order: **Anthracosauria**
Suborder: **Embolomeri**
Family: **Eogyrinidae**

Diplovertebron punctatum *Fric 1885*



Class: **Tetrapoda**
Order: **Anthracosauria**
Suborder: **Gephyrostegida**
Family: **Gephyrostegidae**

Gephyrostegus bohemicus *(Fric) 1885*

Length: 21 cm - snout to pelvis

Length: 30 cm - snout to pelvis Horizon: Westphalian D Locality: Nýrany, Czech Republic Comments: open-water/lacustrine semi-aquatic	Horizon: Westphalian D Locality: Nýrany, Czech Republic Comments: a medium-sized insectivorous/carnivorous amphibian that frequented pond margins. The ecological equivalent of the modern lizard. A fairly common species, about a dozen specimens have been found at this locality

Almost unnoticed amongst the tetrapods, an important event was taking place. Alongside the Protorothyridid Captorhinids (Eureptilia), and barely distinguishable from them, was the earliest known Pelycosaur (Synapsida), *Archaeothyris*. The interplay between these two great divisions of amniotes - the Sauropsida (or Eureptilia) and the Theropsida (or Synapsida) will characterize tetrapod evolution up until the present day.

Resources

Links and References

Mazon Creek Fossils - A window into the Carboniferous period

Reference - Andrew R. Milner, "The Tetrapod Assemblage from Nýrany, Czechoslovakia", in *Systematics Association Special Volume No.15*, "The Terrstrial Environment and the Orogin of Land Vertebrates", ed. by A. L. Panchen, 1980, pp.439-496, Academic Press, London and New York

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The Kasimovian
(Upper Pennsylvanian Epoch)

The Kasimovian Age of the Pennsylvanian Epoch: 307 to 303 million years ago

The Kasimovian is the third stage in the Pennsylvanian (late Carboniferous), lasting from 306.5 ± 1.0 to 303.9 ± 0.9 Ma. The Kasimovian stage follows the Moscovian and is followed by the Gzhelian.

Coal Forests covered tropical Euramerica (Europe, eastern North America, northwesternmost Africa) and Cathaysia (mainly China). Climate change devastated these tropical rainforests in the late Moscovian early Kasimovian ages. This climate change caused by a cooler, drier climate severely affected the lycopsids which dominated the wetland areas (they were subsequently replaced by opportunistic ferns). By the late Kasimovian rainforests were fragmented, forming shrinking patches further and further apart. There was also a great loss of amphibian diversity while simultaneously, the drier climate spurred the diversification of reptiles. Terrestrial invertebrates were diverse and included annelids, molluscs, and arthropods, including the giant arthropleurids. Most were detritivorous, eating 'litter' off of the forest floor however, some had evolved herbivorous and predatory forms. By the end of the age, the Arthropleurids went extinct. Yogi111211

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The Gzhelian
(Upper Pennsylvanian Epoch)

The Gzhelian Age of the Pennsylvanian Epoch: 303 to 299 million years ago

Meganuera monyi
wingspan 75 cm
Stephanian of France.

Eastern Euramerica (modern day Europe) as it appeared in the Gzhelian. Map © Ron Blakey

The Gzhelian is the youngest stage of the Pennsylvanian, the youngest subsystem of the Carboniferous. The Gzhelian lasted from 303.9 ± 0.9 to 299.0 ± 0.8 Ma. It follows the Kasimovian age/stage and is followed by the Asselian age/stage, the oldest subdivision of the Permian system. The Gzhelian is more or less coeval with the Stephanian stage of the regional stratigraphy of Europe.

The aridification of the climate which began in the Kasimovian, continued in the Gzhelian. This change resulted in a major turnover in the structure of the Coal Swamps. The Lycopsids which so dominated the Baskirian and Moscovian ages were practically reduced to one genera *Sigillaria*. Ferns replaced the Lycopsids in abundance with the latter being reduced to the wettest parts of the swamps. The dominance of the Ferns was only temporary as Seed Plants eventually supplanted them, remaining dominant to the present day.

At the very end of the age, the Coal Forests underwent a resurgence, expanding mainly in eastern Asia, notably China; they never recovered fully in Euramerica. The Chinese Coal Forests continued to flourish well into Permian times. This resurgence of the Coal Forests seems to have coincided with a lowering of global temperatures, coinciding with a return of extensive polar ice in southern Gondwana. This lessening of the greenhouse effect maybe due to massive coal deposition extracting much carbon dioxide from the atmosphere.

The Gzhelian was also a time of glaciation with the poles extremely cold (particularly in the south). The equatorial regions remained wet and warm. This period of glaciation persisted into the Permian. Yogi111211

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Behrensmeyer, AK, JD Damuth, WA Dimichele & H-D Sues (1992), **Terrestrial Ecosystems Through Time : Evolutionary Paleoecology of Terrestrial Plants and Animals**, Univ. Chicago Press, 568 pp.

Grossman, EL, P Bruckschen, H-S Mii, BI Chuvashov, TE Yancey & J Veizer (2002), *Carboniferous paleoclimate and global change: Isotopic evidence from the Russian Platform* **in Carboniferous Stratigraphy and Paleogeography in Eurasia**. Inst Geol. & Geochem, Russ. Acad. Sci, pp. 61-71.

Mii, H-S, EL Grossman, TE Yancey, B Chuvashov & A Egorov (2001), *Isotopic records of brachiopod shells from the Russian Platform -- evidence for the onset of mid-Carboniferous glaciation*. **Chem. Geol.** 175: 133�147.

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Permian period

Palaeos com is currently undergoing a major revision and update. For this reason, you may find many blank pages, broken links, etc. We hope to have some material on this page soon. Thank you for your patience.

Permian Period

The Permian Period: 1

The Permian Period of the Paleozoic Era: 299 to 251 million years ago

Introduction

image from Earth History Resources

Permian scene

two large finback pelycosaurs of the genus *Dimetrodon* sun themselves on a river bank.

To the left is a stand of Calamite trees.

The Permian period was named in 1841 by the geologist Murchison after a tour of Imperial Russia to include the "vast series of beds of marls, schists, limestones, sandstones, and conglomerates" that overlay the Carboniferous formations in the eastern part of thecountry. He named it after the ancient kingdom of Permia and the present city of Perm near the Ural mountains.

Geography

During the Permian all the world's land masses joined together into a single supercontinent, Pangea. The collision between Laurasia and Siberia-Kazakhstania and China finalized assembly of Pangaea by end of Permian. This was the first time since the late Proterozoic supercontinent of Rodinia that such a landmass had formed. Pangea was shaped sort of like a giant "Pacman", with the mouth on the east. There was a correspondingly large single ocean, called Panthalassa. The body of water enclosed by the pacman mouth constituted a smaller sea, the Tethys, which covered much of what is now southern and central Europe.

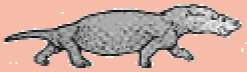
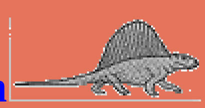
Throughout the Permian, Europe was covered by a very salty inland sea, the *Zechstein sea*, which advanced and receded at least twice. This was home to an impoverished fauna, mainly brachiopods and bivalves, which were able to cope with the hypersaline conditions.

Due to the formation of the supercontinent Pangea, the sea level drops and the warm shallow seas decline in extent. This is one of the factors that may have led to the extinction of many life-forms at the end of the period

There were at least two major extinction events, one in the middle of the period, and a better known one at the end. Various explanations have been offered, from the mundane, such as continental shelf environments being reduced, to the reasonable (Greenhouse events and superanoxia), to the imaginative (Superplume activity in the Earth's mantle) and the extreme (Strangelove Ocean); although it may have been a combination of all these factors and more as well.

Stratigraphy

Unlike most other geological periods which have a three-part division into early, middle, and late, the Permian Period was conventionally divided into early and late only. The more recent arrangement has a three-fold division. Although the earlier part is well documented, there have recently been some controversies regarding the relative dating of the late Permian, and of the Permian-Triassic boundary in general. The following table presents the various periods, epochs, and ages, along with a drawing of a representative animal from that time. The dating (in millions of years ago) is of course approximate, as are all such ancient dates. We have used the most recent ICS dates, which quite plausibly allow rather more time to the later Permian ages then some of the earlier timescales.

Period	Epoch	Age	When began	Duration
Triassic	**Early Triassic**	**Induan**	251.0 Mya	1.3
Permian	**Lopingian** 	**Changhsingian**	253.8	2.8
		Wuchiapingian	260.4	6.6
	Guadalupian 	**Capitanian**	265.8	5.4
		Wordian	268.0	2.2
		Roadian	270.6	2.6
	Cisuralian  	**Kungurian**	275.6	5.0
		Artinskian	284.4	8.8
		Sakmarian	294.6	10.2
		Asselian	299.0	4.4
Carboniferous	**Pennsylvanian**	**Gzhelian**	303.9	4.9

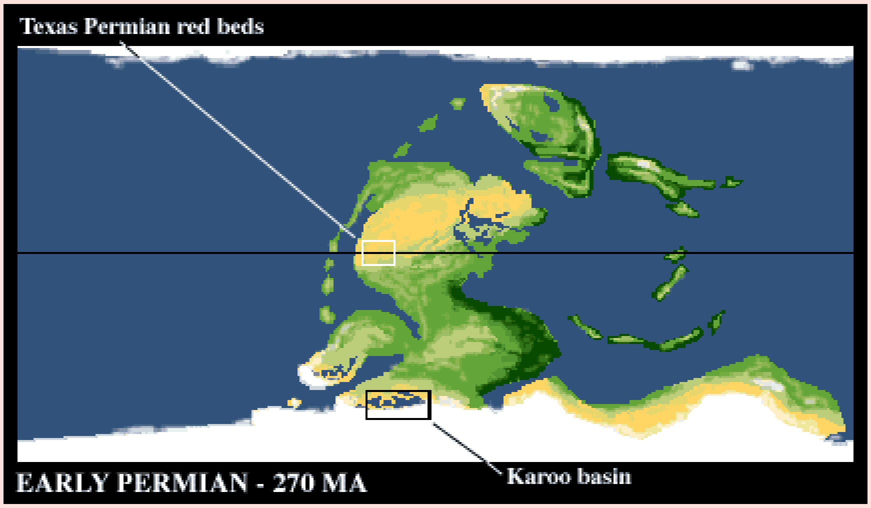
Climate

As the Permian opened, the Earth was still in the grip of an ice age, so the polar regions were covered with deep layers of ice. Glaciers continued to cover much of Gondwanaland, as they had during the late Carboniferous . At the same time the tropics were covered in swampy forests.

Towards the middle of the period the climate became warmer and milder, the glaciers receded, and the continental interiors became drier. Much of the interior of Pangea was probably arid, with great seasonal fluctuations (wet and dry seasons), because of the lack of the moderating effect of nearby bodies of water. This drying tendency continued through to the late Permian, along with alternating warming and cooling periods.

Permian Sites

The Permian has few sites with exceptional preservation. Some exceptional arthropod specimens are known from Kansas and Oklahoma (south-central US). The Permian is best known for its vertebrate fossils .



Map from lecture 8 of DINOSAURS AND THE HISTORY OF LIFE - GEOLOGY V1001x by Professor Paul Eric Olsen

Three important areas for Permian vertebrate fossils are the Early to middle Permian equatorial Red Beds of Texas and Oklahoma, the middle to late Permian Kazanian and Tatarian zones on the Russian platform (not shown on this map, but it is just north of the paleoequator, on the north-east of the large continent (near the lakes), and the Late Permian Karoo series (Lower Beaufort) of southern Africa (bottom center of map).

The Red Beds are full of the fossil remains of Pelycosaurs like the finbacks like *Dimetrodon*, which was clearly the dominant predator of these environments for some 20 million years. The Russian and South African sites contain the remains of many therapsids. These creatures succeeded the basal synapsids as the rulers of the land, until they in turn were supplanted by the Archosaurs during the Early Triassic.

Permian Life

The warm shallow oceans swarmed with many kinds of life, basically very similar to Carboniferous forms (*see left*). Sedentary organisms like stromatolites, algae, foraminifers, sponges (*Heliospongea* (yellow) shown here), corals, bryozoa, and brachiopods (including the spiny *Edriosteges*) shown here), built great reefs which in turn provided homes and shelter for active animals like ammonoids, nautiloids, gastropods and fish. Ammonoids differed from their Carboniferous predecessors in that they had far more complex suture lines, frequently with many-pointed lobes

and rounded saddles.

The giant Carboniferous insects continued for a while, before also disappearing during the Guadalupian. Meanwhile, important new groups of insects like beetles and flies, with more complex life cycles, emerged.

Plants

An Early Permian landscape in Europe. The form in the right foreground is the seed fern *Autunia* (=*Callipteris*), and in the left background is a marattialean tree fern. The conifer in the right background is *Walchia*, while the herbaceous plants around the pond are sphenophytes. This community represents a seasonally dry savanna-like biome of the tropics.

illustration © Sergei Naugolnykh, from the Paleographic Atlas Project. Text from the same site. Reproduced with permission.

This was a period of transition. The early Permian saw the continuation of the Carboniferous biomes, with polar tundra regions and warm wet tropical swamp forests. But the drying climatic tendency during the mid Permian spelled death for the mighty swamp forests. Water loving plants like Lycopods and Sphenopsids were greatly reduced in size, becoming mere shrubs. The old tropical coal swamps (with their giant lycopods, calamites, and cordaitales) declined and disappeared with the drier and cooler climate, surviving only in China and in high latitudes of Pangaea. Plant life consisted mainly of ferns and seed-ferns, with new plants like conifers and ginkgos coming into prominence. The *Glossopteris* flora predominating in Gondwanaland (the southern portion of Pangaea). It is gradually replaced by the seed-fern *Dicroidium* as the climate dries in the Late Permian.

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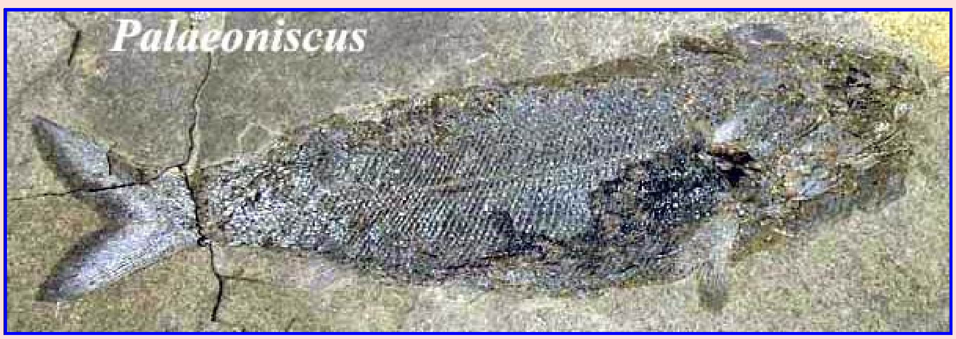
The Permian Period: 2: Tetrapods, and Biostratigraphy

Vertebrates



The great diversity of near-shore and fresh water Chondrichthyans which characterized the Carboniferous began to decline during the Permian. In the oceans, xenacanth sharks dominated until the Guadalupian, when they were replaced by hybodonts. A few acanthodians also lingered into the Cisuralian. Lungfishes and coelacanths were more diverse than they are today, but all of the other Sarcopterygian fishes had already become extinct. The Permian oceans were dominated by a diverse group of spiny-finned (actinopterygian) fishes, most of which had thick, heavy scales and rather basic jaw structures (if you look carefully, you can see this in the image of *Palaeoniscus*). Neopterygians with more derived jaw structures probably began to appear by the end of the Lopingian.

The increasing aridity of the Permian not only affected plants. The tetrapods suffered as their swamps and pools shrunk and dried out. Those surviving forms included big-headed temnospondyls two to three meters in length, as well as long-snouted forms (the archegosaurs) superficially resembling small crocodiles. Many of the non-amniote reptilomorphs, such as anthracosaurs and embolomeres, continued in to the Permian.

But it was the amniotes that took over as the dominant land animals, adapted to life on land (thanks to water-retentive dry skin and the amniotic egg). Although there were a number of different types of amniotes, the largest and most diverse belonged to the Synapsida, which were ancestral to the mammals.

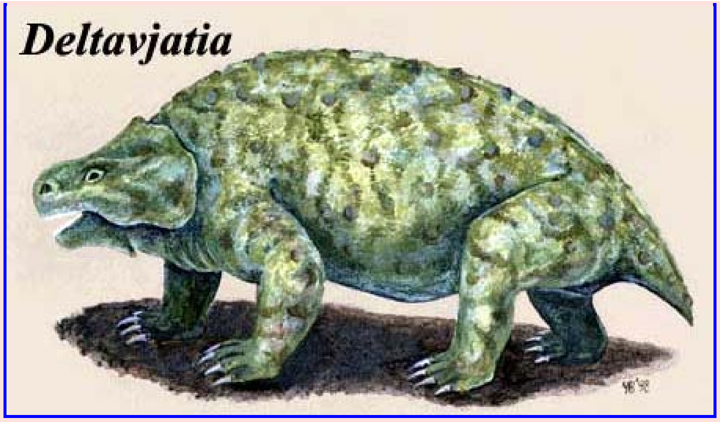
There were several distinct evolutionary dynasties of synapsids as the Permian progressed.

The first, the pelycosaur dynasty, included the large finbacks of the early Permian such as *Dimetrodon*, *Edaphosaurus*, *Ctenospondylus*, and *Secodontosaurus*, all of which attained a lengths some 3 meters, as well a similar types that lacked a "sail". The large dorsal "sails" were most certainly thermoregulatory devices that would heat up the animal in the cold morning, making it more active and giving it an advantage over it's more sluggish sail-less relatives. These animals were limited to the equatorial tropics.

Following this was the Dinocephalian dynasty of the middle Permian (Guadalupian epoch). The Dinocephalians were among the most primitive of the therapsids or "mammal-like reptiles". Some grew to huge size (3 to 5 meters) with 50 to 80 cm long heads full of wicked teeth (the name Dinocephalian means "fearsome head"). These creatures succeeded the Pelycosaurs, being both larger in size and more metabolically active. There were several different types, the primitive anteosaurs (see *Anteosaurus*, left) being carnivores, and the ox-sized tapinocephalia being herbivores.

The Dinocephalians all died out suddenly, perhaps as a result of unusual climatic factors, at the end of the Guadalupian.

The Therapsids that followed them were smaller, and more mammal-like. Some may even evolved fur and the ability to control their temperatures metabolically. These included the large gorgonopsians (the Permian equivalent of the "saber-toothed tiger"), the small to medium-sized Therocephalia, and the herbivorous dicynodonts. These creatures had previously lived alongside the giant Dinocephalians, but came into their own when the latter had died out.



In addition there were many types of non-synapsid amniotes. The pareiasaurs, a group of big, armored herbivores probably related to turtles, reached enormous sizes (length up to 3 meters). Smaller, lizard-like reptiles were probably common, but they are very poorly known. These included the bolosaurs and procolophonids -- both also turtle relatives. During the Permian, the crocodile-bird lineage (Archosauromorpha) had not yet diverged from the lizard-snake (Lepidosauromorpha) clade. The primitive reptiles were represented by lizard-like captorhinids and basal diapsids. The latter included a number of marine or amphibious forms: younginiforms, *Claudiosaurus*, and perhaps the earliest members of the ichthyosaur group.

Image credits: *Palaeoniscus* from the **Essex Rock & Mineral Society**. *Deltavjatia* from the **University Museum of Zoology Cambridge**.

MAK 2002. Revised ATW050604.

Tetrapod Fossil Sites

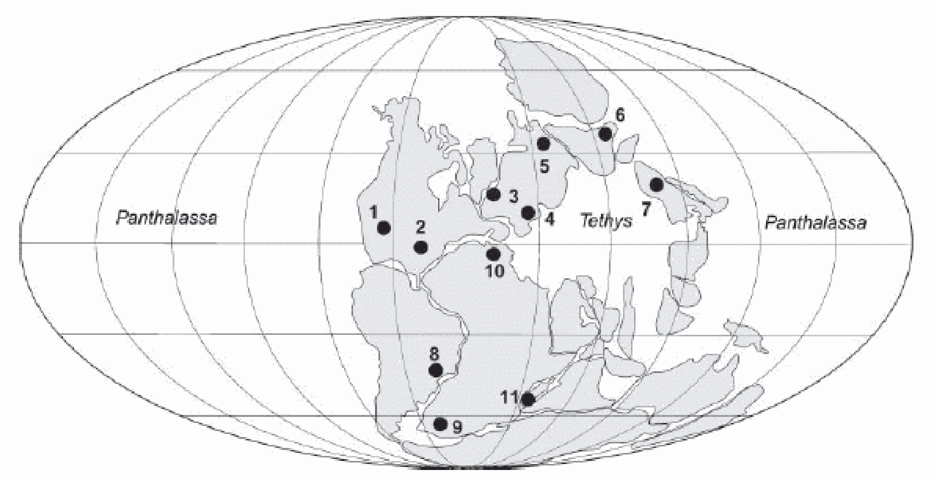


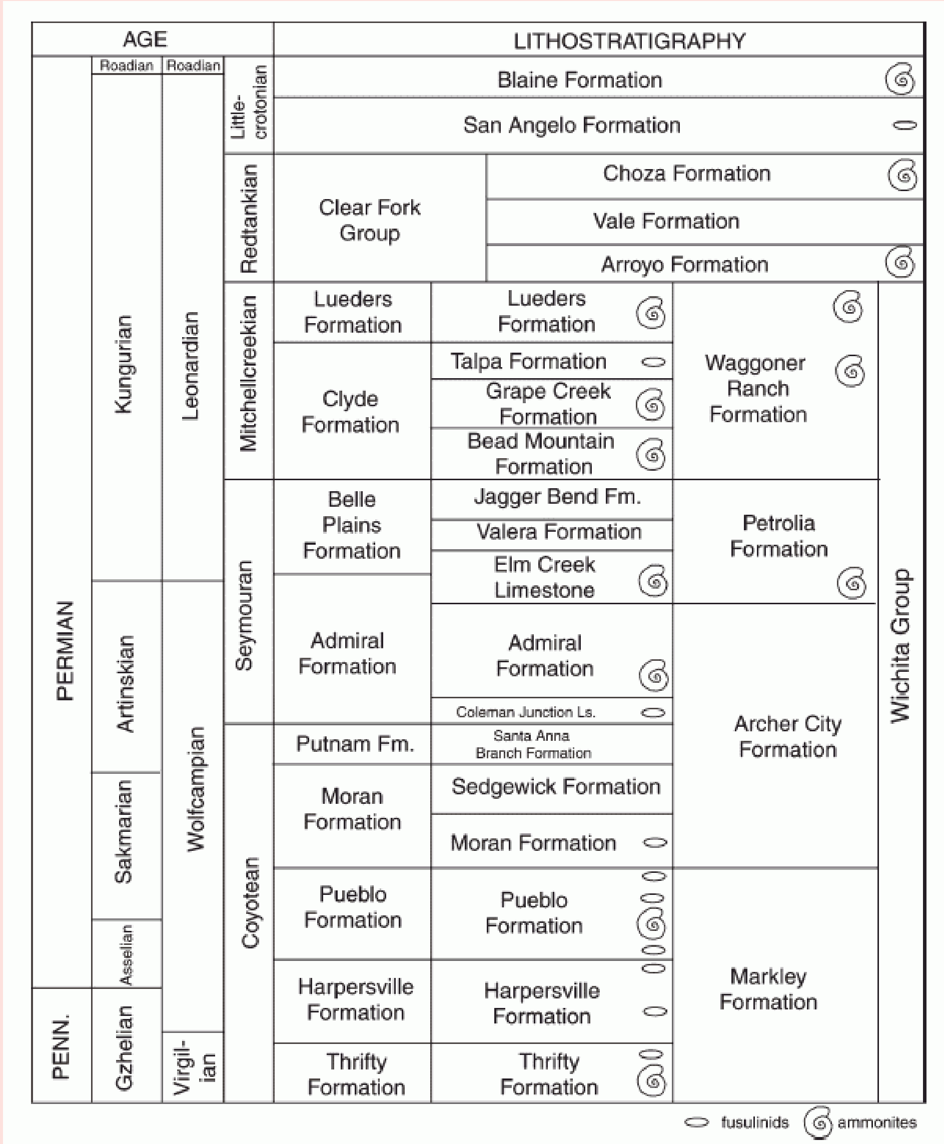
Fig. 1. Map of Permian Pangaea showing principal tetrapod localities. 1, western USA; 2, eastern USA (Dunkard); 3, Scotland; 4, western Europe (Rotliegend); 5, Russian Urals; 6, Junggur Basin, China; 7, Ordos Basin, China; 8, Paraná Basin, Brazil; 9, Karoo Basin, South Africa; 10, Morocco; 11, southern Madagascar.

