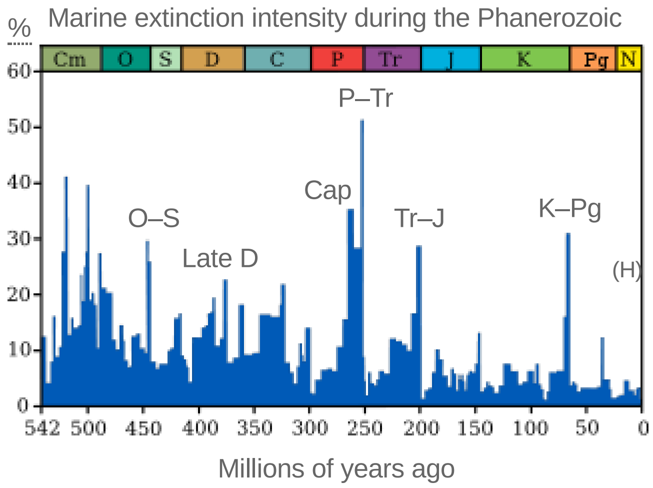
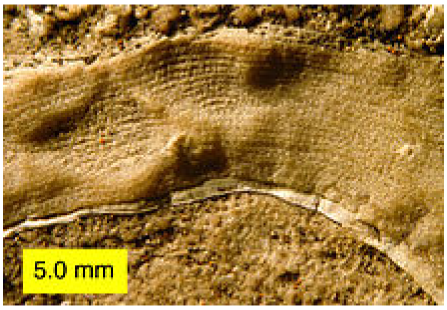
Late Devonian extinction

The **Late Devonian extinction** was one of five major extinction events in the history of life on Earth. A major extinction, the Kellwasser event, occurred at the boundary that marks the beginning of the last phase of the Devonian period, the Famennian faunal stage (the Frasnian–Famennian boundary), about 376–360 million years ago.[1][2] Overall, 19% of all families and 50% of all genera became extinct.[3] A second, distinct mass extinction, the Hangenberg event, closed the Devonian period.[4]



Comparison of the three episodes of extinction in the Late Devonian (Late D) to other mass extinction events in Earth's history. Plotted is the extinction intensity, calculated from marine genera.

Although it is clear that there was a massive loss of biodiversity in the Late Devonian, the timespan of this event is uncertain, with estimates ranging from 500,000 to 25 million years, extending from the mid-Givetian to the end-Famennian.[5] Nor is it clear whether there were two sharp mass extinctions or a series of smaller extinctions, though the latest research suggests multiple causes and a series of distinct extinction pulses during an interval of some three million years.[6] Some consider the extinction to be as many as seven distinct events, spread over about 25 million years, with notable extinctions at the ends of the Givetian, Frasnian, and Famennian stages.[7]

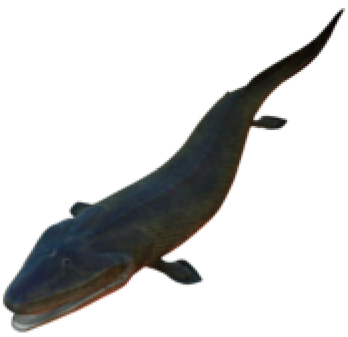


Side view of a stromatoporoid showing laminae and pillars; Columbus Limestone (Devonian) of Ohio

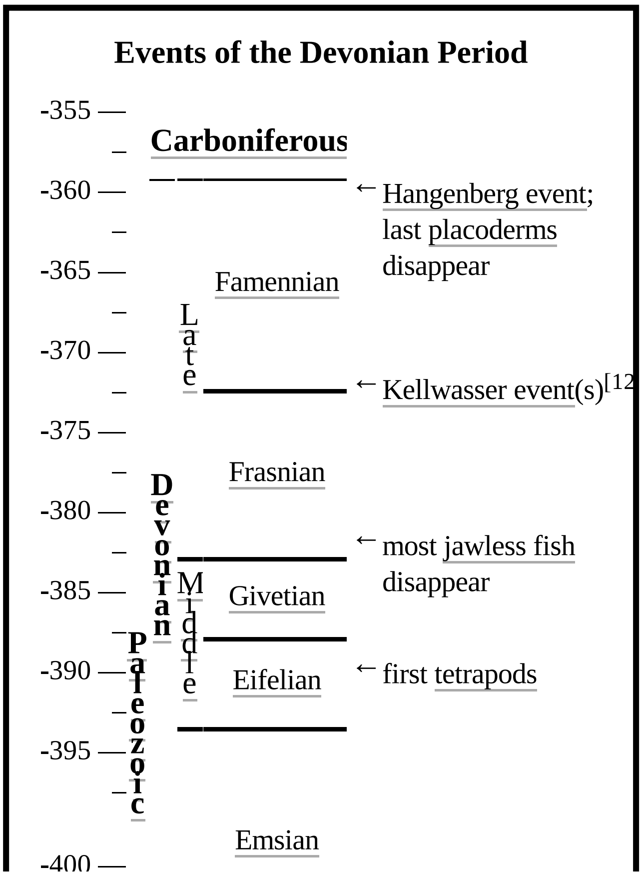
By the Late Devonian, the land had been colonized by plants and insects. In the oceans were massive reefs built by corals and stromatoporoids. Euramerica and Gondwana were beginning to converge into what would become Pangaea. The extinction seems to have only affected marine life. Hard-hit groups include brachiopods, trilobites, and reef-building organisms; the reef-building organisms almost completely disappeared. The causes of these extinctions are unclear. Leading hypotheses include changes in sea level and ocean anoxia, possibly triggered by global cooling or oceanic volcanism. The impact of a comet or another extraterrestrial body has also been suggested,[8] such as the Siljan Ring event in Sweden. Some statistical analysis suggests that the decrease in diversity was caused more by a decrease in speciation than by an increase in extinctions.[9][5] This might have been caused by invasions of cosmopolitan species, rather than by any single event.[5] Surprisingly, jawed vertebrates seem to have been unaffected by the loss of reefs or other aspects of the Kellwasser event, while agnathans were in decline long before the end of the Frasnian.[10]

Contents