Permian tetrapod localities - from Lucas 2006 p.66.

The Permian is richly represented by fossil tetrapods, which enables us to trace the transformation of life during this important time. The main localities are in south-west United States (the famous Red Beds of texas and New Mexico), Southern Africa, the Urals region of Russia (from which the name "Permian" is derived), and more recently China, among other places, as shown in the above map. However, correlating these varying stratigraphic sequences has often proved a challenge, especially because the fauna of each tend to be highly endemic

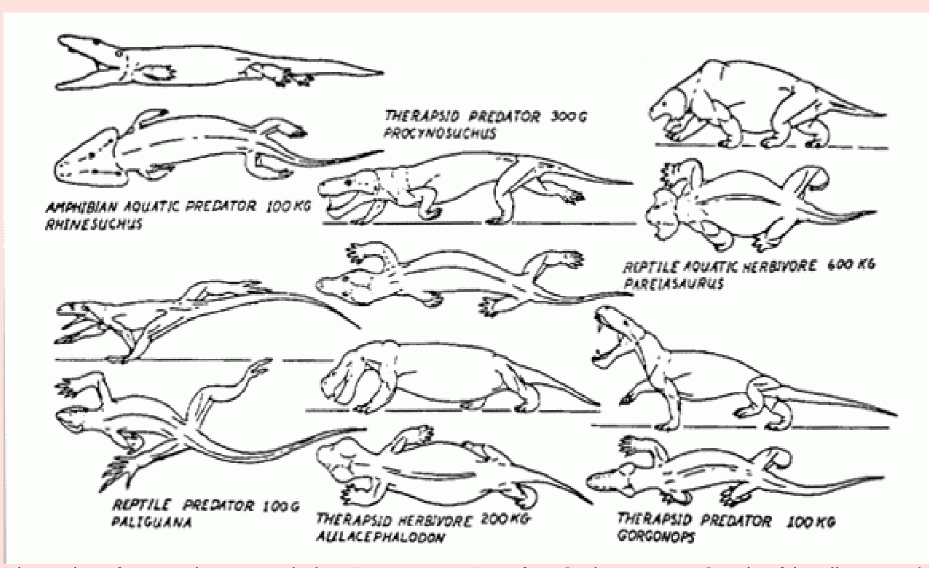
The Red Beds

The biostratigraphy of the Texas and New Mexico Red Bed section has been reviewed by Lucas 2006, who notes that marine biostratigraphy has shown that the youngest strata are no younger than the late Kungurian. The Kungurian in fact was a time of rapid evolutionary turn-over. The various stratigraphic stages and biozones are correlated as follows:



the above diagram shows Lower Permian stratigraphic section in north-central Texas showing cross-correlation of vertebrate biochronology (land vertebrate faunal zones - 4th column from the left) and marine biostratigraphy and dating (shown by fusulinids and ammonoids). Formations on right of diagram are tetrapod-bearing units. From Lucas 2006 p.71

The Karroo



Representative Endothiodon-Dicynodont fauna - (*Daptocephalus* Zone, Lower Beaufort Series, Karoo, South Africa (late Wuchiapingian/early Changhsingian of south-central Gondwana). These represent the type of animals whose remains are preserved in the Upper Permian Karoo sediments, and constitute a cross-section of the terrestrial fauna of the time.

From top left to bottom right: *Rhinesuchus* (Rhinesuchidae - a large fish-eating Temnospondyl); *Procynosuchus* (Procynosuchidae, a small advanced cynodont therapsid carnivore/piscivore/insectivore); an ox-sided herbivorous *Pareiasaurus* (Pareiasauridae - anapsid herbivore); a small diapsid *Paliguana*

("Paliguanidae" - diapsid/"eosuchian" insectivore); a large herbivorous Dicynodont, *Aulacephalodon* (Aulacephalodontidae therapsid herbivore); and a Gorgonopsian therapsid, *Gorgonops* (Gorgonopsidae), which was very much the top predator of this environment

illustration from Robert T. Bakker, "The Need for Endothermic Archosaurs"

The Karroo deposits of Southern Africa are very rich in bones, especially those of therapsid synapsids, and trace the evolution of these animals over a period of some 30 million years or more. The Beaufort beds have produced a remarkable array of synapsids as well as some important archosauriform reptiles (thecodonts) and an assortment of tetrapods. Plants like *Glossopteris* are also well represented

Middle Permian to Early Triassic

graphic from the Bernard Price Institute

Past and Present biostratigraphic divisions of the Karoo Supergroup

Broom (1906)	Watson (1914)	Kitching (1970, 77)	Keyser & Smith (1977-8)	Keyser (1979)	Cooper (1982)	Rubidge 1996
Cynognathus	Cynognathus	Cynognathus	Kannemeyeria	Kannemeyeria - Diademodon	Tetragoia	Cynognathus
					Kannemeyeria	
Procolophon	Procolophon	Lystrosaurus	Lystrosaurus	Lystrosaurus - Thrinaxodon	Lystrosaurus	Lystrosaurus
Lystrosaurus	Lystrosaurus					
Kistecephalus	Cistecephalus	Daptocephalus	Dicynodon lacertips	Dicynodon lacertips - Whaitsia	Dicynodon	Dicynodon
		Cistecephalus	Aulacephalodon baini	Aulacephalodon - Cistecephalus	Cistecephalus	Cistecephalus
Endothiodon	Endothiodon		Tropidostoma microtrema	Tropidostoma - Endothiodon		Tropidostoma
Pareiasaurus	Tapinocephalus	Tapinocephalus	Pristerognathus - Diictodon	Pristerognathus - Diictodon	Robertia	Pristerognathus
			Dinocephalian	Dinocephalian		Tapinocephalus
						Eodicynodon

Table modified from - Hancox and Rubidge, 1997.

Problems of East European Stratigraphy

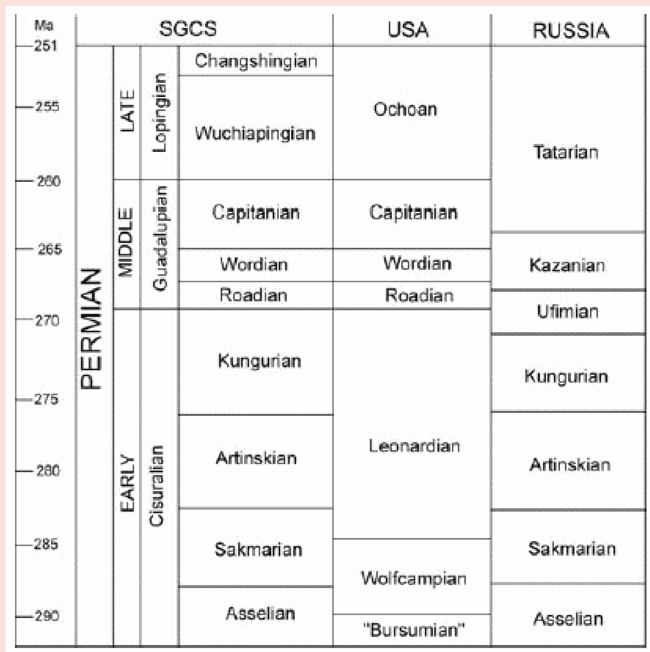
The region around the Ural Mountains - called the Cis-Urals by Russian paleontologists - is an important region of Permian geology and paleontology. Because of the importance of East European deposits in Permian stratigraphy (indeed, the Permian period was named by Murchison after the Perm region in eastern Russia), these became the basis for a global standard. The local geological stages here - the Asselian, Sakmarian, Artinskian, and Kungurian, were incorporated into the International stratigraphic tables, and the whole Early Permian officialy called the Cisuralian. Unfortunately, correlations with the "Upper Permian" stages are less clear, because of a paucity of index fossils (e.g. conodonts, ammonites, etc), due to these sequences being mostly terrestrial. This is unfortunate, because these rocks - rich in tetrapod fossils - trace the evolution of reptiles and amphibians throughout the middle and late Permian, in a manner like the equivalent Beaufort Series of the South African Karoo.

The Russian late Permian strata are traditionally divided into the Ufimian (the earliest, immediately succeeding the Kungurian), the Kazanian, and the Tartarian (the latest, corresponding to the uppermost Permian deposits). Because of the importance of East European deposits in Permian stratigraphy (indeed, the Permian period is named after the Perm region in eastern Russia), these became the basis for a global standard. Unfortunately, the exact details of where each begins and ends is unfortunately somewhat obscure.

There is some controversy regarding the end of the Tartarian. According to Kozur 1998 the Tartarian ends some considerable time before the end of the Permian, so that the uppermost Tartarian is only earliest Wuchiapingian, which seems implausible in view of the advanced tetrapod fauna. Lozovsky 1998 in contrast indicates (at least from the diagrams) the Tartarian seems to stop at the middle Changhsingian, or thereabouts. However, a more recent stratigraphic and biostratigraphic tabulations (see e.g. Benton *et al* 2004, Lucas 2004, Kotlyar and Pronina-Nestell 2005, Taylor *et al* 2009 and link) extend the Tartarian right up to the P-T (Permian-Triassic) boundary. In that table (shown below), the Tartarian includes all the substages from the Wordian upto the Wuchiapingian

map of Permian and Triassic East European fossil localities
(from mathematical.com) (original page)

The following tables are from Lucas 2004 and Kotlyar and Pronina-Nestell 2005 and present two very different correlations, especially as regards the Kazanian, and important stage for Middle Permian tetrapods in East Europe.



Permian marine timescales relevant to this article. The standard global chronostratigraphic scale (SGCS) is from Wardlaw (1999), as is the numerical calibration, which is tentative. Correlation of the North American and Russian scales to the SGCS is that of Glenister *et al.* (1992), Kozur (1995) and Kotlyar (2000).

References:
Glenister, B.F. *et al.* 1992. The Guadalupian. Proposed international standard for a Middle Permian Series. *International Geology Review*, 34: 857-888.
Kotlyar, G.V. 2000. Permian of the Russia and CIS and its interregionalcorrelation. In: Yin, H., Dickins, J. M., Shi, G. R. and Tong, J., Eds., *Permian-Triassic evolution of Tethys and western circum-Pacific*. Amsterdam: Elsevier, 17-35.
Kozur, H. 1995. Permian conodont zonation and its importance for the Permian stratigraphic standard scale. *Geologische Palaeontologische Mitteilungen Innsbruck*, 20: 165-205.
Wardlaw, B.R. 1999. Notes from the SPS chair. *Permophiles*, 35: 1-2.
caption and table from Lucas 2004

According to the above table, the beginning of the Tatarian is around the early-middle Capitanian. However, the paleomagnetic lllawarra Reversal, an important mid-Permian marker, has been found within the Tatarian rocks of Russia (*Permophiles* #31 Januray 1998 pp.35-6.). Since the Illawara Reversal is located (by conodont biostratigraphic dating) just below the base of the Capitanian (i.e., the latest Wordian), the Tatarian must therefore also include all of the Capitanian and at least some of the Wordian. The following table appeared in *Permophiles* #46 2005.

Global Stratigraphic Scale 2004				East-European Stratigraphic Scale 1992			East-European Regional Horizon 1992	New East-European Stratigraphic Scale 2005		
System	Series	Stage	Biostratigraphic boundary marker	Series	Stage	Substage	Horizon	Series	Stage	Substage
Permian	Lopingian *	Changhsingian *	*Clarkina wangi*	Upper	Tatarian	Upper	Vyatkian	Tatarian	Vyatkian	Upper
		Wuchiapingian *	*Clarkina postbitteri postbitteri*							Lower
							Severodvinian		Severodvinian	Upper
	Guadalupian *	Capitanian *	*Jinogondolella postserrata*							Lower
		Wordian *	*Jinogondolella aserrata*			Lower	Urzhumian	Biarmian	Urzhumian	
		Roadian *	*Jinogondolella nankingensis*		Kazanian		Povolzhian		Kazanian	Upper
							Sokian			Lower
	Cisuralian *	Kungurian	*Neostreptognathodus pnevi*		Ufimian		Sheshmian	Cisuralian	Ufimian	
							Solikamian			
				Lower	Kungurian		Irenian		Kungurian	
							Filippovian			
							Saranian			
		Artinskian	*Sweetognathus whitei*		Artinskian		Sargian		Artinskian	
							Irginian			
							Burtsevian			
		Sakmarian	*Sweetognathus merrili*		Sakmarian		Sterlitamakian		Sakmarian	
							Tastubian			
		Asselian *	*Streptognathodus isolatus*		Asselian		Shikhanian		Asselian	
							Kholodnolozhian			

* GSSP

Kotlyar and Pronina-Nestell 2005 (*Permophiles* #46 December 2005.)

Molostovskii, 2005 argues that Upper Permian paleomagnetic zones establish that the upper Tatarian Substage of the stratotype region corresponds to the uppermost Middle–Upper Permian of the international marine scale. The Vyatka Horizon is similar in stratigraphic range to the Changhsingian, while the Severnayadvina regional stage corresponds to both the upper Capitanian Substage and the Wuchapingian Stage.

Minikh et al 2008 point to new data on asynchronous biozonal and paleomagnetic boundaries at the boundary of the Urzhumian and Severodvinian stages which show the Kiaman-Illawarra boundary occurs within the Urzhumian stage (the upper third according to Urzhumian ostracod assemblages), with Severodvinian ostracods, fishes and tetrapods only occuring far above the boundary. This implies that the upper part of the East European Urzhumian can be correlated with the upper Capitanian.

Biostratigraphy of Tetrapods from East Europe

The chart on the left, from Lucas 2004, gives the various iterations of the biozonation of East European (Cis-Uralian) Tetrapods by successive Russian workers. Zone I is upper Kazanian, and hence mostly Wordian (and perhaps latest Roadian). Zone II is Urzhumian, and hence mostly Capitanian, and Zone IV is Severnayadvian and Vyatskian (Lopingian). The earlier fauna can be plotted by Dinocephalian index fossils (apart from *Clamorosaurus*, an endemic Euskelian temnospondyl amphibian of uncertain dating), the later faunas by Pareiasaur and reptiliomorph amphibians (Chroniosuchia). "Zone III" is non-fossilferous

Efremov (1937)	Chudinov (1975)	Ivakhnenko et al. (1997)		
Zone IV	North Dvina Pareiasaur Complex	*Scutosaurus* Superzone	*Archosaurus rossicus* Zone	
			Scutosaurus karpinskii Zone	*Chroniosuchus paradoxus* Subzone
				Jarilinus mirabilis Subzone
			Proelginia permiana Zone	*Chroniosaurus levis* Subzone
				Chroniosaurus dongusensis Subzone
			Deltavjatia vjatkensis Zone	
"Zone III"	fauna not known			
Zone II	Isheevo Deinocephalian Complex	*Titanophoneus* Superzone	*Ulemosaurus svijagensis* Zone	
			Estemmenosuchus uralensis Zone	
			Parabradysaurus silantjevi Zone	
Zone I	Ocher Deinocephalian Complex		*Clamorosaurus nuctumus* Zone	

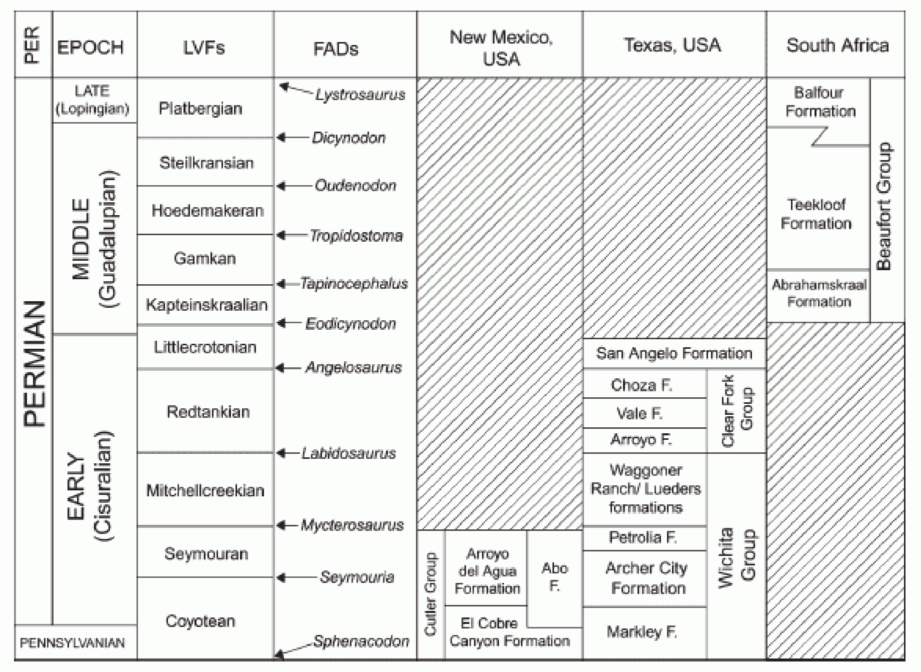
The following table, based mostly on information in Olson, 1962, King, 1990, Lozovsky, 1998, and Kurkin, 2001, and Tverdokhlebov et al 2005 provides a more detailed listing of the tetrapods in East Europe. The various locality columns give the ranges for tetrapods found in those localities (see map, Permian localities in red).

ICS Age	Russian Age (Ural Mts)	Horizon	Zone	Biozone	Assemblage	Cis-Uralian Dinocephalian Complex	Ezhovo (Ocher)	Belebei, Mezen, Pechora	Isheevo	Kotelnik	Sokolki	Vyazniki
Changhsingian Age	Tartarian	Vyatskian	Zone IV	*Archosaurus*	Vyazniki Assemblage Zone							Vyazniki assemblage
Wuchiapingian Age				*Scutosaurus*	Sokolki Assemblage Zone						Sokolki Subassemblage	
		Severodvinian		*Proelginia*							Ilinscoe Subassemblage	
				Deltavjatia						Kotel'nich Subassemblage		
Capitanian			Zone III									
		Urzhumian (lower Tartarian)	? ? ? ? Zone II	*Ulemosaurus*	? ? ? ? Isheevian (Ulemosaurus A.Z.)	? ? ? ? Upper Zone II CDC (Karglaian)			? ? ? ? Isheevo Dinocephalian Complex			
Wordian					Karagalian							
					Bashkirian	Lower Zone II CDC (Bashkir)		? ? ? ? Cotylosaur Complex ? ? ? ?				
	Kazanian	Upper										
Roadian			Zone I ? ? ? ?	*Estemmenosuchus Parabradysaurus*		Zone I CDC	Ocher fauna ? ? ? ?					
		Lower		? ? ? ? *Clamorosaurus* ? ? ? ?								
Kungurian	Ufimian Kungurian											
Artinskian	Artinskian		Zone 0									

Here the *Deltavjatia* biozone can be considered either middle or late Capitanian or early Wuchiapingian, depending on how you want to interpret things.

Permian global tetrapod correlations

The following diagram by Lucas 2006 p.67 compares American (equatorial West Pangea) with African (south central Pangea) sequences.



Ten land vertebrate zones are plotted, representing the transition from pelycosaur- to dinocephalian- to advanced therapsid dominated faunas. Because of the endemic nature of the Russian fauna, Lucas did not attempt a comparison. However I consider there is enough comparitive material to do so, because even if there is not a species or often no genus level match, there is a definite common pattern of faunal change, as well as climatic, paleomagnetic, and other factors.

The following useful table is from Ochev 2001 and gives Cis-Ural - Karoo correlations

East Europe				South Africa		
stage	sub-stage	province zone	genera-correllants	genera-correllants	assemblage zone	group
Tatarian	Upper	Archosaurus	7		Dicynodon	Lower Beaufort
		Scutosaurus	7, 13'	7, 10, 13"		
		Proelginia	6?7, 9, 10, 13	6, 13"	Cistecephalus	
		Deltavjata	5	5, 13"	Tropidostoma	
			12	12'	Pristerognathus	
	Lower			2, 8', 12'	Tapinocephalus	
		Ulemosaurus	1, 3, 4, 8	1', 3', 4', 8'	Eodicynodon	
Kazanian	Upper	Estemmenosuchus				Ecca
	Lower	Parabradysaurus				
Ufimian		Clamorosaurus				

Biozone stratigraphic correlations between Eastern Europe (left) and South Africa (right). Numbers designate the genera of the families common for the regions compared. Primed numbers designate the South African genera close to the East European ones under the same numbers in their evolutionary levels. Dinocephalia: Fam. Ulemosauridae: 1 – Ulemosaurus, 1' – Tapinocaninus; Fam.Tapinocephalidae: 2 – Moschops; Fam. Anteosauridae: 3 – Titanophoneus, 3' – Australosyodon. Anomodontia: Fam. Venyukoviidae: 4 – Ulemica, 4' – Patronomodon. Fam. Dicynodontidae: 5 – Tropidostoma, 6 – Oudenodon, 7 – Dicynodon. Therocephalia: Fam. Pristerognathidae: 8 – Porosteognathus, 8' – Glanosuchus. Gorgonopia: Fam. Gorgonopidae: 9 – Sauroctonus, 9' – Scylacops. Eotheriodontia: Fam. Burnetiidae: 10 – Proburnetia, 11 – Burnetia. Pareiasaurida: Fam. Pareiasauridae: 12 – Deltavjatia, 12' – Bradysaurus, 13 – Proelginia, 13' – Scutosaurus, 13" – Pareiasaurus.

In addition, it seems implausible to place the transitional forms from the Dashankou locality in China (Xidagou Formation) in the Gamkan (equivalent to *Tapinocephalus* zone) Lucas 2006 does; Liu et al 2009 attribution of Roadian age is probbaly better. This would allow a further stage can be plotted between the Littlecrotonian and the Kapteinskraalian, which can (for sake of a better name) be called the "Dashankouan".

By comparing these different fossil sequences, one particular chapter in life's epic saga, life on land during the Permian, can be traced and studied in detail

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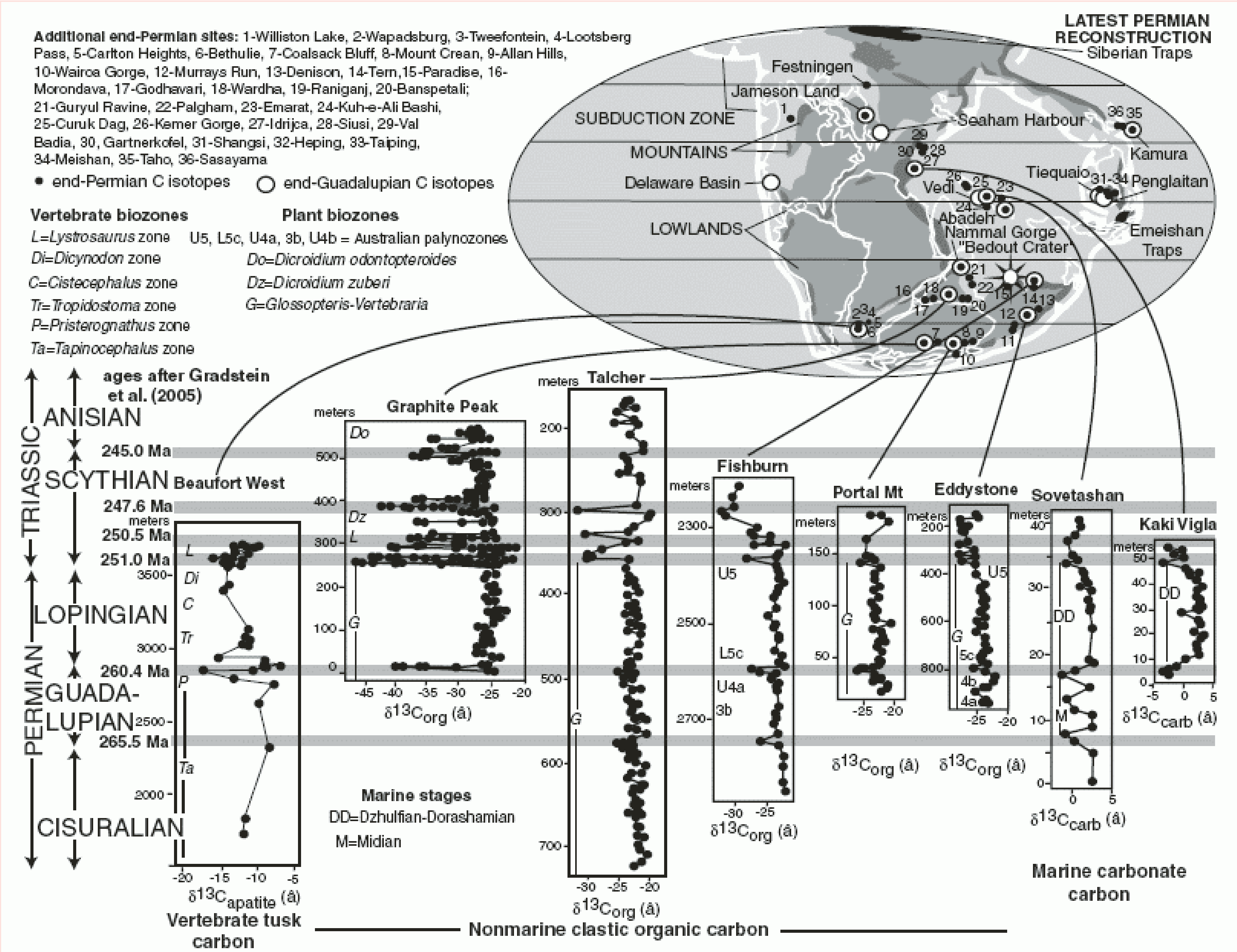
The Permian Period: 3 - Extinction Events

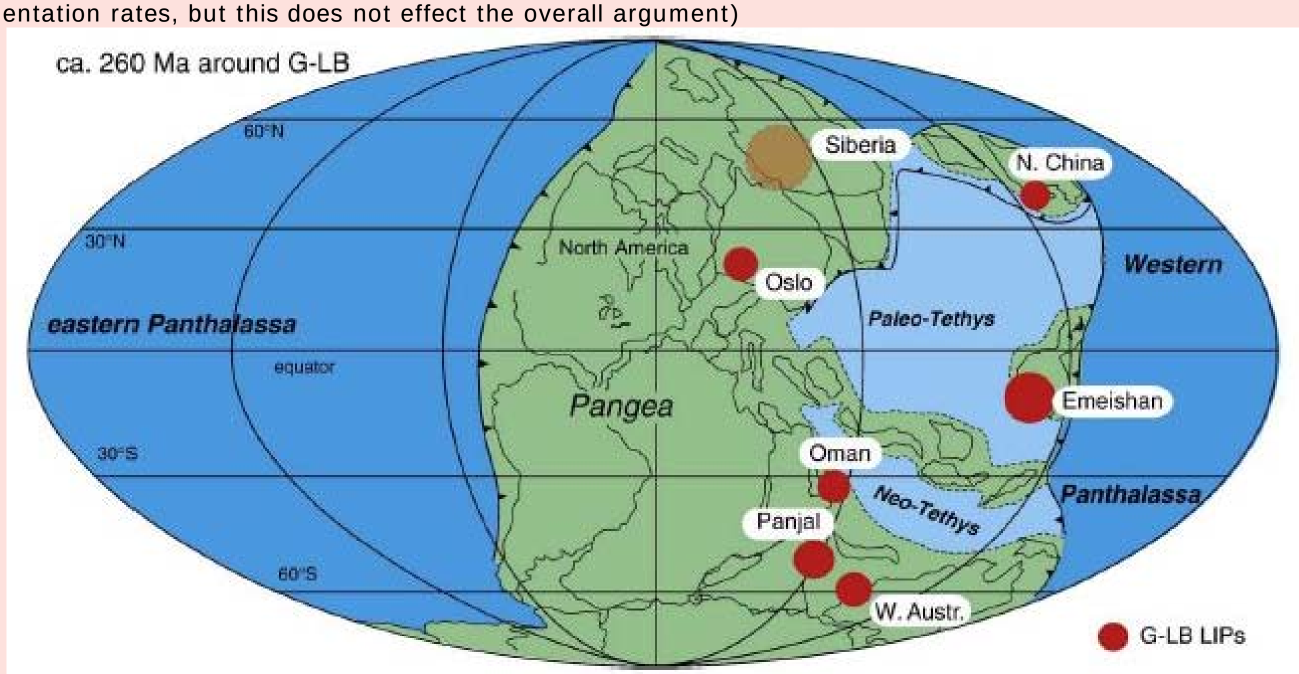
Not one but two Permian Extinction Events

Originally there was thought to be only a single end Permian mass extinction. More accurate stratigraphic resolution reveal two huge mass extinction events, one at the end of the Guadalupian epoch and the other at the end of the Permian (and because taxonomic losses were divided between the two crises and the intervening interval, the terminal extinction eliminated only about 80 percent of marine species, not 95 or 96 percent as previously estimated) (Stanley & Yang 1994, although this thesis is not without its critics, e.g. Clapham et al 2009). Gregory Retallack (a specialist in fossil soils) and co-workers have associated these mass extinctions with catastrophic greenhouse events and herperanoxia. Retallack 2005 Retallack et al 2006. They use new paleobotanical, paleopedological, and carbon isotopic studies of Portal Mountain, Antarctica, and comparable studies in the Karoo Basin, South Africa to shown that there were two separate abrupt mass extinctions on land, which can also be linked to corresponding marine invertebrate extinctions. One was the end Guadalupian (end Capitanian), the other the better known end Permian extinction. Both were times of short-lived warm and wet greenhouse climate, marked soil erosion, transition from high- to low-sinuosity and braided streams, and wetland soil stagnation. Retallack et al 2006 (abstract)

This research with carbon isotopes also hints at a further, earlier mass-extinction at the end of the Cisuralian. If so, these extinction events would explain the three radically different dynasties of terrestial life duriong the Permian - the pelycosaur, dinocephalian, and advanced therapsid. Retallack et al 2006 give the following diagram, which is reproduced here



Negative carbon isotope anomalies, indicating extreme Greenhouse conditions resulting in a series of mass extinctions during the Permian. from Retallack et al 2006 p.1400 (note, the Tapinocephalus zone here is incorrectly shown extending down into the Cisuralian (see left-most graph), obviously the graphs do not take into account differing sedimentation rates, but this does not effect the overall argument)



Middle-Late Permian large igneous provinces.) G–LB = Guadalupian–Lopingian boundary). Diagram from Isozakia 2009 p.425

In order to explain how the necessary amounts (a hundred to a thousand gigatons) of methane could be released into the atmosphere within a period of 10 to 100 thousand years, Retallack et al 2006 p.1409 suggest catastrophic methane outbursts to the atmosphere from from Volcanic intrusion (feeder dikes and flood basalts) into massive coal deposits. They mention that both the end-Guadalupian Emeishan Basalt (Zhou et al., 2002) and end-Permian Siberian Traps (Kamo et al., 2003) (see illustration above) erupted through pre-existing coal measures.

Another (perhaps complementary) cause, suggested by Isozakia 2009 was mantle superplume activity, which also led to the Illawarra Magnetic Reversal

For much of the Triassic, oxygen levels remained low, and according to Ward 2006, this favoured dinosaurs which - like birds would have had a more efficient aerobic metabolism, over mammals. Early Triassic survivors of the mass extinction like *Lystrosaurus* and *Proterosuchus* had stocky bodies and barrel-chests indicating increasing lung capacity, while therapsid carnivores like *Galesaurus* and *Thrinaxodon* had reduced lumbar ribs which, along with thickened thoracic ribs and higher thoracic vertebral spines may well indicate enlarged lungs and a muscular, mammal-like diaphragm, allowing more efficient respiration. Retallack et al 2003 p.1148

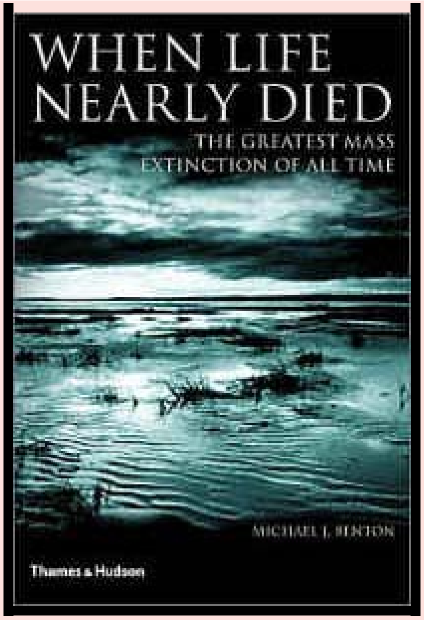
The big one

Disaster movies are a staple of Hollywood today, and it might be plausibly suggested that the depth and complexity of their stories and their degree of realism varies in inverse proportion to the size of their special effects budget. The genre being as popular as it is, few subjects in earth history excite the imagination of the average person as much as the terminal Permian extinction (which corresponds to the third of the carbon isotope anomalies shown in the previous diagram). This is a shame, because the Permian is an amazing chapter in the history of life, and it is rather limiting to focus so much on its final pages.

But the allure of disaster movies being what it is, real-life equivalents of the subject continues to fascinate. To get a better perspective on the end-Permian disaster blockbuster, it may be useful look at two (or more) very different accounts, in two very different books, each by a paleontologist, and each on thr same subject (well, more or less...) (The Benton review has been filched from the Book Reviews section)

Benton, Michael J. (2003), **When Life Nearly Died: the Greatest Mass Extinction of all Time**. Thames & Hudson, 336 pp. ISBN 0-500-05116-X

Michael Benton's latest book is a semi-popular explanation of the end-Permian extinction. Over the last two decades, paleontologists have reached consensus that the end-Permian ("PT") event was the greatest biotic disaster of the Phanerozoic, and possibly of all time. It is hard to know how seriously to take figures of this sort, but Benton cites species extinction rates of 95% and more. Even this figure, he suggests, is conservative because it does not take into account additional pulses of extinction, including a slightly later Olenekian event. He describes the PT devastation as world-wide, non-selective, and so thorough that



ten million years were required to recover to more or less normal levels of biodiversity.

Explaining why and how the PT extinction happened is a difficult task, but Benton does it very well indeed. More than half of the book is history and background. Normally, this would be irritating, but Benton covers it so fluidly that one doesn't really mind. The heart of the PT problem is stratigraphy -- both the science of stratigraphy and the philosophical bias of the stratigraphic community. Benton has an almost unmatched ability to tell the science part of any paleontological tale in plain, straightforward prose. In this book, Benton shows us that he can also produce, at the same time, a well-structured story about the interaction between philosophy and science in the geological community, as well as the interplay between geologists, paleontologists, and others. In short, this is that rare book, a really balanced and compelling study of a scientific idea, including both its content and its history.

Personally, I am perhaps even more impressed with Benton the historian than with Benton the writer or Benton the paleontologist. He never bogs down in personalities. He tries to understand both Victorian Englishmen and Soviet apparatchiks on their own terms and usually succeeds. True, he inserts the conventional reminder that the former were arrogant imperialists, and he does gloss over some uncomfortable truths about Soviet science -- all according to the latest academic fashion. However, Benton's writing is too clear and honest to allow even self-deceptions to cloud the facts.

If there is any disappointment in the book, it is on the science side. However, this was intended to be a semi-popular book, and it would be churlish to expect too much. Benton concludes that the Siberian Traps were responsible for the PT extinction. If his marshalling of the evidence for this hypothesis is less than compelling, it is probably only because the evidence itself is still less than compelling.

He is probably correct, but there are aspects of the PT event which are still very unclear. Unfortunately, most of these issues remain unresolved due to the same problems which have bedeviled the PT question from the very beginning -- the intractable issues of dating and stratigraphy around the PT boundary. We just don't know, not even to an order of magnitude, how long the die-off took. Our knowledge of the recovery phase is just as bad. Everyone agrees that the recovery took a long time. Certainly it took over a million years, but whether it was 1, 5, 10, or 20 My depends on what one's criteria are and on the uncertainties of Early Triassic stratigraphy.

A few examples will suffice. The Induan Age, the first age of Triassic, has been shrinking. Not very long ago, it was supposed to have lasted about 5 My. Now, the best estimate is 1.3 My and possibly as little as 0.2 My. Obviously this makes a huge difference in how one views the initial post-PT world. Another problem is the supposed Late Olenekian extinction. Benton views it as a mass extinction. Others see it (as Benton is fair enough to state) as faunal turnover connected with recovery, much like a succession series in any ecological recovery (see our discussion at Olenekian). Which view is correct depends critically on what organisms were where and at what time. The issue simply cannot be resolved without a much finer parsing of the stratigraphic record.

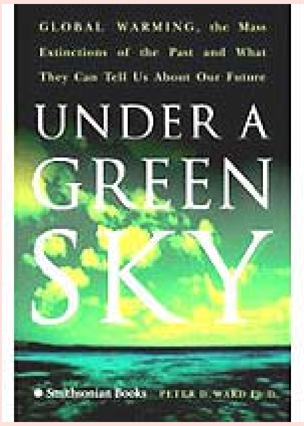
But enough of that sort of thing. The scientific issues are sometimes frustrating and difficult. The book, on the other hand, is simply a really good book. At the moment, its US$30 price is a bit steep for many of us; but, by all means, get it when you can. ATW040209.

Postscript: very recent dating of the Siberian flood vulcanism places this series of events at about 251.3 Mya, with most locations dating between 251.7 and 251.1 Mya (all dates ±0.3 My), resulting in the extrusion of 2-4 million cubic *kilometers* of volcanic material. Kamo *et al*. (2003). This is extremely close to the currently accepted date for the end-Paleozoic of 251.0. Unfortunately, the Permo-Triassic boundary is placed about 1My *after* the main pulse of extinction. So we still have a small, but annoying gap, with the extinctions taking place slightly *before* Central Siberia turned into an incandescent mud bath. In addition, the figures sound large, but amount to no more than a single Krakatoa-size (20 km^3 ejecta) event every 4 years, on the average. Maybe enough to threaten the existence of life, but maybe not. Once again, we just don't have the temporal resolution down fine enough to tell. If, for example, 100 Krakatoas, had exploded during even one of those 500-600 ky, we might well not be around today to discuss the matter today. The odds are that no more than 10-15 or so would have occurred in even the worst year, if the distribution were random. [Check my math: I make it 3,000,000 km^3/ 20 km^3 = 150,000 Krakatoa-equivalents. 150,000 Keq / 600,000 yr = 0.25 Keq/yr on the average. The chance of 10 in any given year is then $(0.25)^{10} = 9.54 \times 10^{-7}$. The chance of ten *not* happening at all in 600,000 years is $(1 - 9.54 \times 10^{-7})^{600,000} = 0.564$] However this assumes that the rate of vulcanism was randomly distributed, which is a very, very bad assumption.

Kamo, SL, GK Czamanske, Y Amelin, VA Fedorenko, DW Davis & VR Trofmov (2003), *Rapid eruption of Siberian flood-volcanic rocks and evidence for coincidence with the Permian-Triassic boundary and mass extinction at 251 Ma*. **Earth & Planet. Sci. Lett.** 214: 75-91.

ATW041004. No rights reserved.

Now for something a bit different - a bit more impalusible and eccentric



Paleontologist and Science writer Peter Ward proposes the theory (in his book *Under a Green Sky*), that the Permian mass-extinction, along with the other four major extinctions, were the result of runaway greenhouse effect, which heated the oceans and shut down the ocean conveyor belt. This is the phenomenon by which warm and hence poorly oxygenated surface water cools when it approaches the poles, taking in oxygen and sinking to the bottom, where it carries the oxygen rich watre to the equator. At the equator it warms and rises, repeating the cycle.

Without this cycle, the oceans become berift of oxygen (this is called the "Strangelove Ocean", after the famous Stanley Kubric Cold War black comedy *Dr Strangelove*), life suffocates and dies, and anaerobic archaea and bacteria flourish. This is deadly for two reaons. First, some of these microrganisms (the methanogens) produces huge amounts of methane, further adding to the greenhouse effect. Others, the sulfate-reducing organisms, generate vast amounts of hydrogen sulfide, better known as rotten egg gas. Ward describes a nightmare scenario, with poisonous oceans belching methane, turning the sky green and hazy and poisoning plants and animals.

Personally, I find it hard to believe that *any* higher life and developed ecosystems could make it through such conditions. Which is not to say that it can't happen, or that it hasn't happened at some stage in Earth history. Perhaps this was how life was for periods of the early Earth (the Archaean aeon with its reducing atmosphere). But, given Phanerozoic conditions, there is some controversy over whether it is even possible to shut down the the ocean conveyor belt. In any case, Ward's more extereme scenario makes an interesting complement to more mainstream scenarios.

But it gets stranger; there is also the possibility of mantle superplume activity.

MAK091115

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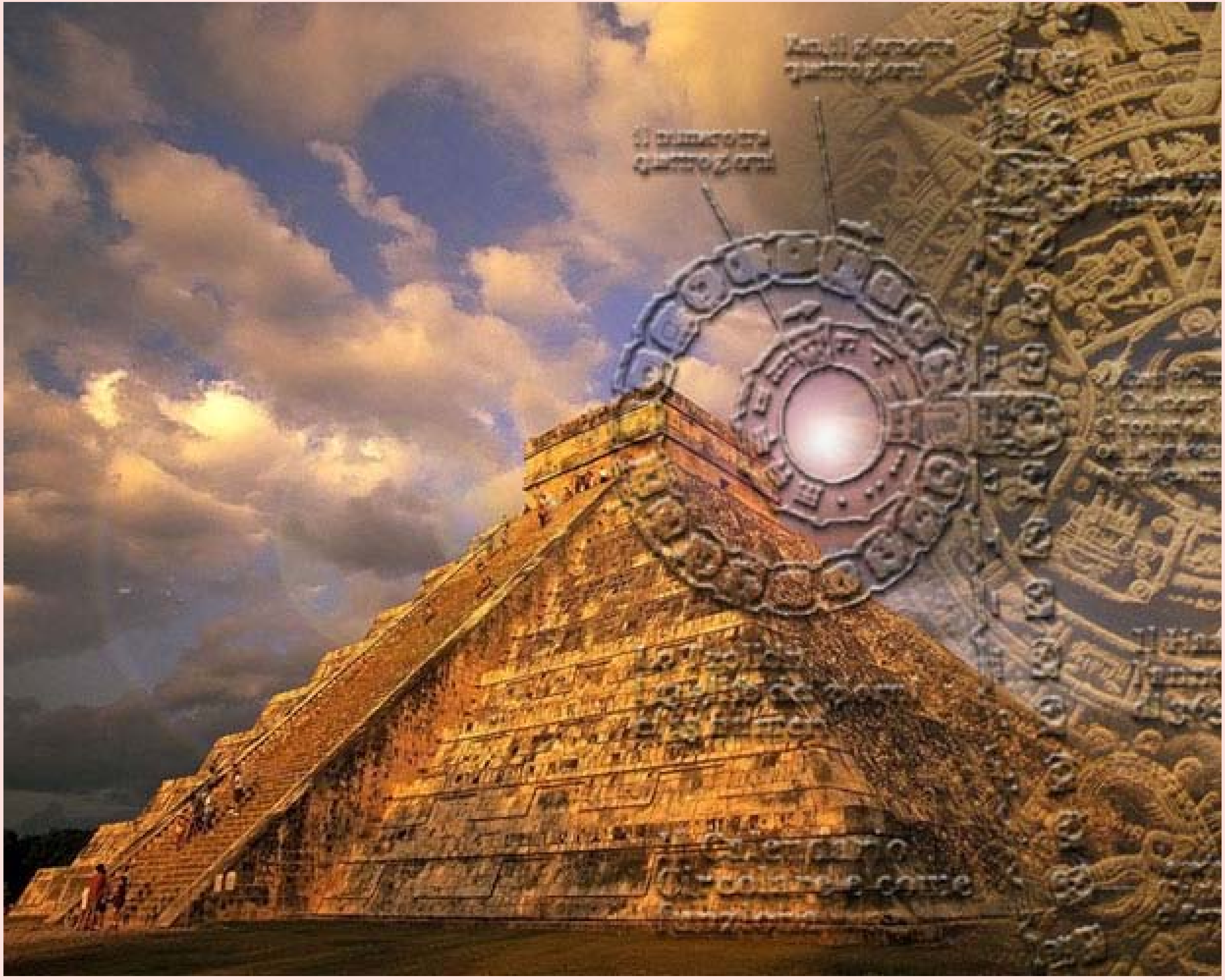
text content ATW 2004, M. Alan Kazlev 2009

The Permian Period: 4

Geomagnetic Polarity, the Illawarra Reversal and Superplume activity

Every so often, the Earth's poles reverse the orientation of their magnetic field, so the north magnetic pole becomes the south and vice-versa. There is a rich and enthusiastic mythology about this in the New Age movement, according to which this event will mean the end of the world as we know it, and usher in a new



spiritual age. The original idea of tying magnetic pole shift to "Earth Changes" derives from Edgar Cayce, an important American spiritual healer of the early 20th century, who became known as "the sleeping prophet" because he would deliver all his messages while in trance. More recently, the Mexican-American author and artist José Argüelles added his own idiosyncratic interpretations of this with the Mayan Calender, which conveniently ends in 2012, thus allowing three years from the time of writing (November 2009) before either the world as we know it ends or more uncritical New Age proponents have to seriously revise their mythology. In fact, the poles have switched their magnetic orientation at irregular intervals throughout the Earth's history, and not once did the world end. This can be dated through determining the magnetic orientation of crustal sea floor spreading zones and ferrimagnetic minerals in sedimentary or volcanic rock on land.

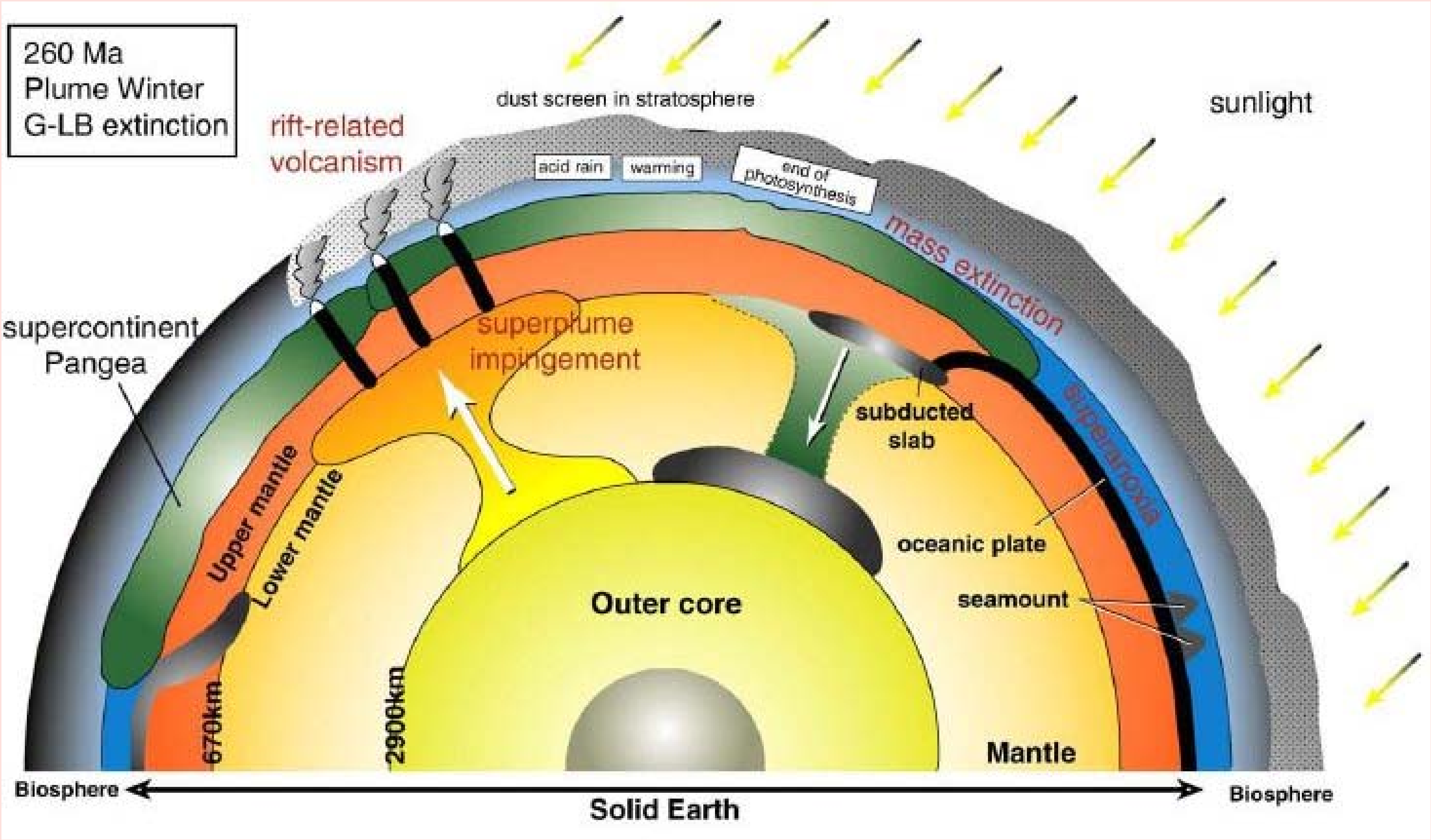
One of the most interesting and significant of these magnetic field reversals was the Capitanian age (mid Permian) Illawarra Reversal, which ended the Kiaman Reverse Superchron. (the Kiaman and Illawarra Superchrons are named after Australian localities where geological evidence of these magnetic events were first detected).

The Kiaman Superchron was a 50 million year long period of stable geomagnetism, with few or no geomagnetic reversals. It lasted from the late Carboniferous to the Middle Permian. During this period the magnetic field polarity was the opposite of what it is now. Therefore in the format of geomagnetic charts it is drawn white (whereas current north-south orientation is drawn black).

Japanese Earth Sciences researcher Yukio Isozaki has developed the intriging theory (Isozakia 2007, Isozakia 2009 link) that ties in the Illawarra Reversal, global cooling, vulcanism, the Permian mass extinctions, and the resulting radical change of conditions on Earth. His theory is that around the time of the Wordian/Capitanian boundary a plume of super-hot material fomed in the molten outer core of the Earth. The resulting thermal instability made the magnetic geodynamo in the outer core unstable, the first polarity switch being the Illawarra Reversal, which was the "fingerprint" of this event. The weakening of Earth's magnetic field exposed the surface to increased cosmic radiation. The radiation ionised the atmospheric nitrogen, which seeded for clouds. The more cosmic rays that penetrated the atmosphere, the more clouds developed, which increased the albedo (reflectivity). This in turn cooled the Earth's surface, because the sun's rays couldn't get through (the opposite of a greenhouse effect, which traps heat within the atmosphere). This resulted in the Kamura cooling event (Isozaki et al 2007). Meanwhile, the plume was slowly rising through the mantle, upsetting convection in the core, and causing the frequent polarity reversals that characterised the

Late Permian to Triassic Mixed Superchron. After about five million years it reached the upper mantle, triggering supervolcanoes and causing further cooling.

This is explained in the following diagram Isozakia 2009 p.428:



Massive vulcanism could also create a greenhouse effect, which brings us to the events documented by Retallack 2005 and Retallack et al 2006

Isozaki considers the same superplume triggered the Siberian Traps and hence the end-Permian extinction. Retallack however disputes Isozakia' thesis, because life recovered and flourished between the two mass extinctions. But I don't see why these two respective hypotheses (superplume vulcanism/cosmic ray induced cooling and greenhouse/anoxic triggered extinctions) should be mutually exclusive.

The same superplume activity, according to Isozaki, triggered the breakup of Pangea, while the change in cosmic radiation may explain not only global climatic changes in the end-Guadalupian but also long-term global warming and cooling trends in Earth's history in terms of cloud coverage over the planet. The Illawarra Reversal and the Guadalupian-Lopingian boundary event thus represent the transition processes from the Paleozoic to Mesozoic and Modern world. MAK091115

Update: Jason R. Ali (2009) has pointed out a number of problems inherent in Isozaki's hypothesis, including a three million year hiatus between the end-Kiaman reversal and the mid Capitanian extinction, the time required for the plume to travel from the Core-Mantle Boundary to the surface being certainly greater than the 10 Million or spo years of the late Permian, problematic statements regarding the streingth of the geomagnetic field as reveiled through paleomagnetism, the timing of vulcanism worldwide, and the main Mid Permian extinction event associated with vulcanism being middle Capitanian rather than end-Guadalupian. MAK120127

text content M. Alan Kazlev 2009, 2012

The Cisuralian (Rotliegendes)

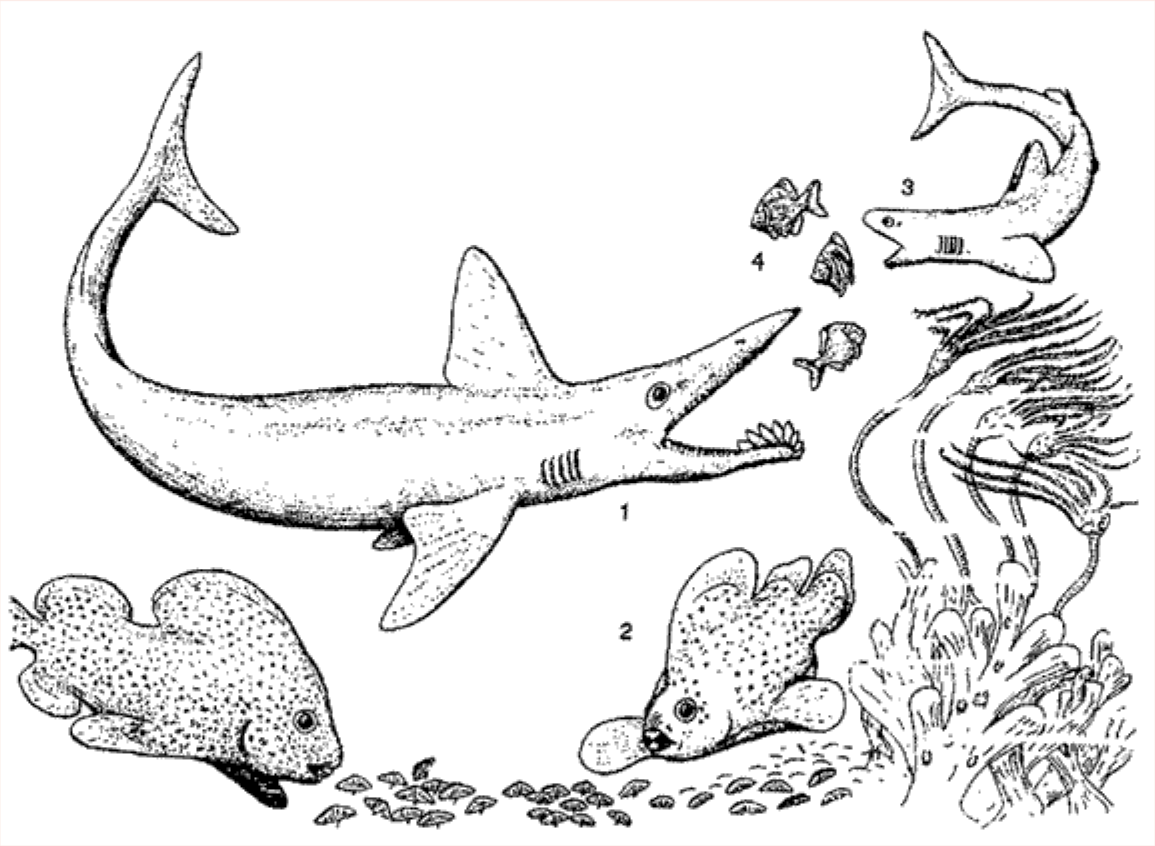
The Cisuralian Epoch of the Permian Period: 299 to 271 million years ago

Marine Invertebrate Life

A Permian reef (Artinskian of Texas), showing an abundance of sponges, rugose corals and brachiopods, a gastropod (left)), a spiny-shelled nautilid *Cooperoceras* (right foreground) and a smooth shelled ammonoid (center background).

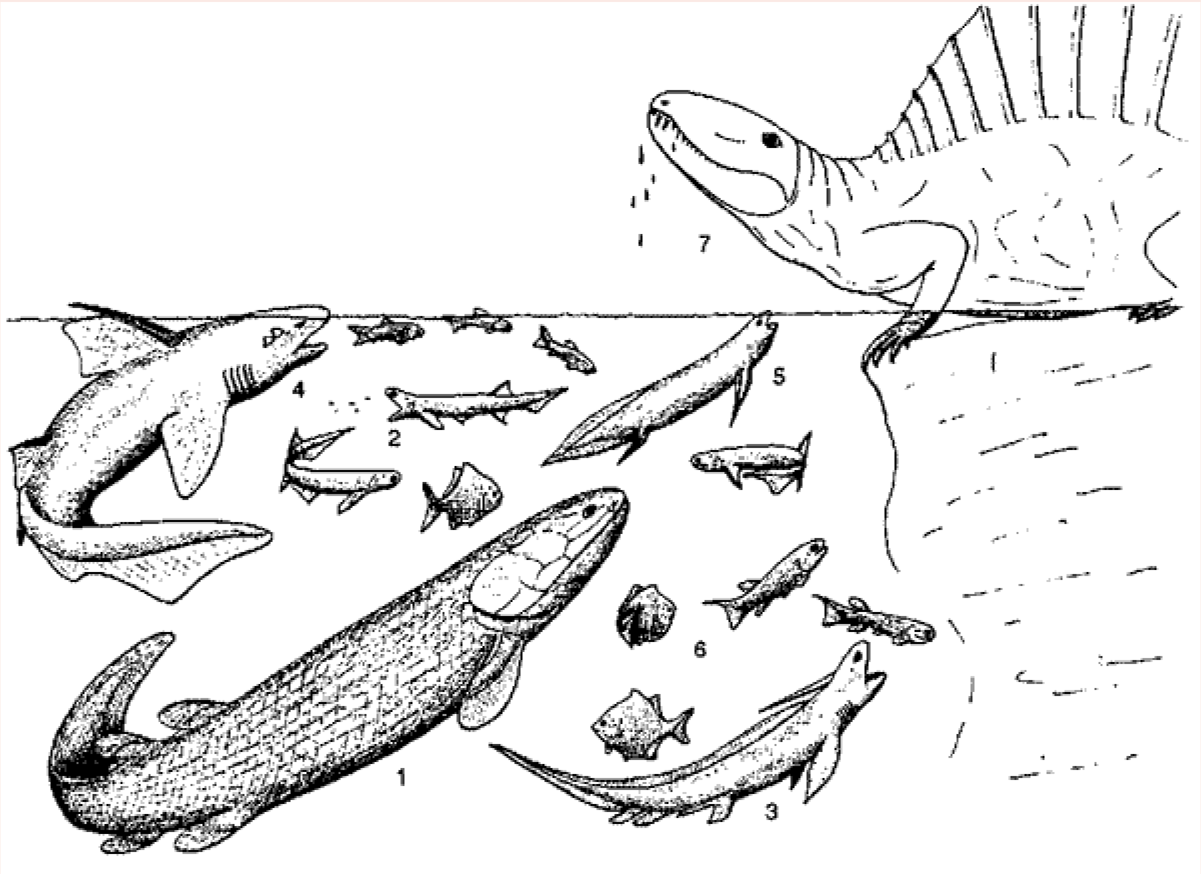
source - Earth History Resources

Marine Fishes of the Early Permian



Early Permian fishes from the Copacabana Formation of Bolivia. The fauna still includes some of the peculiar chondrichthyans of the Carboniferous, such as huge engeneodontids (1. *Parahelicoprion*) and petalodontids (2, *Megactenopetalus*) along with primitive sharks (3) and a variety of ray-finned fishes (4, platysomids).

Fresh Water Fish



In the Early Permian, the last refuge for some of the vertebrate taxa that were widespread in Devonian times was the marginal, possibly brackish or freshwater, environment. exemplified here by the red beds of the Wichita Group of Texas. In this environment survived the youngest osteolepiform (1. *Ectosteorhachis*) and acanthodians (2. *Acanthodes*) in association with xenacanthiform (3) and hybodontiform sharks (4). as well as with coelacanths, lungfishes (5), and various ray-finned fishes (6). Various tetrapods (stem tetrapods and early synapsids, 7) also occur together with this fish fauna

this and previous image and (most of) the associated text from Philippe Janvier's superb *Early Vertebrates*, pp.22-23 (Clarendon Press, Oxford, 1996).

An Early Permian Bestiary

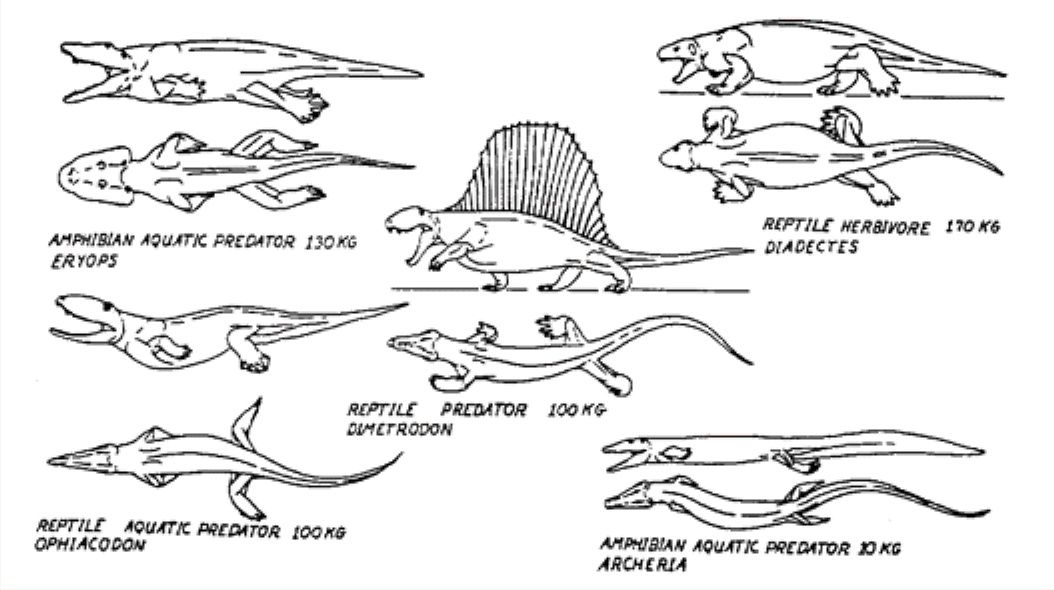


Illustration by Dr Bob Bakker

The early Permian age, a period of well over 20 million years, was - as far as the terrestrial ecosystem went - a fairly stable period ruled over by a diverse selection of pelycosaurs, including the large sphenacodontid finbacks such as the carnivorous *Dimetrodon*, *Ctenospondylus*, and *Secodontosaurus*, all of which attained a lengths of up to 3 meters, as well as semi-aquatic ophiacodonts and the big temnospondyl *Eryops* and smaller eel-like anthracosaur *Archeria*. This was a biome strongly tied to water and to a plant-arthropod-fish food chain; *Diadectes* and *Edaphosaurus* were the only herbivores. In this respect it continued the pattern of the great Carboniferous coal swamps. The drier upland was inhabited by a different fauna, mostly smaller insectivores with the herbivorous caseids and proto-therapsid *Tetraceratops* as significant newcomers. Both in the uplands and the lowlands insects continued to represent an astonishing diversity of forms.

Substages:

Click on the names of the stages given below for more detail regarding the stratigraphy and animals living at that time (note: these pages are still under construction)

Period	Epoch	Age	When began	Duration
Permian	**Guadalupian** (Middle Permain)	Roadian	270.6	2.6
	Cisuralian (early Permian)	Kungurian	275.6	5.0
		Artinskian	284.4	8.8
		Sakmarian	294.6	10.2
		Asselian	299.0	4.4
Carboniferous	Pennsylvanian	Gzhelian	303.9	4.9

The Permian - a brief but very readable introduction to some of the major animals and plants of early Permian time, with illustrations from the Age of Reptiles mural by Rudolph F. Zallinger

American Permian Vertebrates - an electronic reprint of Williston's classic (1911) monograph on American Permian Vertebrates (includes *Eryops*, *Aspidosaurus*, *Nothodon*, *Seymouria*, *Clepsydrops*, *Ophiacodon*, *Varanosaurus*, *Casea*, and others) can be purchased here for an inexpensive fee.

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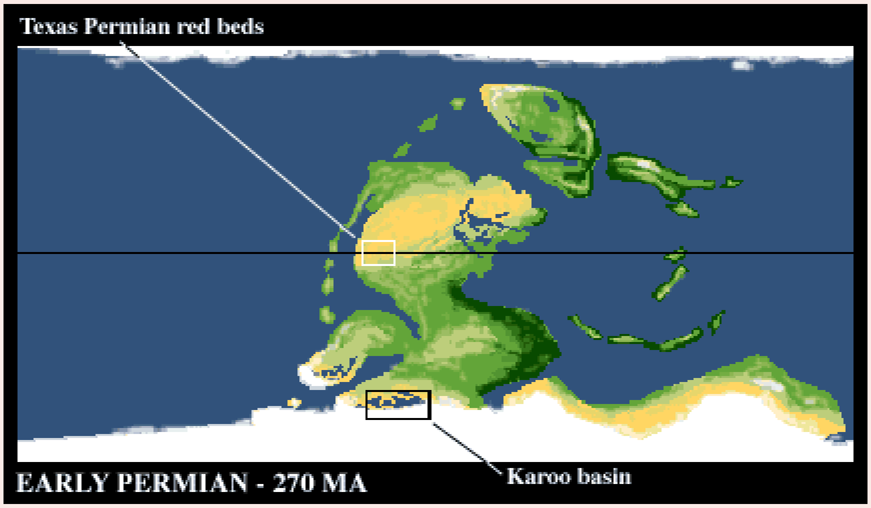
The Asselian

The Asselian Age of the Cisuralian Epoch (Early Permian): 299 to 295 million years ago

Archegosaurus, a large (about 1.5 metres) semi-aquatic predator, a sort of stem tetrapod crocodile
Family Archegosauridae, (Order TEMNOSPONDYLI)
central equatorial Pangea (Europe)

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. Yogi111212



A map of the globe during earliest Permian (Asselian-Sakmarian) times.

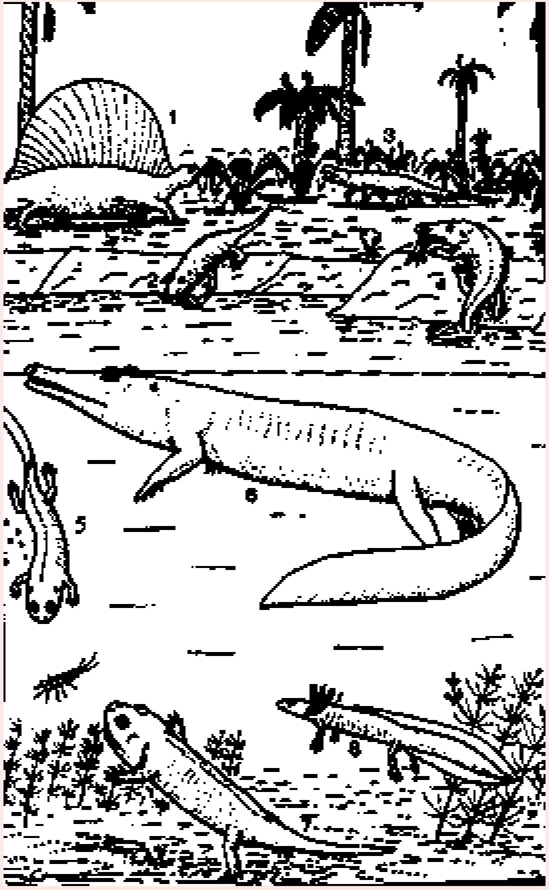
black: mountains higher than 2000 metres
brown: low mountains
light green: uplands
dark green: lowlands
light blue: shallow continental seas
medium blue: deep ocean
white: glacial icecap

Straddling the equator you can see the C-shaped supercontinent of Pangea, which formed during the late Paleozoic when the globe's major landmasses collided.

from Mapping a Planet's Restless Past -The University of Chicago Magazine December 1995
see also the accompanying article by Andrew Campbell

An Asselian (earliest Permian) bestiary

Life in the Asselian times had not changed much from the latest Carboniferous. There were still swampy forests of huge trees, and a fauna dominated mostly by stem tetrapods with only a few medium-sized reptiles



This scene shows some of the inhabitants of a mountain valley community in eastern Euramerica (what is now Germany).
top left to right:
1. *Edaphosaurus*, a herbivorous pelycosaur;
2. an unnamed seymouriamorph amphibian;
3. an unnamed captorhinid reptile;
4. an unnamed trematopid temnospondyl amphibian;

center
5. *Micromelerpeton*, a micromelerpetontid temnospondyl;
6. *Sclerocephalus*, an aquatic actinodontid temnospondyl;

bottom
7. *Discosauriscus*, an aquatic seymouriamorph;
8. *Apateon*, an aquatic branchiosaurid temnospondyl.

From A. R. Milner, "Biogeography of Palaeozoic Tetrapods" fig.13.5; in J.A. Long (ed.) *Palaeozoic Vertebrate Biostratigraphy and Biogeography*, 1993, John Hopkins University Press, Baltimore

Known Occurrence of Asselian Tetrapod Faunas

Note: the following is based on J. M. Anderson & A. R. I. Cruikshank, "The Biostratigraphy of the Permian and Triassic, Part 5, a review of the classification and distribution of Permo-Triassic Tetrapods," in *Paleontologica Africana*, **21**, 15-44 (1978); slightly modified.

Location	tetrapod zone	approx time	USA				Western Europe			Eastern Europe
Age			Utah, Colorado	New Mexico	Texas	Pennsylvania	England	France	Germany	Russian platform
Asselian	P 2	288	Hotgaita shale		Moran formation	Washing-ton formation				
	P 1	289		Abo (Cutler group)	Pueblo					
		290 291					Kenilworth Sandstone	lower Rottliegendres	lower Rottlie-gendres	"Asselian"

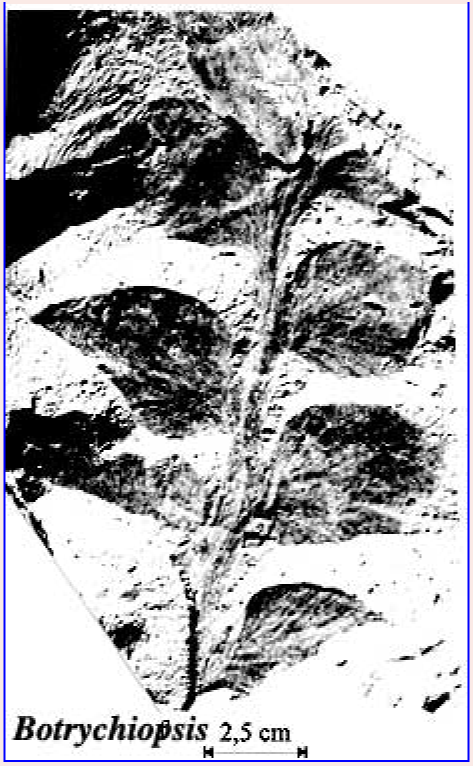
* approximate time in MYA (millions of years ago) - nearest million year intervals

* In their chart Anderson & Cruikshank, locate the Abo formation in tetrapod zone 3. However the fact that many of the same species occur in the late Carboniferous El Cobre formation shows that the two strata cannot be that far apart in time

Asselian Links

GeoWhen Database - Asselian: GeoWhen's usual concise and authoritative placement of the age in geochronological context. *See also* the coverage of the stratotype at Carboniferous - Permian Boundary Stratotype

DinoData: Earth History Maps of Jan Golonka: See Slice 14. These wonderful maps are our primary source for paleogeographical information. Another large-scale map can be found as part of a series reproduced in Mei, S-L, CM Henderson & YG Jin (2004?), *Permian conodont provincialism, zonation and global correlation*, published on line by the Applied Stratigraphy Research Group of the University of Calgary, Dept Geology & Geophysics.



One of our favorite places on the web is the History of Insects site maintained by the Paleoentomology Institute in Moscow. Among the other treasures on this site are a number of papers -- not always on the subject of insects. For example, this study of Early Permina climate: Chumakov, NM & MA Zharkov (2002), *Climate during Permian–Triassic biosphere reorganizations, article 1: Climate of the Early Permian*. **Strat. Geol. Correl.**, 10: 586–602.

Upper Palaeozoic floras of SE Asia: pdf Rigby, JF (1998), *Upper paleozoic floras of SE Asia*, **in** R Hall & JE Holloway [eds.], **Biogeography and Geological Evolution of SE Asia**. Backhuys Publ. pp. 73-82. Indispensible data for reconstructing the flora of the period. Not fun reading -- just data. Permian marine biogeography of SE Asia, an article from the same collection by Shi & Archbold, puts the information in paleogeographical context. Prof. Archbold has done a great deal of work in this area. More references can be found at Research Output for Neil Archbold. Another on-line study of the earliest Permian flora can be found at Jasper, A, M Guerra-Sommer, M Cazzulo-Klepzig & R Menegat (2003), *The **Botrychiopsis** genus and its biostratigraphic implications in Southern Paraná Basin*. **An. Acad. Bras. Ciênc.**, 75:.513-535 with maps and some nice fossil plant images (see example at right).

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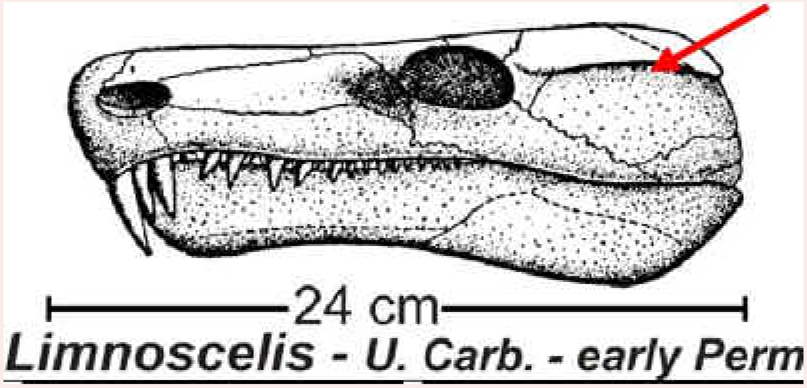
The Sakmarian

The Sakmarian Age of the Cisuralian Epoch: 295 to 284 million years ago

Sakmarian Tetrapod Faunas



Limnoscelis - a large reptile-like tetrapod

Note: the following is based on J. M. Anderson & A. R. I. Cruikshank, "The Biostratigraphy of the Permian and Triassic, Part 5, a review of the classification and distribution of Permo-Triassic Tetrapods," in *Paleontologica Africana*, **21**, 15-44 (1978); slightly modified.

Location	tetrapod zone	approx time	USA					India
Age			Utah, Colorado	New Mexico	Texas	Oklahoma	Pennsylvania	Himalayas
Sakmarian	4	283 284 285 286 287 288	Organ rock shale;		Admiral formation	Wellington formation		Kashmir
	3			Abo formation (Cutler group)	Putman formation		Green Formation (Dunkard group)	
	2		Hotgaita shale		Moran formation			

* approximate time in MYA (millions of years ago) - nearest million year intervals

Tetrapods

Class Tetrapoda
Order Temnospondyli
Superfamily Eryopoidea
Family Eryopidae

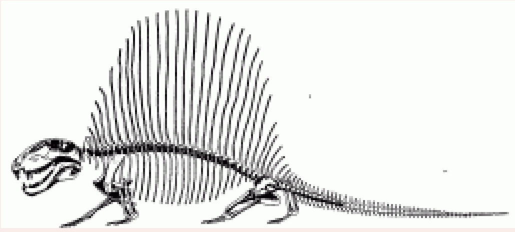
Eryops megacephalus *[Cope]*

Horizon and Locality: Witchita Series (Wolfcampian age), Texas Red Beds
Locality:
Specimens:
Length (skull):
Length (total): 1.5 to 2 meters
Weight: about 130 kg
Diet: other stem tetrapods
Comments: a large carnivorous aquatic tetrapod, which seems to have persisted with no change for some 20 million years or so

Plesion Synapsida (Theropsida)
Order Pelycosauria
Suborder Eupelycosauria
Family Sphenacodontidae

Sphenacodon ferocior

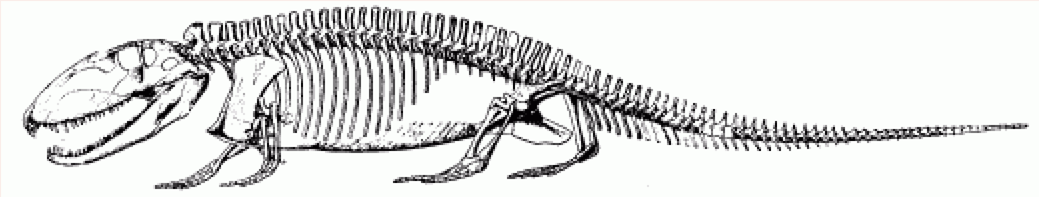
Horizon and Locality: from the Abo/Cutler Formation, New Mexico, USA
Adult Length: 225 cm
Adult Mass: 129 kg
Diet: other stem tetrapods
Comments: Almost identical to *Dimetrodon*, except that it lacks the famous "sail". *Sphenacodon* lived in a different region (separated by an expanse of sea) from most species of *Dimetrodon* (apart from the small contemporary *D. occidentalis*), and was the size of larger and later species of the latter.
References: Romer and Price 1940, Reisz 1986



Plesion Synapsida (Theropsida)
Order Pelycosauria
Suborder Eupelycosauria
Family Sphenacodontidae

***Dimetrodon* milleri** *Romer 1937*

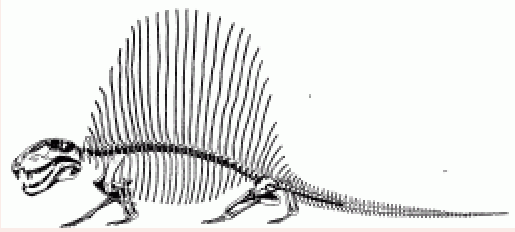
Horizon: from the Putnam Formation, Wichita Group, Texas, USA
Specimens: one nearly complete and two partial skeletons
Adult Length: 174 cm
Adult Mass: 47 kg
Diet: smaller Tetrapods
Comments: a small, rare form, this is the stratigraphically earliest of the many *Dimetrodon* species recovered from Texas.
References: Romer and Price 1940, Reisz 1986



Plesion Synapsida (Theropsida)
Order Pelycosauria
Suborder Eupelycosauria
Family Ophiacodontidae

Ophiacodon retroversus *[Cope]*

Horizon and Locality: Admiral Formation, Witchita Series (Wolfcampian age), Texas Red Beds
Adult Length: 2.5 meters
Adult Mass: 120 kg
Diet: mostly fish, perhaps also small aquatic tetrapods
Comments: a large species of the Ophaicodontid lineage. These creatures apparently grew progressively bigger through time.
The skull is very deep and long, not unlike phytosaurs such as *Nicrosaurus*. It has been suggested that *Ophiacodon* was a fish-eating form that lived largely along the shores of streams and ponds.
References: Romer and Price 1940, Reisz 1986



Plesion Synapsida (Theropsida)
Order Pelycosauria
Suborder Eupelycosauria
Family Sphenacodontidae

***Dimetrodon* limbatus** *[Cope]*

Horizon: Admiral and Bell Plains Formations, Wichita Group,
Locality: Texas, USA
Specimens: Skull and skeletal elements

Adult Length: 256 cm
Adult Mass: 146 kg
Diet: other Tetrapods
Comments: a large animal, representing the trend in increase in size of successive *Dimetrodon* species. It seems to be less common than smaller contemporary species
References: Romer and Price 1940, Reisz 1986

Resources

Some Links and References

Romer, A.S. and Price, L.I. *Review of the Pelycosauria*, Geological Society of America Special Papers,. no.28,

Robert R. Reisz, *Pelycosauria*, Encyclopedia of Paleoherpetology, Part 17A, 1986, Gustav Fischer Verlag, Stuttgart and New York

The Sam Noble Oklahoma Museum of Natural History - Collections - Vertebrate Paleontology - Lists a number of specimens of late Sakmarian age (Wellington Formation)

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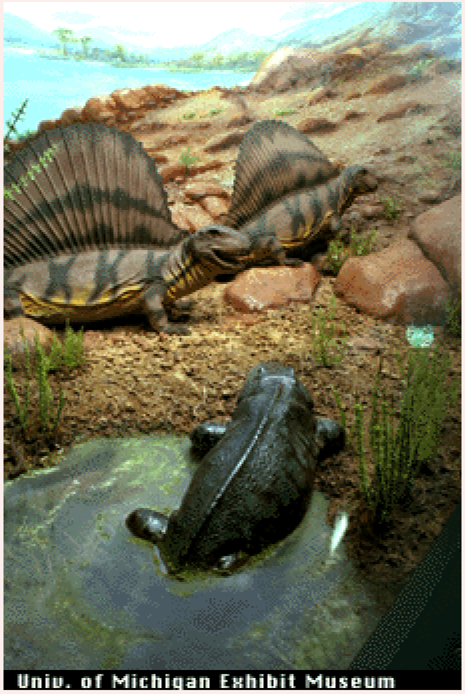
The Artinskian Age

The Artinskian Age of the Cisuralian Epoch: 284 to 276 million years ago

Introduction



As the climate became drier, the early Permian semiaquatic and lowland floodplain *Dimetrodon* and *Eryops* dominated fauna shown here, which had flourished for some 25 million years, was replaced by the more advanced floodplain and upland caesid and therapsid fauna.

An Artinskian bestiary: Edaphosaurid-Nectridean Province

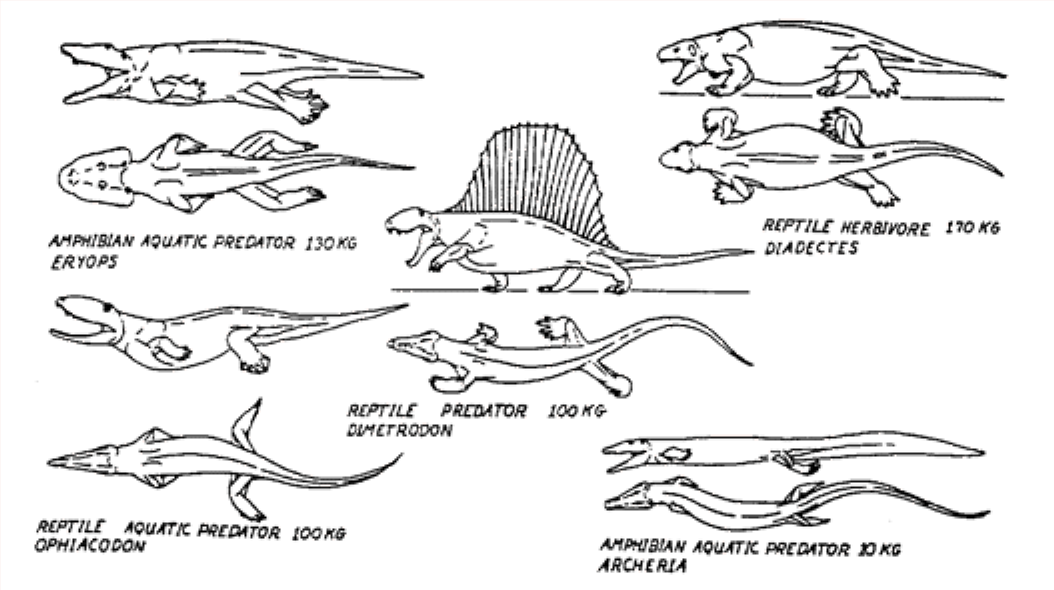
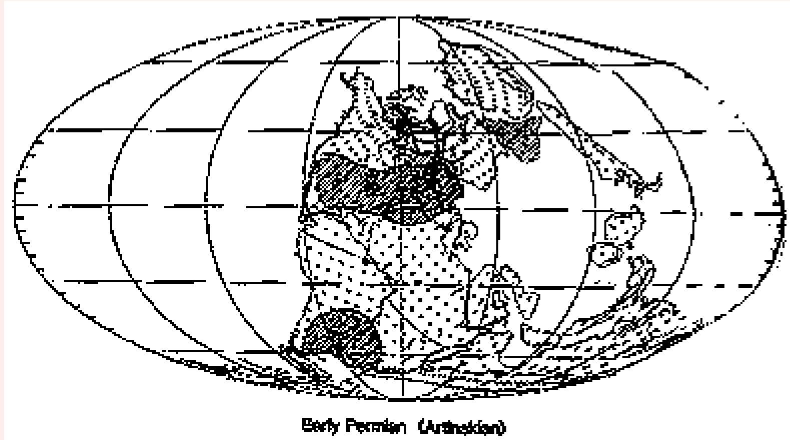


Illustration by Robert Bakker



This map shows the three known tetrapod provinces (shaded) of the early Permian -
the tropical Edaphosaurid (centre),
the Kazakhstan Seymouriamorph province (upper right),
and the high latitude Gondwana Mesosaurid province (bottom)

From A.R. Milner, "Biogeography of Palaeozoic Tetrapods" fig.13.3; in J.A. Long (ed.) *Palaeozoic Vertebrate Biostratigraphy and Biogeography*, 1993, John Hopkins University Press, Baltimore

Known Occurrence of early Permian Tetrapod Faunas

Note: the following is based on Anderson and Cruikshank 1978 slightly modified.

Location	tetrapod zone	approx time *	USA		Western Europe	Eastern Europe	Brazil	southern Africa	India
Age			Texas	Oklahoma	Germany	Russian platform	Parana Basin	South Africa / South-West Africa	Himalayas
biotic province			Edaphosaurid province (equatorial Euramerica)				Mesosaurid province (south-west Gondwanaland)		
Baigendzhinian	10	277	Choza	Hennesey					
	9	278	Vale						
	8	279	Arroyo	Garber		zone 0			
Aktasinian	7	280	Ludens	West Grandfield					
	6	281	Clyde	Deep Red Run			Irati	White band	
	5	282 283	Belle Plains	Wellington formation					

* approximate time in MYA (millions of years ago) - nearest million year intervals

Class Chondrichthyes
Subclass Elasmobranchii
Order Xenacanthida
Family Xenacanthidae

Xenacanthus

Length (total): about 1 to 2 meters
Diet: aquatic vertebrates
Comments:

Some Tetrapods - Aktasinian (Early Artinskian)

Class Tetrapoda
Order Temnospondyli
Superfamily Eryopoidea
Family Eryopidae

Eryops megacephalus *[Cope]*

Horizon: Wichita Series (Wolfcampian age), Texas Red Beds
Locality:
Specimens:
Length (skull):
Length (total): 1.5 to 2 meters
Weight: about 130 kg
Diet: other tetrapods
Comments: a large long-lived aquatic temnospondyl

Arroyo Formation - Early Baigendzhinian Age

Plesion Synapsida (Theropsida)
Order Pelycosauria
Suborder Eupelycosauria
Family Sphenacodontidae

Dimetrodon grandis *(Case, 1907)*

Horizon and Locality: Arroyo Formation, Clear Fork Group, Texas, USA
Specimens:
Length (skull): 42 cm
Length (total): 3.2 metres
Weight: around 250 kg
Diet: other tetrapods
Comments: The last and largest of the long-skulled, stocky-bodied lineage of dimetrodonts. Apart from *D. angelensis* this was the largest species of *Dimetrodon*. A large, heavily-built, very common species, it is close to the earlier *D. limbatus*, with which it differs in larger size, more elongate and stouter neural spines, and fewer premaxillary teeth (only two on either side, the fewest for any species of the genus). It is associated with the slightly smaller but equally successful *Dimetrodon gigashomogenes*
References: Romer and Price 1940, Reisz 1986
Links:

Plesion Synapsida (Theropsida)
Order Pelycosauria
Suborder Eupelycosauria
Family Sphenacodontidae

Dimetrodon gigashomogenes *Case, 1907*

Horizon and Locality: Arroyo, Vale and Choza Formations, Clear Fork Group, Texas, USA
Specimens:
Length (skull):
Length (total): 328 cm
Weight: around 166 kg
Diet: other tetrapods
Comments: A large representative of the short-skulled lineage of dimetrodonts. Possibly ancestral to *D. angelensis*. Although similar in size to *Dimetrodon grandis*, it differs in the shape of the neural spines, the length of the vertebrae centra, and the lighter overall build. *D. gigashomogenes* would seem to be a descendent, or possibly even the same species, of the preceding *D. dollovanus*, from which it differs mainly in larger size.
References: Romer and Price 1940, Reisz 1986

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The Kungurian Age

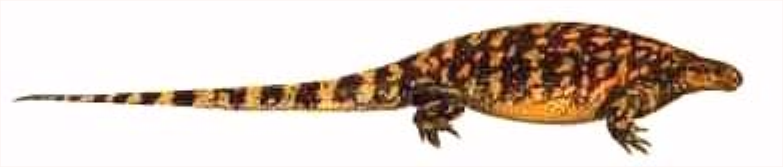
The Kungurian Age of the Cisuralian Epoch: 276 to 271 million years ago

Kungurian Life

Plants

Paleozoic vascular flora, which appeared in the Middle Ordovician epoch, died out quite a few millions of years before the end of the Paleozoic, in the Kungurian or earlier. In theGuadalupian, the gymnosperm-dominated Mesophytic flora emerges (although Mesophytic type plants go back to the Carboniferous, just as some Paleophytic plants survive even to this day), and this flourishes right up until the middle and later Cretaceous. MAK010115.

Tetrapods



A typical caseid synapsid. During the Kungurian these herbivores were generally 2 to 4 meters in length with the largest species reaching 5 or 6 meters

illustration by Steve Kirk, from *The Illustrated Encyclopedia of Dinosaurs and Prehistoric Animals*, ed. by Barry Cox

During this period, for the first time, herbivores established themselves as a major part of a terrestrial ecosystem. Although herbivorous reptilomorphs (*Diadectes*) and synapsids (*Edaphosaurus*) appeared during the latest Carboniferous, they remained a minority element of the "Edaphosaur - Nectridean" fauna. But now in the Kungurian we see an environment dominated by medium to large sized herbivores (the pelycosaur family Caseidae). This very important event marked the shift from a food chain based on detritus and carnivory (insectivore/ piscivore/ carnivore) to a more efficient one in which plants as primary producers provide the main input. The Lopingian Epoch (Late Permian) witnessed a succession of impressive medium to large herbivores - caseids, estemmenosuchids, deuterosaurs, tapinocephalids, and dicynodonts - with (apart from the dicynodonts) each "dynasty" flourishing briefly than dying out after only a few million years, to be replaced by a new wave. The reason for this may perhaps be related to the instability of these early ecosystems, which had not yet developed the complexity and stability of a long-range ecology. A similar situation was evident with the first waves of Metazoa (marine invertebrates) during the late Vendian (Edicarian) through to Furongian time.

Class Tetrapoda
Order Temnospondyli
Superfamily Trimerorhachoidea
Family Trimerohachidae

Slaugenhopia texensis *Olson 1962*

Horizon: Upper San Angelo Formation, Pease River Group
Locality: Knox County, Texas, USA
Specimens: skull fragments and some postcrania
Diet: aquatic invertebrates
Comments: The only stem tetrapod from this locality. Known from very scrappy remains. Olson, 1962 suggests that this species is quite similar to *Trimerohachis*, and could be a descendant
References: Olson, 1962

The captorhinid reptile *Labidosaurus*. *Rothaniscus* and *Kahneria* would have been very similar in appearance. In lifestyle these animals were comparable to large tropical lizards

Class Reptilia
Plesion Eureptilia
Order Captorhinomorpha
Family Captorhinidae

Rothaniscus *multidonta (Olson and Berrbower, 1953)*

Horizon: Upper San Angelo Formations, Pease River Group
Locality: Hardemann County, Texas
Specimens: several partial skulls and postcrania
Length (skull): 25 cm
Length (total): about 1.5 metres long
Diet: omnivorous
Comments: Previous described as *Rothia*, this is the largest member of the Captorhinidae. The rather light structure of the limb bones suggest an agile reptile
References: Olson, 1962

Class Reptilia
Plesion Eureptilia
Order Captorhinomorpha
Family Captorhinidae

Kahneria seltina *Olson 1962*

Horizon: Upper San Angelo Formation, Pease River Group
Locality: Knox County, Texas, USA
Specimens: several partial lower jaw and postcrania
Length (total): about 1.2 metres long
Comments: Known from scrappy remains, this appears to be an animal similar to (but a little smaller than) *Rothaniscus*
References: Olson, 1962

Plesion Synapsida (Theropsida)
Order Pelycosauria
Suborder Eupelycosauria
Family Sphenacodontidae

Dimetrodon angelensis *Olson 1962*

Horizon: Upper San Angelo Formation, Pease River Group
Locality: Knox County, Texas, USA
Specimens: Skull and skeletal elements
Length (skull): 58 cm long
Length (total): about 4 metres
Weight: about 300 kg
Diet: other Tetrapods
Comments: the last and largest of the fin-back synapsids; creatures that were so successful for some 30 million years.
References: Olson 1962

Plesion Synapsida (Theropsida)
Order Pelycosauria
Suborder Caseasauria
Family Caseidae

Caseoides sanangelensis *Olson and Berrbower, 1953*

Horizon: Middle San Angelo Formation, Pease River Group
Locality: Knox County, Texas, USA
Specimens: partial skeletons of two specimens
Length (total): about 3 metres
Weight: about 150 to 200 kg
Diet: herbivore
Comments: Very similar to, perhaps a descendent of, the Artinskian *Casea halselli*, but rather larger in size. A very typical

Caseid; a fairly large, heavily built, herbivorous lizard-like animal. In the development of its proportionally thick, stout limbs it represents the culmination of the *Casea* lineage. The Roadian Phreatophasma aenigmaticum, although smaller and more lightly built, may tentatively be a relative.
References: Olson 1962

Plesion Synapsida (Theropsida)
Order Pelycosauria
Suborder Caseasauria
Family Caseidae

Caseopsis agilis *Olson 1962*

Horizon: near top of Middle San Angelo Formation, Pease River Group
Locality: Knox County, Texas, USA
Specimens: partial skull and postcrania
Length (total): about 3 metres
Diet: herbivore
Comments: In contrast to other members of the family, this is a lightly built, agile animal. It's direct antecedents are not known. *Caseopsis c.f. agilis* (either the same species or a very similar one) is known from the slightly later Lower Flowerpot Formation, same locality
References: Olson 1962

Plesion Synapsida (Theropsida)
Order Pelycosauria
Suborder Caseasauria
Family Caseidae

Cotylorhynchus hancocki *Olson and Berrbower, 1953*

Horizon: Upper San Angelo Formation, Pease River Group
Locality: Hardemann County, Texas
Specimens: postcrania
Length (total): about 6 metres
Weight: about 2 tonnes
Diet: herbivore
Comments: Probably a descendent of the latest Artinskian age *Cotylorhynchus romeri*, this is likewise a very large, heavily built animal. In fact this huge but gentle herbivore is the largest known caseid, the largest known pelycosaur, and for its time the largest tetrapod ever. In fact it was so big that adults had nothing to fear from any contemporary carnivores. This was a very common animal, and Olson, in his monograph on Late Permian Vertebrates [ref] has created a number of false species based on misinterpretations of this and other species ("chimeras"). The giant dinocephalians *Driveria*, *Mastersonia*, and *Tappenosaurus*, each provided with its own family and since referred to in subsequent paleontological works, were probably based on misinterpretations of this Caseid. This is all the more surprising considering that Olson wrote a monograph on the family.
References: Olson 1962

Plesion Synapsida (Theropsida)
Order Pelycosauria
Suborder Caseasauria
Family Caseidae

Angelosaurus dolani *Olson and Berrbower, 1953*

Horizon: Middle San Angelo Formation, Pease River Group
Locality: Knox County, Texas, USA
Specimens: partial skull and postcrania
Length (total): about 3 to 3.5 metres
Weight: about 300 kg
Diet: herbivore
Comments: A large, heavily built form

References: Olson 1962

Plesion Synapsida (Theropsida)
Order Therapsida?
Suborder "Biarmosuchia"? (basal Therapsids)
Family Phthinosuchidae?

Gorgodon minutus *Olson 1962*

Horizon: Upper San Angelo Formation, Pease River Group
Locality: Knox County, Texas, USA
Specimens: partial skull
Length (skull): 6 cm
Comments: It is not clear whether this small, very scrappy specimen really is a proto-therapsid or simply a misidentified pelycosaur
References: Olson 1962

Later Early Kungurian Age

This is the youngest occurrence of the American sequence of Texas Red Beds and equivalent formations. The animals here are very similar to those of the preceding San Angelo Formation (Earliest Kungurian), and clearly part of the same chronofauna.

Plesion Synapsida (Theropsida)
Order Pelycosauria
Suborder Caseasauria
Family Caseidae

Cotylorhynchus bransoni *Olson and Barghusen, 1962*

Horizon: Chickasha Tongue of the middle Flowerpot Formation
Locality: Kingfisher County, Oklahoma
Specimens: postcrania
Length (total): about 3 metres
Weight: about 250 kg
Diet: herbivore
Comments: This is not only the last member of the genus but also, curiously, the smallest and most lightly built. But in characteristics such as the phalangeal formula and tooth structure it is the most advanced. It seems that the Cotylorhynchines, having reached the maximum size in the Early Kungurian *C. hancocki*, now began to shrink, culminating in the diminutive *Ennatosaurus* of the late Roadian/early Wordian
References: Olson 1962

Plesion Synapsida (Theropsida)
Order Pelycosauria
Suborder Caseasauria
Family Caseidae

Angelosaurus greeni Olson 1962

Horizon: Lower Flowerpot Formation, Pease River Group
Locality: Knox County, Texas, USA
Specimens: scrappy postcrania
Length (total): about 4 metres
Weight: about 500 kg
Diet: herbivore
Comments: This is the largest of the Angelosaurs. It is known only from very scrappy remains. Apart from larger size, there is little to distinguish this species from the slightly earlier *Angelosaurus dolani*
References: Olson

Plesion Synapsida (Theropsida)
Order Pelycosauria

Angelosaurus romeri *Olson and Barghusen, 1962*

Horizon: Chickasha Tongue of the middle Flowerpot Formation
Locality: Kingfisher County, Oklahoma
Specimens: postcrania
Length (total): about 2.5 metres
Weight: about 150 kg
Diet: herbivore
Comments: This is the smallest of the Angelosaurs. The vertebrae can only be distinguished with difficulty from those of the contemporary *Cotylorhynchus*
References: Olson

Late Kungurian Age

There are no tetrapod beds of undoubted middle or late Kungurian Age. It may be that Ocher fauna of Russia may occur at this level rather than during the Early Roadian, but that is probably not likely. In any case, even if it was the case, there is still a great morphological gap between the early Kungurian caseid fauna, and the Latest Kungurian/ Early Roadian Bairmosuchian- Estemmenosuchid fauna

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The Guadalupian Epoch

The Guadalupian Epoch of the Permian Period: 271 to 260 million years ago

Introduction

The Guadalupian Stage was named after the Guadalupe Mountains of New Mexico, U.S.A., where rocks and fossils of this age are known. These rock strata and fossils were formed during the middle Permian period, and as part of the recent revision of Permian stratigraphy (in order to attain a standard global correlation) the old division of lower and upper Permian has been supplemented, if not replaced, by a newer arrangement.

***Titanophoneus* potens**
Early Capitanian epoch - length approximately 3 meters
image copyright © Kelly Taylor - reproduced with permission

In this the Guadalupian epoch refers to the Middle Permian (with the Lopingian as the Late Permian).

The first two-thirds of this epoch were characterized by a continuation of the temperate and tropical climate zones established during the preceding Kungurian Age. But the drying climate meant the end of the great tropical coal forests that had dominated the equatorial belt for so long and provided a haven for numerous stem tetrapods, reptiles, fish, invertebrates, and plants. The last third experienced a drop in temepratures, the Kamura cooling event (Isozaki et al 2007), during which tropical coral reefs and many marine organisms died out. Finally, vulcanism led to a Greenhouse crisis, anoxia, and a mass-extinction at the end of the epoch (Retallack 2005 Retallack et al 2006)

During this period, evolutionary turn-over was high, and on land a series of animal dynasties successed each other.

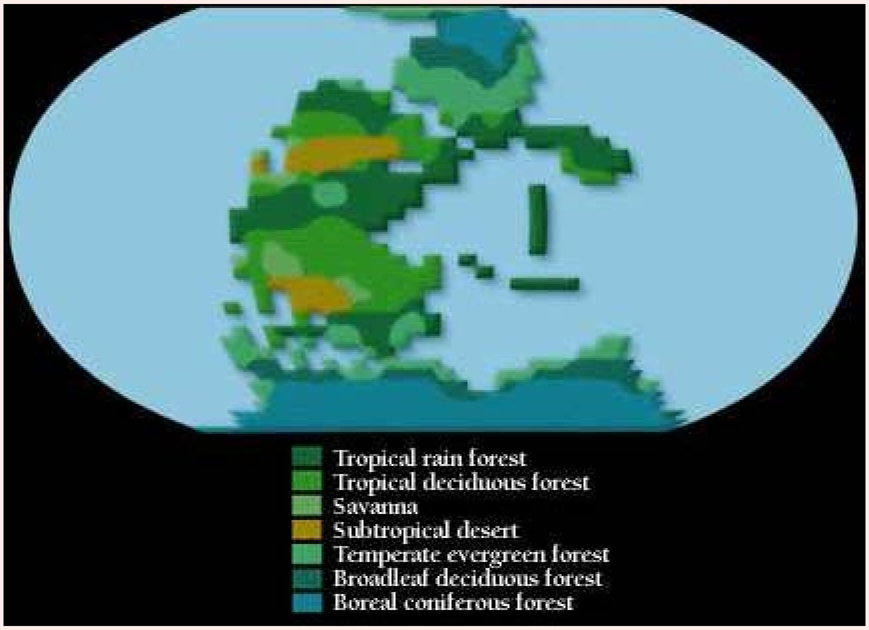
At the top of the middle Permian food chain were giant carnivores, such as the Eotitanosuchids and the appropriately named "terrible heads" or Dinocephalians. These latter included *Titanophoneus* pictured above) and *Anteosaurus*. Some, such as *Ivantosaurus* and *Anteosaurus* were the largest land carnivores of the Permian period, reaching 5 or more meters in length, and dwarfing even the bigger fin-back *Dimetrodons* of the Early Permian.

These animals were among the most primitive of the therapsids. In older books they are called "mammal-like reptiles" because they were on the evolutionary road to mammals, and may have even had the very beginnings of a primitive warm-blooded metabolism, although the presence of fur (shown in the *Titanophoneus* illustrated above) at this early stage is probably dubious. These creatures preyed on their equally if not bigger herbivorous contemporaries, the moose-like Estemmenosuchids, the great Tapinocephalids (upto 2 tonnes live weight) with their immensely thickened skulls allowing head-butting territorial behavior, and the bizarre armoured and possibly semi-aquatic pareiasaurs.

In addition to this megafauna a diverse selection of smaller reptiles inhabited the undergrowth, and stem temnospondyl amphibians, although diminished from their early Permain heyday, still frequented ponds, rivers, and lakes. Some, like the aquatic *Melosaurus*, was an *Eryops*-type predator reaching 2 to 3 meters . This creature was clearly able to eat just about anything it could wrap its huge mouth around (mostly fish and smaller tetrapods and reptiles).

Among the smaller animals that would have ended up in*Melosaurus*' stomach were *Discosauriscus*, an aquatic batrachosaur (Seymouriomorpha) that was very close to the base of the true reptiles. Ironically, whilst reptiles had evolved from batrachosaurs millions of years earlier, these Carboniferous relics had continued as "living fossils", retreating back to the ponds as their last refuge

While animals were undergoing a change so were plants, with xerophyletic (dry-adapted) species of ferns, seed-ferns, conifers and ginkgos coming into prominence. The *Glossopteris* flora dominates in Gondwanaland. These new plants mark the transition between the Paleophytic (the old spore-bearing moisture loving coal swamp plants) and the Mesophytic (gymnospermous) era of plant evolution. Significantly, whereas animal life has its big transition at the very end of the Permian, plant life switches over to a more modern flora some ten to twenty million years previous. The same pattern is seen in in the late Mesozoic era, where modern flowering plants appear long before the extinction of the dinosaurs and their contemporaries.



> "Life on much of the supercontinent Pangea resembled central Asia today: Large inland areas, far from moderating oceans, suffered baking summers and bitter winters. At tropical and subtropical latitudes, summer monsoon rains bathed the continent's east coast. Those conjectures come from a computer model that uses coastlines and topography-plus a few laws of physics, like the equations for air movements and heat transport-to predict the climate 250 million years ago. The idealized, squared-off coastline of this map simplified the calculations done in 1993 by Chicago's Alfred Ziegler and John Kutzbach of the University of Wisconsin-Madison (illustration by Allen Carroll). Rainfall and temperature data determine the biome regions where evolution unfolded, from tundra to tropics. Wind patterns can predict ocean currents like the upwellings that fostered plankton, a clue to today's oil deposits. And comparisons to the actual climate and biome, deduced from fossil and geologic evidence, improve the computer model-refining predictions of future climate change, like global warming."

This map and the above text are from Mapping a Planet's Restless Past -The University of Chicago Magazine December 1995 - see also the accompanying article by Andrew Campbell

The Guadalupian epoch ended with a deteriorating environment, Greenhouse conditions, and several series of mass-extinctions; both the great dinocephalians and other taxa on land, and varuious invertebrates in the sea. In teh following, Lopingian, age, new types of mammal-like reptiles would dominate the land.

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text content M.Alan Kazlev 2000-2009

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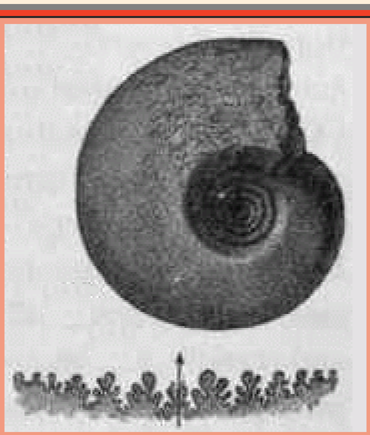
The Roadian Age

The Roadian Age of the Guadalupian Epoch: 271 to 268 million years ago

Introduction



The Roadian is the first of the three ages of the Middle Permian (Guadalupian epoch). It takes its name from the Road Canyon Member, the lower (oldest) part of the Word Formation. It was established in 1968, but only added to the international IUGS timescale in 2001, when the International Commission on Stratigraphy established the Global Stratotype Section and Point (GSSP) in the Cutoff Formation (Guadalupe Mountains of Texas). The base of the Roadian is defined as the appearance of the conodont *Jinogondolella nankingensis*.. Other important fossils characteristic of the stage include the ammonoids *Demarezites* and *Waagenoceras* (*right*) and the foramnifers *Neoschwangerina tenuis* and *Afganella tereshkovae*. The top of the Roadian and base of the Wordian is given by the first appearance of fossils of conodont species

Jinogondolella aserrata. (online refs - Britannica, Wikipedia, Upper Paleozoic timescale)

Waagenoceras cumminsi **White, x 4/5., and suture line -**
from William B. Scott, 1907, 1921 , *An Introduction To Geology*, Macmillan image ©
StasoSphere original page

Russian terrestrial stratigraphy, the Ufimian and Kazanian

The Russian terrestrial late Permian strata are traditionally divided into the Ufimian (the earliest), the Kazanian, and the Tartarian. There has however been some difficulty mathching these with the International scale. Whereas the Kazanian and the Tartarian are secure, the fate of the Ufimian is uncertain, It is generally considered equivalent to perhaps the lower part of the Roadian, but has sometimes also considered belonging to the next older age (Kungurian) or the next younger, the Wordian (e.g. Gilmour and Morozova 1997). On the basis of conodont zonation, Chernykh 2002 says:

> "The upper Kazanian substage is most probably also Roadian, because *Merrillina galeata*, which is characteristic of higher stratigraphic horizons (Wordian) is absent in the Upper Kazanian of the Mid-Volga Region. Because the lower Kazanian correlates with the lower Roadian and I suggest the upper Kungurian correlates with the Cathedralian, it appears the Ufimian may lose its status as a stage."

However another paper (which considers vertebrates and strata of the South Urals) by Tverdokhlebov et al 2005 p.30 retains the Ufimian, noting that fishes have been found from deposits of this age north of the region being considered, but no tetrapods.

The problem is that the Kungurian, which is one of the stages shared with both the International Scale and East-European Scale, has a different definition with which. Hence (as recommended in the *Permophiles Newsletter of the Subcommission on Permian Stratigraphy* #46) in order to have uniformity the Ufimian is either removed, or reduced to a substage in the East-European Time Scale equivalent to the upper part of the Kungurian Stage (Latest part of the Early Permian) in the International Time Scale.

Finally, the Kazanian, the middle of these three stages, has been equated with the Wordian, the latest Roadian to Early Capitanian (Lucas 2004), the Middle Roadian to Early Wordian (Benton et al 2004), and the Roadian (*Permophiles* #46 2005). The Russian commission on Permian Stratigraphy considers that the Kazanian and Roadian Stages are equivalent, based on new discoveries of Roadian conodonts and ammonoids in the lower Kazanian (Kotlyar and Pronina-Nestell 2005).

"Olson's Gap"?

There is some controversy over the Roadian tetrapod fauna, which is due to the problem of correlating East European tetrapod faunas with the international stratigraphic standard.

Dr Spencer Lucas (2002 and 2004) argues that no tetrapods are known from the Roadian, and thus there is a hiatus between the Pelycosaur dominated Early Permian (up till the Kungurian) and the Therapsid dominated middle and late Permian (beginning in the Wordian). He refers to this as "Olson's Gap", after Everett C. Olson, who investigated these stratigraphic levels in the search for tetrapods intermediate between pelycosaurs and therapsids and wrote a number of important monographs on the subject (e.g. Olson, 1962). Dr Lucas' arguments have been challenged by Reisz and Laurin 2002 who have described a typically Russian middle Permian fauna from North America, and argue that this is Roadian, not Kungurian in age. A recent issue of the *Permophiles Newsletter of the Subcommission on Permian Stratigraphy* (no. 46, December 2005 - correlation table reference) argues that the the Kazanian and Roadian Stages are equivalent. If so this means that there is no Olson's Gap, because the Kazanian tetrapods that were previously thought to be Wordian are actually Roadian. This does not mean that all the Kazanian faunas are Roadian, since the best known ones are late Kazanian, which may mean they overlap with the Early Wordian. See also Lozovsky 2005

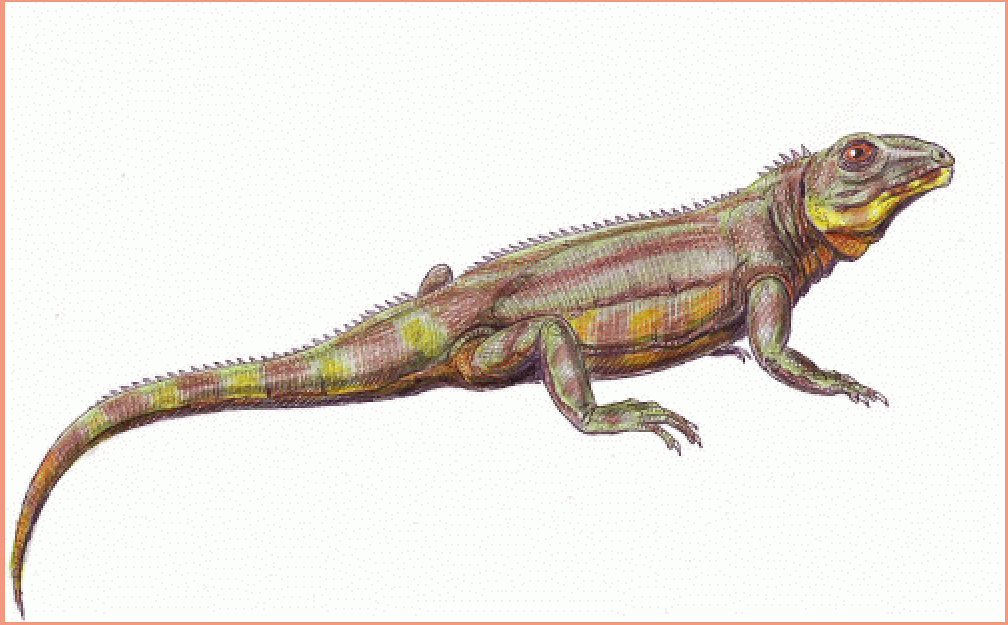
Not to be outdone, Lucas met these arguments with Lucas 2004, Lucas 2005. More recently it has been argued that the very primitive Therapsida of the Xidagou Formation (Dashankou locality) in China are of Roadian age (Liu et al 2009). I have to admit I feel biased towards acknowledging Roadian tetrtrapod faunas, if only because the the morphogenetic (evpolutionary) difference between primitive Chinese and Russian faunas and the more advanced but traditionally Wordian Eodicynodon fauna of South Africa. Here I assume here that the Dashankou, Lower Kazanian, and part of the Upper Kazanian are of Roadian age, with the Russian Ocher fauna on the Roadian/Wordian boundary or thereabouts.

Roadian tetrapod faunas

One example of this therapsid-dominated fauna tetrapod assemblage is in the Lower Kazanian stage of the Russian Cisurals. The Golyusherma locality is correlated with the Baitugan horizon at the base of the Kazanian, and hence is Earliest Roadian Kotlyar and Pronina-Nestell 2005, reveals a tetrapod assemblage of diverse amphibians: archegosaurid and melosaurid temnosondyls and leptorophid seymouriamorphs; and reptiles: bolosaurid parareptiles, captorhinid eureptiles, and primitive estemmosuchud and brithopodid therapsids. Specimens were collected during mining operations at Bashkirstan (also Russian Ural region) may be just as old. These include fragmentary remains of temnospondyls, the dinocephalian "Brithopus" and phreatosuchids (possibly Caseid pelycosaurs although this is not certain Olson 1962). (Lucas 2004 - note that Lucas considers all these Lower Kazanian faunas no earlier than early Wordian; however according to the contributers of *Permophiles* (#46) the Kazanian is actually Roadian. See also see also East European Stratigraphy - Notes)

***Platyoposaurus stuckenbergi*, a common Roadian Temnospondyli Archegosauroid amphibian from central low latitude northern Pangea (now Perm region of Ruussia). Length about 2.5 meters**
illustration from Mathematical com

During this period the low diversity and very poorly known amphibian and parareptile fauna that characterized the Kungurian age is supplanted (and for the most part replaced) by a rich range of early therapsids. There seems to be a great morphological gap between even the latest Kungurian caseid fauna, and the Roadian therapsid fauna. The therapsids of this time belonged to several distinct (albeit related) lineages, none with clear antecedents.



The small lizard-like parareptile Belebey, which seems to have had a ubiquitous distribution during this time. Illustrated is the Cisuralian species *Belebey vegrandis*
artwork by Dmitry Bogdanov - Wikipedia

The late Kazanian Belebey Community (also in the Cis-Urals region, Russia) provides another glimpse of the various organisms and trophic interactions of this time (V.P. Tverdokhlebov *et. al.* 2005 - see diagram below). This fauna would seem to be the same age, or possibly a bit earlier, than the Ocher assemblage. Various species of fishes, especially palaeonisciforms, fed on water plants, insects, and other invertebrates. These in turn were preyed upon by batrachomorph amphibians. Procolophonomorph anapsid reptiles such as nycteroleterids, *Belebey*, *Davletkulia*, and *Tokosaurus* filled the terrestrial small lizard niche. There were doubtless carnivorous biarmasuchians and brithopodids but these are not known from this locality. The largest animal, and the only therapsid, is a medium-sized (see XLS data file - Ecological Sort) herbivorous dinocephalian, listed as *Estemmenosuchus* sp. (Tverdokhlebov et al 2005 p.45), which at Beleby seems to have been free of predation, although at Ocher it would have faced large Eotitanosuchids. Possibly these animals were here too but have not been preserved.

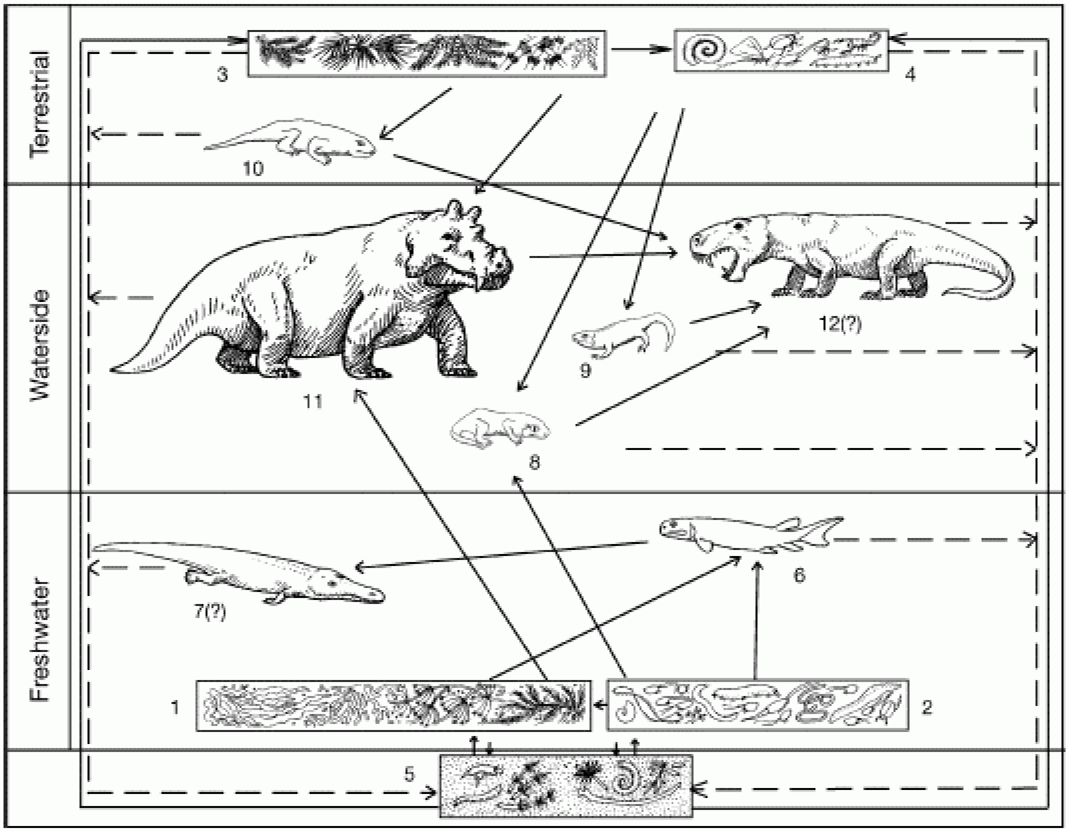


image © from V.P. Tverdokhlebov *et. al.* (2005) Upper Permian vertebrates and their sedimentological context in the South Urals, Russia

"Reconstructed food web for the terrestrial and aquatic components of the Belebey Community (Belebey Svita; Late Kazanian) of the SE of European Russia. Lines with arrows indicate the movement of energy through the community: solid lines show feeding pathways, and dashed lines show decay pathways. Aquatic components: (1) aquatic plants, (2) invertebrates, taxa whose role in terrestrial food chains is insignificant. Amphibious components: taxa which play a significant role in both aquatic and terrestrial food chains. Terrestrial components: (3) plants, (4) invertebrates, taxa which play a role in terrestrial food chains; (5) plant and animal detritus; (6) palaeonisciform, (7) probable batrachomorphs, (8) nycteroleretids, (9) *Tokosaurus*, (10) *Belebey*, *Davletkulia*, (11) *Estemmenosuchus*, (12) probable carnivorous eotheriodonts."

The basal dinocephalian *Stenocybus acidentatus*. Compared to some of the later giants, this was a relatively small animal, probably no more than a meter in overall length.
artwork by Dmitry Bogdanov - Wikipedia

Of very similar age, if not even slightly earlier, to these Russian faunas is the rich fuana of the Xidagou Formation (Ordos Basin of northern China). This includes the dissorophoid temnospondyl *Anakamacops*, an *Intasuchus*-like temnospondyl, the anthracosaurs *Ingentidens* and *Phratochronis*, the bolosaur *Belebey* (as menationed this is also known from the Russian Kazanian - both bolosaurs and dissorophids otherwise occur together only in the Early Permian), a captorhinid, the basal theraspid *Raranimus*, dinocephalian *Stenocybus* and anteosaur *Sinophoneus*, and the anomodont *Biseridens*. (Lucas 2006 p.81, Liu et al 2009 p.397)

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Wordian Age

The Wordian Age of the Guadalupian Epoch: 268 to 266 million years ago

Introduction

The Wordian stage was introduced in 1916. It is named after the Word Formation of the North American Permian Basin.

This was an important period in the history of life on Earth, as it marked the consolidation of the Roadian therapsids, and the appearance of many new forms.

Stratigraphy

Harried editor's note: I am going to be extermely lazy and quote direct from Wikipedia *If you knew how many pages I have to get through here you would understand :-). Besides, why reinvent the wheel?* MAK091116

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, the regional timescale used for the southeastern US had the Wordian and Capitanian as subdivisions of the Guadalupian. 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 also contains two fusulinid biozones: *Afganella tereshkovae* and *Neoschwagerina tenuis*

References: Glenister & Furnish 1961, Glenister et al 1991, Gradstein et al 2004

The Illawarra Reversal

During the middle Wordian, , there was a reversal of the Earth's magnetic field. The Earth's magnetic field, which jhad been stable for a long time, began to flip polarities frequently. This event, known as the Kiaman-Illawarra boundary, marked the end of a long period of magnetic stability and the beginning of a period of rapid polarity shifts in the Earth's magnetic field, and may have been caused by superplume of magma deep within the Earth. This may have allowed more cosmic radiation to reach the Earth's surface, bringing about global cooling Isozakia 2009. The first magnetic flip, known as the Illawarra reversal, and is an important stratigraphic marker when dating terrestrial and marine rocks.

Marine Life

Brachiopod Provinces

An aalysis by Shena et al 2009 of Roadian and Wordian occurrences of 381 brachiopod genera from 44 different geographical stations was revealed four distinct brachiopod biogeographical realms and nine provinces, and 11 brachiopod associations. The Boreal Realm in the Northern Hemisphere includes two provinces and is characterized by cold-water brachiopod associations. The Gondwanan Realm in the south also includes two provinces, the Westralian Province with biogeographical links to the Tethys. The Palaeoequatorial Realm is located mainly in the tropics and contains highly diverse and abundant brachiopod faunas. The brachiopod fauna from the Mino Belt in Japan is distinct from the other regions, and assigned to the palaeoceanic Panthalassan Realm. The major determining factor would seem to be temeprature related, with decreasing diversity from the equator to the poles. Geographic factors and oceanic currents may also have played some role.

Tetrapods

The Wordian saw the continuation of the earlier Roadian age fauna, but with even more types of therapsids. So astonishing is this sudden evolutionary radiation that Bob Bakker refers to it as the "Kazanian Bloom". Dr Bob Bakker argues that these early therapsids were able to flourish because of their advances in metabolic development towards the mammalian condition. But in view of the fact that even advanced later therapsids like Gorgonopsids still seemed to have many ectothermic features (Freeman 1994/95) it is very unlikely that they were already partially or fully endothermic. In any case, these animals quickly radiated into an extraordinary variety of large and small terrestrial herbivores and carnivores. The Early Permian ectothermic families died out early during, or perhaps prior to, this time.

In considering Wordian faunas and communities, it seems to me that a distinction can be made between the Biarmosuchid - Estemennosuchid dominated faunas of the Latest Roadian and Early Wordian, and the more progressive dinocephalian faunas of the middle to late Wordian. These would constitute two distinct Tetrapod empires (communities)

The Latest Roadian and Early Wordian

I have assumed here that the Ocher (Ezhovo) fauna (Late Kazanian or earliest Tatarian) from which many important archaic therapsids are known, is late Roadian, although it has been also considered middle or late Wordian. (see also East European Stratigraphy Notes)

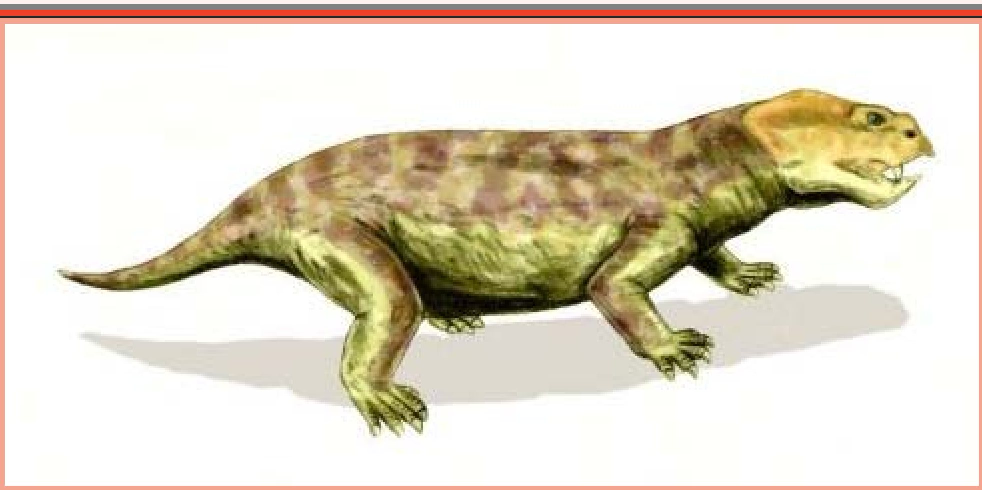
image from Les Thérapsides

Kazanian scene. The large animals with moose-like "antlers" are *Estemmenosuchus mirabilis*. A predatory *Eotitanosuchus* watches from the cover of some sphenopsids

The above scene, a reconstruction of the Ocher assemblage, is probably a little later than the Belebey Community, around the Roadian/Wordian boundary. This is very similar to the Beleby fauna, except that there are larger and more diverse Estemmenosuchids, and also the presence of a number of Biarmosuchian and anteosaur carnivores, graded in size according to preditor guilds

The carnivores include the modest-sized Biarmosuchidae, relatively long-limbed lightly-built hunters of small game (a kind of therapsid dog perhaps), representing a persisting primitive lineage from which the other groups may have developed, the huge carnivorous eotitanosuchians (essentially biarmosuchids grown large), the bizarre estemmenosuchids, herbivores that seem to have frequented a marshy environment, and possessing strange bony head growths, not unlike antlers, and the large brithopodids, representing another carnivorous lineage, more heavily built than the biarmosuchids. Note that apart from the estemennosuchids, which replaced the cotolyhunchines as great lumbering herbivores, all these animals were carnivores. As with the Early Permian pelycosaur-dominated fauna, this was a primitive ecosystem with a preponderance of meat-eaters over herbivores.

The Middle to Late Wordian - Tapinocephalid and Anteosaur empire



The basal dicynodont *Eodicynodon*. This was the first appearance of a very successful type of animal that would dominate terrestrial ecosystems right up until the end of the Cranian (late Triassic)

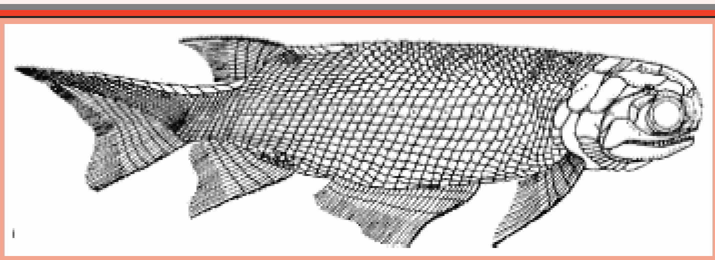
For a long time, the South African Beaufort Series that traces the evolution of life from the Middle Permain to the Middle Triassic was thought to only begin with the *Tapinocephalus* zone. In 1995 a distinct, more archaic fauna was described from the lower Abrahamskraal Formation (Rubidge 1995). This has been called the *Eodicynodon* Assemblage Zone. Although considered older than the Russian Zone I and II assemblages (Lucas 2004; Rubidge 1995, Lucas 2006), it would seem to me to be more advanced than the Russian Ocher and Chinese Dashankou faunas, and lence later, not earlier, as shown by the presence of primitive theriodonts (gorgonopsian,

artwork by Arthur Weasley - Wikipedia

the therocephalians) and tapinophalids (specialised herbivorous dinocephalians) and the early dicynodont, the eponymous *Eodicynodon* itself. On the basis of its very primitive elements, Liu et al 2009 considers the Dashankou fauna Roadian, and hence older than the Eodicynodon, fauna.

A syodont anteosaur. These medium-sized unspecialised carnivores may have had a ubiquitious distribution.
artwork by Dmitry Bogdanov - Wikipedia

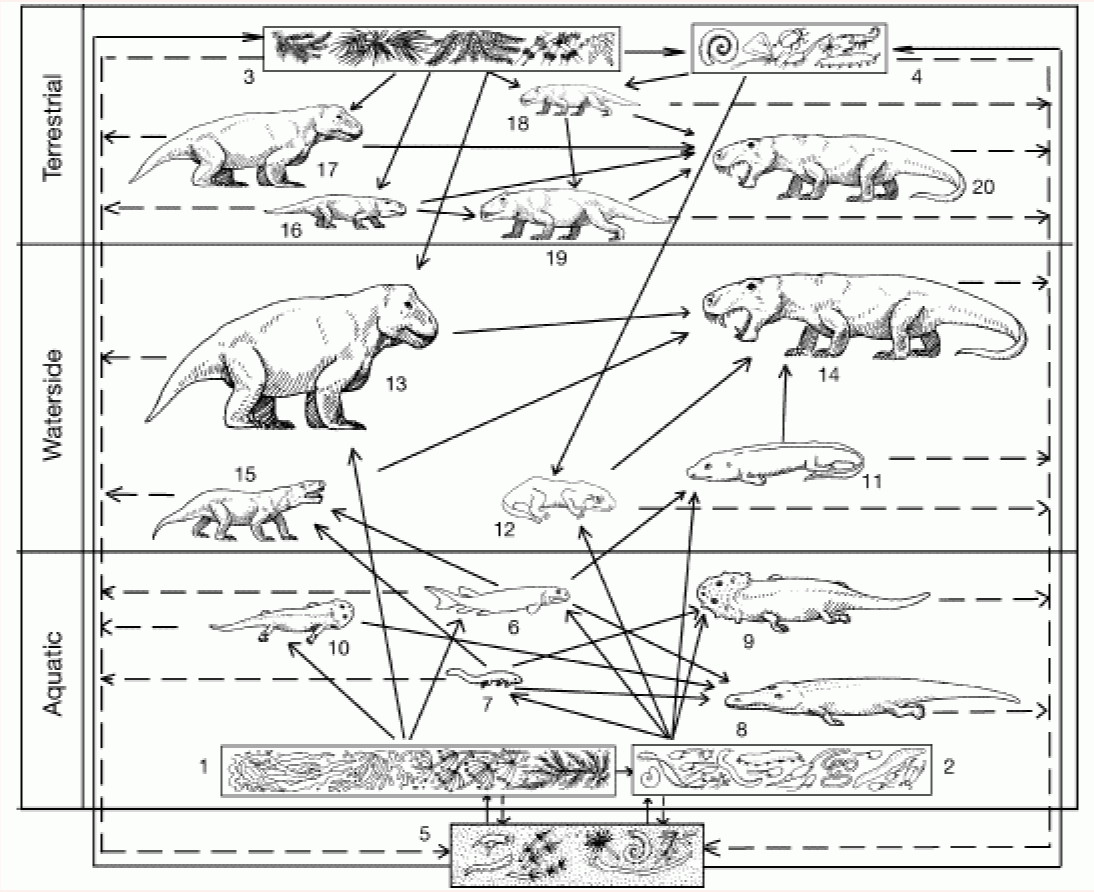
This diverse fauna includes a large number of herbivores, including small primitive anomodonts (*Eodicynodon*, *Otsheria* and *Patronomodon*) and the huge (3 meters long) dinocephalians (*Tapinocaninus*). Carrnivores include the medium-sized anteosaurid dinocephalian *Australosyodon* (Rubidge 2004), which is very similar to Russian forms like *Notosyodon* and *Syodon*) and the more advanced and mammal-like *Glanosuchus* and *Alopecodon*; the eraliest known therocephalians. Lucas makes the *Eodicynodon* Assemblage Zone the characteristic assemblage for the Kapteinskraalian Land Vertebrate Faunachron (Lucas 2006)



***Varialepis bergi*, length 34 cm;, an actinopterygian from the Bolshekinelskaya Svita of the South Cis-Urals. Order Elonichthyiformes, Family Varialepididae.**
From Tverdokhlebov et al 2005 p.47

In Russia the Bashkirian (Lower Zone II) (Olson, 1962) and Bolshekinelskaya Svita (Formation) (Tverdokhlebov et al 2005) would seem to be equivalent. The Bolshekinelskaya Formation includes Xenacanthiforme sharks, diverse Actinopterygii (*right*), Melosaurid temnospondyls (*Konzhukovia vetusta* and *Tryphosuchus* sp), the Lanthanosuchid *Chalcosaurus lukjanovae*, and several types of Therapsida, including indeterminate Phthinosuchidae (although this is a poorly defined group in any case), carnivorous (identified only as *Titanophoneus* sp.) and herbivorous (*Deuterosaurus jubilaei*) Anteosaurids , Tapinocephalids identified as *Ulemosaurus* cf. *gigas*., but I wouldn't be superpised if they are more equivalent to the South African *Tapinocaninus*, the herbivorous Dinocephalian *Rhopalodon*(?) sp., and the Venyukoviid anomodont *Ulemica efremovi* (Tverdokhlebov et al 2005 p.45). The overlying (and hence more recent) Amanakskaya Svita is better represented, including Melosaurids, Archegosaurids, Seymouriamorphs, Lanthanosuchidae, Biarmosuchidae, Anteosaurids (including Syodon and the superpreditor *Titanophoneus adamanteus*), Tapinocephalids, Microuraniidae (*Microurania minima*), Venyukoviidae, and Pristerognathidae. *Syodon* and *Porosteognathus*? indicate a close connection with the *Eodicynodon* Assemblage Zone fauna. Differences may be due also to climatic and geograpohic factors, Russia at the tiome was very close to the equator, whereas the Karoo was in the high latitudes. Theriodonts and Dicynodonts may thus have begun as cold adapted forms, whereas the dinocephalians were probably tropical war,-weather animals, hence their greater diversity in the Cisurals.

The following diagram shows a suggested ecology of this time.

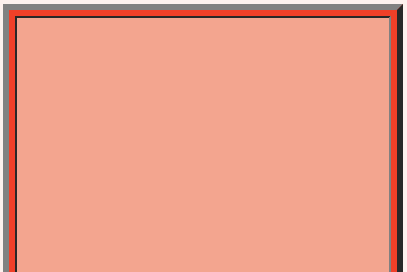


Reconstructed food web for the terrestrial and aquatic components of the Urzhumian Community (Bolshekinelskaya and Amanakskaya svitas; Early Tatarian) of the SE of European Russia. Lines with arrows indicate the movement of energy through the community: solid lines show feeding pathways, and dashed lines show decay pathways. Aquatic components: (1) aquatic plants, (2) invertebrates, taxa whose role in terrestrial food chains is insignificant. Amphibious components: taxa which play a significant role in both aquatic and terrestrial food chains. Terrestrial components: (3) plants, (4) invertebrates, taxa which play main role in terrestrial food chains; (5) plant and animal detritus; (6) palaeonisciform, (7) larva of amphibians, (8) batrachomorphs: *Konzhukovia, Uralosuchus, Tryphosuchus, Platyoposaurus*, (9) *Chalcosaurus*, (10) leptorophids, (11) *Enosuchus*, (12) nycteroleterids, (13) dinocephalians *Ulemosaurus Deuterosaurus*., (14) *Titanophoneus*,, (15) *Syodon*, (16) Ulemica, (17) herbivorous *Rhopalodon* and *Biarmosuchoides*, (18) *Microurania*, (19) *Porosteognathus*, (20) phthinosuchids.

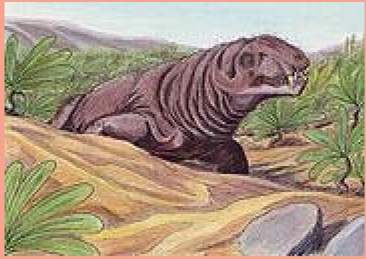
image © from V.P. Tverdokhlebov *et. al.* (2005) Upper Permian vertebrates and their sedimentological context in the South Urals, Russia

As explained by Tverdokhlebov *et. al.*:

Much of the Kazanian ecosystem structure survived in the early Tatarian vertebrate faunas, the Urzhumian Community, seen in the Bolshekinelskaya and Amanakskaya svitas). In the ponds and rivers, palaeonisciform, and other, fishesfed on aquatic plants and insects. But a wider community of batrachomorph amphibians, such as *Konzhukovia*, *Uralosuchus*, and *Tryphosuchus*, and reptiliomorphs, such as *Chalcosaurus* and unnamed leptorophids, preyed on the fishes, as well as on tetrapod larvae. On land, nycteroleterids and the batrachomorph Enosuchus also fed on aquatic plants and animals. The therapsid component of the fauna is much more extensive, with mediumsized herbivores such as the venyukoviid anomodont *Ulemica* and the dinocephalians *Rhopalodon* and *Microurania* feeding on waterside and terrestrial plants. These were preyed on by the anteosaurid dinocephalian *Syodon*, the therocephalian *Porosteognathus* and unnamed phthinosuchids. The largest herbivores are the dinocephalians *Ulemosaurus* and *Deuterosaurus*, and these were preyed on by the large anteosaurid dinocephalian *Titanophoneus*,, a new top-level predator.



Perhaps also of this same age, or a little older (Roadian) are the Various types of stem tetrapods and reptiles are well-represented in the Belebei-Mezen Cotylosaur Complex (the definition of "Cotylosaur" has since changed somewhat), which is difficult to correlate stratigraphically because of a paucity of shared faunas. It can be assumed however that numerous small lizard-like insectivorous Anapsida were an important part of the ecosystem. The Pelycosaurs may (or may not) be represented by a single femur, *Phreatosaurus aenigmaticum* Efremov (1954), which Efremov assigns to the family



The omnivorous short-faced anteosaur *Deuterosaurus*. This was a characteristic animal of low latitude northern Pangea (Cisurals). This was a medium-sized animal, the skull is 23 cm long, so the overall length may have been around one and a half meters.
artwork by Dmitry Bogdanov - Wikipedia

Phraetosuchidae (probably an artificial group based on scrappy postcrania), but Olson, 1962 argues is really a member of the Family Caseidae, a group that is well represented in the Kungurian age.

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The Capitanian Age

The Capitanian Age of the Guadalupian Epoch: 260 to 266 million years ago

Introduction

The Capitanian began on a high note, with a world rich in life in both the sea (with widespread tropical reefs) and on land (with a diverse dinocephalian therapsid fauna). As the age progressed, the climate becaome colder, the sea level fell, and then finally massive volcanos created a sudden greenhouse effect and anoxia. The result was a mass extinction that resulted in a turn-over life on both land and sea.

Stratigraphy

Harried editor's note: As with the Wordian, I am going to be lazy and quote direct from Wikipedia, as this material seems to be well written, and this gives me more time for other pages MAK091116

The Capitanian stage was introduced by George Burr Richardson in 1904. The name comes from the Capitan Reef in the Guadalupe Mountains (Texas, USA). It was first used as a stratigraphic subdivision 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

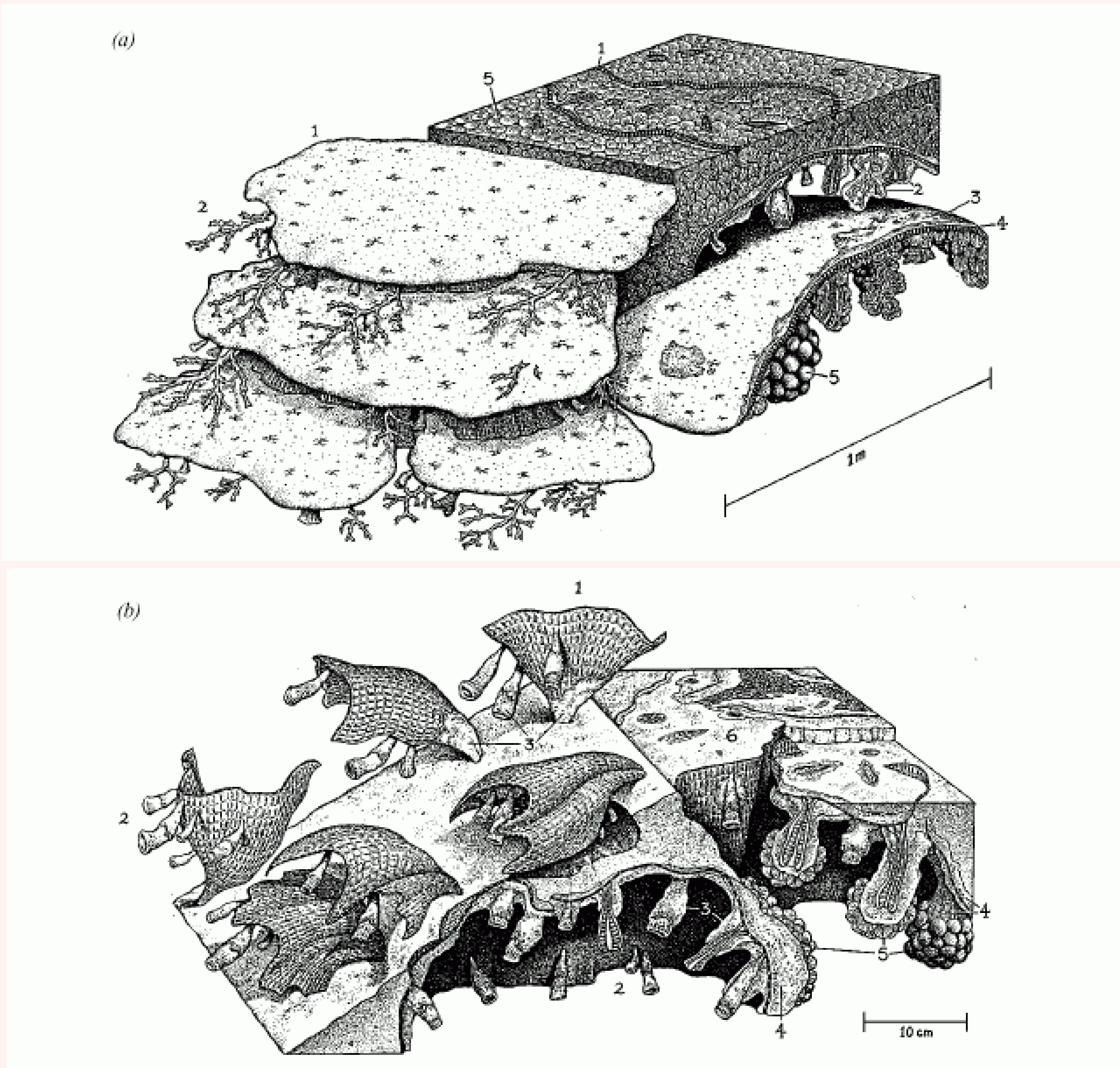
2001.

The base of the Capitanian stage is defined as the place in the stratigraphic record where fossils of conodont species *Jinogondolella postserrata* first appear. The top of the Capitanian is defined by the appearance of the the conodont *Clarkina postbitteri postbitteri* It includes the ammonite zone *Timorites*, the conodont biozones *Clarkina postbitteri hongshuiensis, Jinogondolella altudaensis, Jinogondolella postserrata* and the fusulinid biozones: Rausserella and Afganella schenki

References: Glenister & Furnish 1961, Glenister et al 1991, Gradstein et al 2004

Marine Life

Reefs



Reconstruction of a Permian reef: the Capitan Reef, Texas and New Mexico (260 Ma) (from Wood RA. 1998 *Reef Evolution.* Oxford: Oxford Univ. Press.).
(*a*) Platy sponge community. 1. *Gigantospongia discoforma* (platy sponge); 2: solitary and branching sphinctozoan sponges; 3: *Archaeolithoporella* (encrusting ?algae); 4: microbial micrite; 5: cement botryoids.
(*b*) Frondose bryozoan-sponge community. 1. Frondose bryozoans (*Polypora sp.; Goniopora sp.*) 2: solitary sphinctozoan sponges; 3:*Archaeolithoporella* (encrusting ?algae); 4: microbial micrite; 5: cement botryoids; 6: sediment (grainstone-packstone).

image and caption © xxxxfrom Rachel Wood - The Ecological Evolution of Reefs

Terrestrial life - Tetrapods

The Capitanian marked the greatest diversity of the Dinocephalian megafauna, and also, in teh middle of teh epoch, its extinction.

According to Bakker, a high large herbivore diversity is indicated by the floodplain facies of the *Tapinocephalus* Zone of the South African Karroo, where five families or subfamilies and six genera are rather widespread and common; biomass D is about four. This high level of large herbivore diversity was to be also achieved by the radiations of the succeeding therapsid, therapsid-archosaur, dinosaur, and mammal empires. Each dynasty seems to have ended with a mass extinction, and, following a low diversity period, a new ecological community evolves.

As in the preceeding Wordian age, most of the big herbivores and carnivores were Dinocephalians. These may have attained weights of a tonne or more. The only other animals of comparable size were the Pareiasaurs, armoured herbivores specialised for a semi-aquatic existence, and possessing a truely bizarre cranial ornamentation. Accompanying these strange giants were a variety of smaller therapsids, lizard-like anapsids, and rare synapsids and diapsids.

The giant herbivorous dinocephalian *Ulemosaurus svijagensis*, length 3 meters or more. Late Wordian to Early Capitanian of low latitude northern Pangea. The dinocephalians were the most diverse and successful of the Mid Permian megafauna, f;ourishing for some ten million years, before falling victim to the end-Guadalupian mass extinction
- image from Dinocephalian World (no longer online)

In the equatorial regions (according to Permian geography - the continents have drifted since then!), the Russian Isheevo Megafauna is probably contemporary with the Early Tapinocephalus Zone (*sensu* Boonstra), which is the period of greatest Dinocephalian diversity. Here there are two important genera, *Doliosauriscus* and *Ulemosaurus*, that appear to be synonymous with (although distinct at the species-level) the Karroo *Anteosaurus* and *Moschops* respectively (although it has also been suggestsed that *Ulemosaurus* may be more basal than *Moschops*). The more primitive characteristics of the northern fauna, and the preponderance of carnivores over herbivores, may be due to the more equitable climate and to it being more closely tied to water. Curiously, Pareiasaurs are absent from Isheevo; however they appear in the following, Kotelnich assemblage (perhaps equivalent to the *Pristerognathus* zone), where the epynomous *Deltavjatia* lends its name to the *Deltavjatia vjatkensis* Assemblage Zone

Thus at this time one finds both a cool temperate south Gondwanan and a tropical northern Pangean (what is now Russia) dinocephalian-dominated fauna, with a number of very similar large dinocephalians and other animals. These clearly constitute part of the same extended biogeographical region, the fossil remains of which have been found in the vicinity of the Ural mountains. The stratigraphic level is variously referred to as "Zone II" (by Efremov in 1937, and following him by other writers e.g. E.H. Colbert *The Age of Reptiles*), the Isheevo Deinocephalian Complex (by Tchudinov in the 60s and 70s), and more recently the *Ulemosaurus svijagensis* zone, and is almost unanimously considered to be contemporary with the Tapinocephalus Zone. So worldwide we see a period of great Dinocephalian diversity.

Indications of the common fauna is indicated by the fact that there are two important genera, the apex preditor *Doliosauriscus* and the megaherbivore *Ulemosaurus*, that appear to be congeneric with (although distinct at the species-level) the Karroo *Anteosaurus* and *Moschops* respectively, although it has also been suggested that *Ulemosaurus* may be more basal than *Moschops*, more like Eodicynodon zone genus *Tapinocaninus* perhaps, or maybe transitional between the two. Unfortunately, large impressive fossil tetrapod taxa are seriously oversplit by zealous paleontpologists, each of which prefer their own generic name, so that often a genus only has one species (compare this with modern day mammals where a single genus may have a number of species). This obscures the similarities between them. *Titanophoneus* is another important giant predator, very similar to, but perhaps a little specialised than, *Doliosauriscus* and *Anteosaurus*. When full grown these animals had skulls upto 80 cm long, and overall lengths of 3 to 5 meters. *Porosteognathus* was smaller than these animals, but also evolutionarily more advanced, a medium-sized preditor that may be similar to the South African *Pristerognathus*. The small brithopidid dinocephalian *Syodon* is very similar to the Eodicynodon zone genus *Australosyodon*

Global Cooling

Carbon isotopes in marine limestone from of Capitanian age show an increase in d13C values. The change in carbon isotopes in the sea water indicate severe cooling. This icehouse effect 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. The tropical coral reefs died first, and then fauna from the mid latitudes moved towards the equator.

The cooler temperatures would have also caused massive ice sheets to accumulate, thus causing a fall in sea level. That means less near shore environments and further extinction.

References: Isozakia 2007, link

End-Gaudalupian Extinction

The end of the Capitanian was marked by a marine extinction event distinct from the end Permian mass extinction (Stanley & Yang 1994. There was also a terrestrial mass extinction during the mid Permian (which killed off the dinocephalians and many other large animals), which raises the question of whether they were part of the same event. Lucas 2009a and 2009b considers the terrestrial extinction preceded the Illawara reversal which would make it early to mid Wordian, much earlier than the end-Guadalupian marine extinction. However, Minikh et al 2008 argue that the Kiaman-Illawarra boundary occurs within the Urzhumian stage (dinocephalian fauna), and that the upper Urzhumian can be matched with the upper Capitanian, which indicates that dinocephalians continued throughout at least most of the Capitanian. It still may be the case that the terrestrial and marine extinctions were not necessarily synchronous.

In this current review, I have assumes that dinocephalian extinction event occurred duriong the late or end Capitanian.

The end Capitanian event involved mass extinction, ocean onoxia, sharp isotopic excursions (of Carbon and Strontium, related to vulcanism), sea-level drop, and plume-related volcanism. The remnants of those huge volcanoes can be seen today in India, China and Norway. Retallack 2005 Retallack et al 2006 ties the terrestrial extinction to a greenhouse crisis that he also relates to the end-Guadalupian marine extinction. This is the opposite of Isozakia 2007 and 2009 who refers tpo global cooling. But it may be that first there was a cooling, then a suffered heating, as the temperature fluctuated wildly, further stressing Late Permain environments.

The low diversity Pristerognathus faunal zone would therefore be early Wuchapingian, or at most late Capitanian or early Wuchapingian boundary.

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The Lopingian Epoch

The Lopingian Epoch of the Permian Period: 260 to 251 million years ago

Introduction

A juvenile *Scutosaurus* pareiasaur falls victim to the gorgonopsid superpreditor *Inostrancevia* . An adult Scutosaur wartches helplessly nearby.
Late Wuchiapingian to Changhsingian age - Urals region of Russia (Low latitude northern Pangea)
image by Dmitry Bogdanov - Wikipedia

The Lopingian stage constitutes the later subdivision of the Late Permian, which follows immediately from the Guadalupian. It is divided into two unequal epochs, the long Wuchiapingian and the short (only about 2 million years) Changhsingian. The Lopingian, Wuchiapingian and Changhsingian stages are named after Chinese localities where fossils and rock strata of this age occur in a good and mostly unbroken series. As part of the current revision of Permian stratigraphy, "Lopingian" and "Guadalupian" have replaced earlier terms like "Upper Permian", "Zechstein", "Tartarian", and "Dzulfinan" in international usage (although the latter three terms are still applied locally).

The Lopingian sub-period lasted almost as long as the preceding Guadalupian, approximately 9 million years. This was a period of great stress for eco-systems, as the climate continued to dry and the single large continent of Pangea did not provide much room for diversity (the more isolated islands and continents, the more species). Throughout the Permian period the numbers of invertebrate species tends to decrease. At the end of the Lopingian there is a period of enormous vulcanism (in what is now Siberia), which further stresses ecosystems by introducing acid rain into the atmosphere. Finally, at the end of the period there appears to have been either a tremendous period of vulcanism or an extraterrestrial impact (possibly a comet or giant asteroid similar to the one that killed the dinosaurs), as 95% of species of living beings suddenly die out within a very short period. The Paleozoic era comes to an end and new species inherit the globe.

In the dry late Permian environment many types of synapsids and reptiles flourished. The giant dinocephalians of the Middle Permian had vanished, but the big pareiasaurs were still around, sharing the world with various types of more advanced therapists that had likewise survived, including the large gorgonopsians like *Inostrancevia*, shown above, the small to medium-sized therocephalians, the newly evolved and very mammal-like condones like *Procynosuchus*, and an astonishing diversity of herbivorous dicynodonts (The large *Aulacephalodon* is shown here, but other types were small and rodent-like). A great small many insectivorous lizard-like diapsid reptiles, like *Paliguana*, inhabited the landscape, most of which, curiously, had hind-legs much longer than their forelimbs (clearly an adaptation to bipedal locomotion, like the frill-necked lizard of Australia today). Finally, amphibians, although reduced in numbers, were nevertheless present and included animals of large size. The aquatic rhinesuchid temnospondyls were clearly the successors of the Middle Permian melosaurs and early Permian eryopids, both of which they resembled closely in size, appearance, and no doubt habits as well.

As the biggest animals around, the fearsome looking, but herbivorous, pareiasaurs were nevertheless not free of danger. They had outlasted the carnivorous anteosaurian dinocephalians, but now the previously small and insignificant gorgonopsians had evolved to large forms (up to the size of a modern lion or bear) to take their place. These animals, the equivalent of the sabre-toothed cat of the Cenozoic era, used their enormous canines to bring down the ox-sized pareiasaurs. Gorgonopsians and pareiasaurs may even have formed a "co-adaptive pair"; (like the *Smilodon* - mammoth 'relationship' of the Pleistocene) the gorgonopsians evolved in larger, more robust and larger fanged forms (for example *Dinogorgon* and *Inostrancevia*) whereas their pareiasaur prey become more armoured (for example *Pareiasaurus* and *Scutosaurus*). Both groups became simultaneously extinct and the end of the Permian.

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The Changhsingian Age

The Changhsingian Age of the Lopingian Epoch: 251 to 254 million years ago

Also spelt Changxingian.

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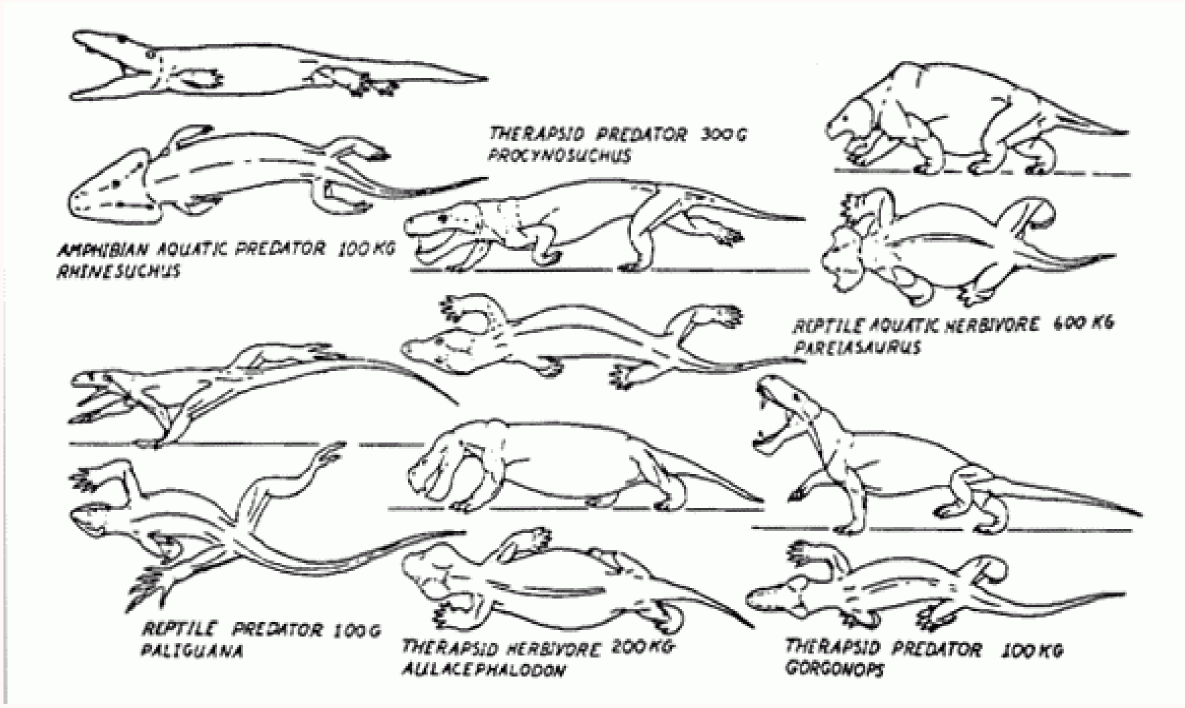
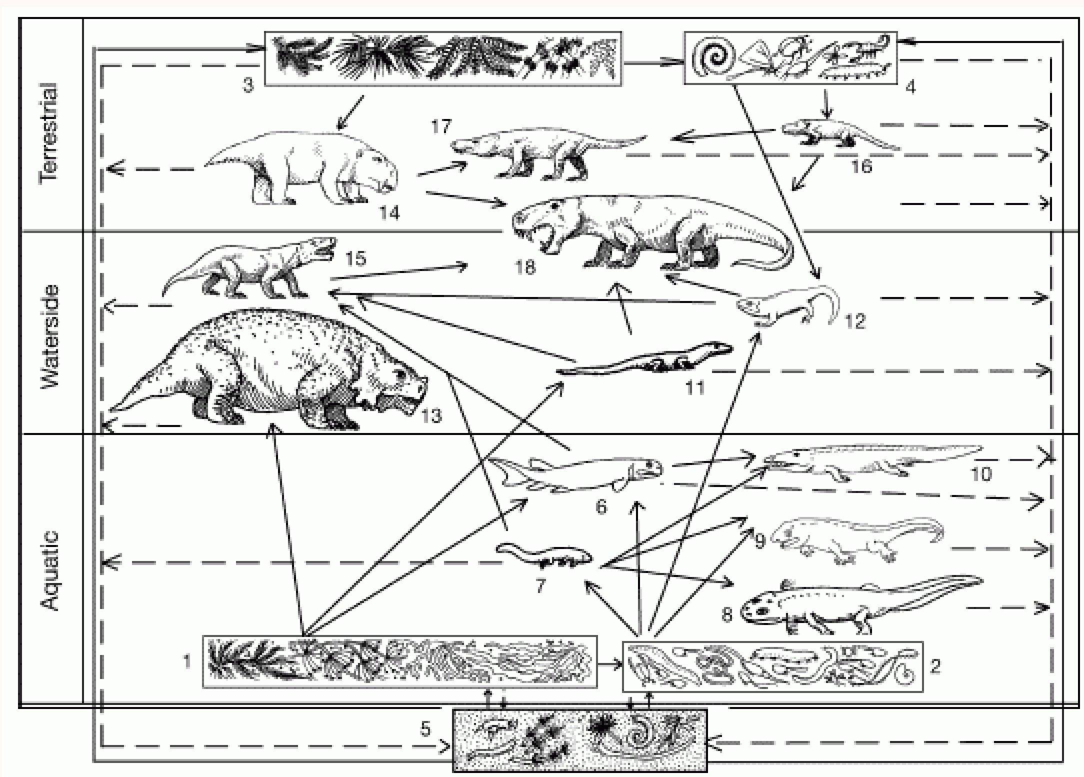


Representative animals from the Daptocephalus/Dicynodon assemblage zone of Gondwana (South Africa) included here is a are large temnospondyl of the rhinesuchid family, a small advanced procynosuchid Therapsid, an ox-sided herbivorous Pareiasaur, a small diapsid lizard (*Paliguana*), a large herbivorous Dicynodont, and a Gorgonopsian therapsid, which was very much the top predator of this environment

Illustration by Dr Bob Bakker



Reconstructed food web for the terrestrial and aquatic components of the Vyatkian Community (Kutulukskaya and Kulchumovskaya svitas; Late Tatarian) of the SE of European Russia. Lines with arrows indicate the movement of energy through the community: solid lines show feeding pathways, and dashed lines show decay pathways. Aquatic components: (1) aquatic plants, (2) invertebrates, taxa whose role in terrestrial food chains is insignificant. Amphibious components: taxa which play a significant role in both aquatic and terrestrial food chains. Terrestrial components: (3) plants, (4) invertebrates, taxa which play a role in terrestrial food chains; (5) plant and animal detritus; (6) palaeonisciform, (7) larva of amphibians, (8) Dvinosaurus, (9) Karpinskiosaurus, (10) chroniosuchids: Chroniosuchus, Jarilinus and Uralerpeton, (11) kotlassiid Microphon, (12) tokosaurids, (13) pareiasaur Scutosaurus, (14) Dicynodon, (15) therocephalians Chthonosaurus and Annatherapsidus, (16) procynosuchid Uralocynodon, (17) therocephalian Scylacosuchus, (18) gorgonopsian Inostrancevia.

image © from V.P. Tverdokhlebov *et. al.* (2005) Upper Permian vertebrates and their sedimentological context in the South Urals, Russia

As explained by Tverdokhlebov *et. al.*:

> The latest Tatarian Vyatkian Community (Kutulukskaya and Kulchumovskaya svitas; Fig. 22) continued at a similar level of complexity. The aquatic component is comparable to previous examples; the fishes and larval tetrapods were fed on by the reptiliomorphs Microphon, Dvinosaurus, Karpinskiosaurus, and the chroniosuchids Chroniosuchus, Jarilinus, and Uralerpeton. Small herbivores on land include unnamed tokosaurids. Larger herbivores are the dicynodont Dicynodon and the pareiasaur Scutosaurus. Terrestrial carnivores include the reptiliomorph Chthonosaurus, the therocephalians Annatherapsidus and Scylacosuchus, and the procynosuchid cynodont Uralocynodon. The top carnivore, capable of preying on the largest of contemporary herbivores was the gorgonopsian Inostrancevia. Immediately following the end-Permian environmental catastrophe, earliest Triassic faunas consisted only of a few fish taxa and small, aquatic tetrapods, in low-diversity, low-abundance assemblages.

During this time, two new large predator families appear - the proterosuchid thecodonts (archosauriforms) and the therapsid moschorhinids (therocephalians). The latter make up about half the predator specimens in the latest *Daptocephalus* Zone faunas (late Wuchiapingian-early Changhsingian).

End of an Era

The Changhsingian age began with the continuation of the successful Therapsid communities of the preceeding Wuchiapingian age. As time progressed, massive vulcanism in what is now Siberia (the Siberian Traps), perhaps in association with other factors, resulted in dramatic greenhouse conditions, with increasing atmospheric carbon dioxide and methane, and decreasing amounts of oxygen Retallack 2005 Retallack et al 2006. The increasingly harsh conditions began to take their toll on the biota, culminating in the worst mass extinction in the histrory of advanced life on Earth.

Unlike the End-Cretaceous Extinction, in which dinosaurs and other animals remained common until the obvious asteroid impact, there seems to have been a gradual decrease in biodoversity, at least as far as terrestrial animals went, culminating in a sudden dramatic extinction that ravaged what was left of the already impoverished fauna Ward et al. 2005. Only those animls that were already pre-adapted for low oxygen conditions, such as burrowers like Lystrosaurus, were able to make it through.Retallack et al 2003

A Late Changhsingian Bestiary

(*Left*) Representative animals (drawn to scale) from the latest Permian of Gondwana (These fossil animals are from near Bethulie, Orange Free State, Southern Africa). Scale bar 10 cm.
Featured here are *Rubigea majora*, a 3 meter long Gorgonopsian therapsid and superpreditor of its environment, *Theriognathus microps*, a tiny but advanced Therocephalian (Family: Whaitsiidae), and - , making up the herbivore contingent. - an abundant small and common large Dicynodont

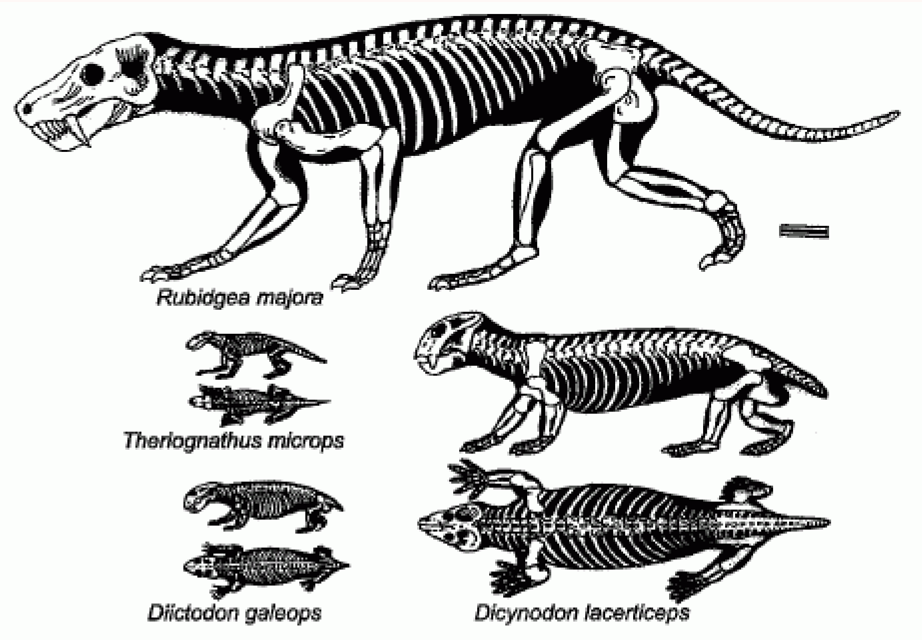


Illustration from Retallack, Smith, and Ward, "Vertebrate extinction across Permian-Triassic boundary in Karoo Basin, South Africa", *Geological Society of America Bulletin*, 115(9): p.1133

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The Wuchiapingian Age

The Wuchiapingian Age of the Lopingian Epoch: 260 to 254 million years ago

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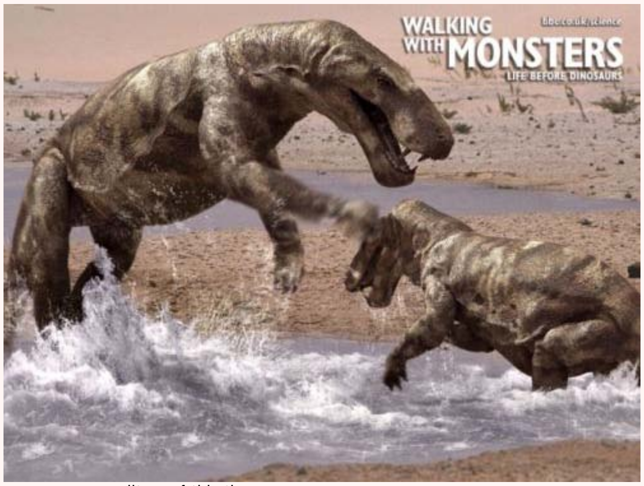
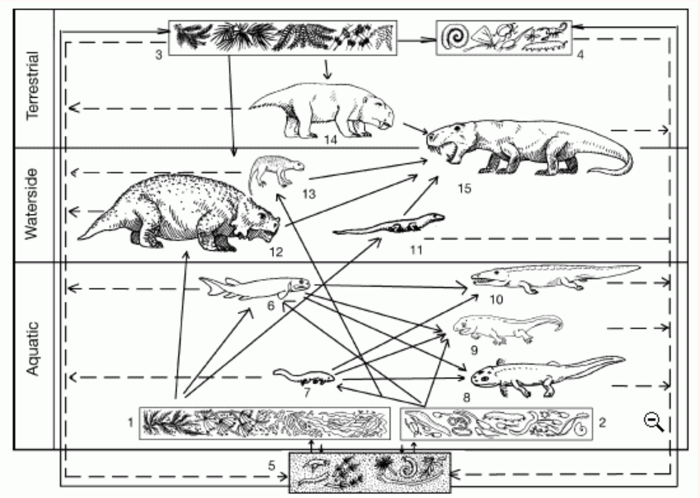
Gorgonopsid and Dicynodont Empire



Gorgonopsid mammal-like reptiles were common preditors of this time
image © BBC, from Walking With Monsters gallery

In the earliest known post-Tapinocephalus Zone fauna of southern Africa (where the fossil record for late Permian tetrapods is most complete), new groups of big herbivores - the beaked and toothless dicynodonts - appear. These were clearly descended from those genera which were common but restricted to small body sizes during the *Tapinocephalus* Zone. Initial diversity of large dicynodonts may have been low, with one genus, *Endothiodon*, dominating some early local faunas. But within a relatively short period more big dicynodont families were added, and at the acme of Endothiodon-Dicynodont Empire (faunal stages 4 and 5 in Fig. 2) four fully terrestrial big families are common, plus pareiasaurs, the big aquatic herbivores that were the only survivors over 15 kg from the Dinocephalian empire. Biomass D rises during this period, and appears to reach maximum in the Capitanian age, some time before end of the Endothiodon-Dicynodont Empire. In the latest fauna (late *Daptocephalus* zone, Wuchiapingian age, stage 5 in Fig. 2) one genus, *Daptocephalus*, increases in relative frequency at the expense of the other big herbivores; thus local diversity, measured by D, decreases although all of the genera and families seem to be present right through to the end of the zone.

Only one family dominates the top predator role, the gorgonopsians, making up nearly all the specimens known (C in Fig. 2). Large gorgonopsids were present but very rare in the preceding *Tapinocephalus* Zone (Dinocephalian empire). The medium-size hipposaurids, also present in the *Tapinocephalus* Zone, were wide-spread but uncommon.



Reconstructed food web for the terrestrial and aquatic components of the Severodvinian Community (Malokinelskaya and Vyasovskaya svitas; Late Tatarian) of the SE of European Russia. Lines with arrows indicate the movement of energy through the community: solid lines show feeding pathways, and dashed lines show decay pathways. Aquatic components: (1) aquatic plants, (2) invertebrates, taxa whose role in terrestrial food chains is insignificant. Amphibious components: taxa which play a significant role in both aquatic and terrestrial food chains. Terrestrial components: (3) plants, (4) invertebrates, taxa which play a role in terrestrial food chains; (5) plant and animal detritus; (6) palaeonisciform, (7) larva of amphibians, (8) Dvinosaurus, (9) Karpinskiosaurus, (10) Chroniosaurus, (11) kotlassiid Microphon, (12) pareiasaur Proelginia, (13) Suminia, (14) dicynodonts, (15) gorgonopsians.

image © from V.P. Tverdokhlebov *et. al.* (2005) Upper Permian vertebrates and their sedimentological context in the South Urals, Russia

As explained by Tverdokhlebov *et. al.*:

By the late Tatarian, the ecosystem had further matured. Vertebrate faunas from the Malokinelskaya and Vyazovskaya svitas, the Severodvinian Community (Fig. 21), show the usual palaeonisciform, and other, fishes and tetrapod larvae feeding on aquatic plants and insects, and they in turn being preyed on by the batrachomorph Dvinosaurus and the reptiliomorphs Microphon, Karpinskiosaurus and Chroniosaurus. Terrestrial herbivores include the basal anomodont *Suminia*, medium-sized dicynodonts, and the giant pareiasaur *Proelginia*. The top predators were gorgonopsians, which could presumably have killed a large, thick-skinned pareiasaur with their sabre teeth.

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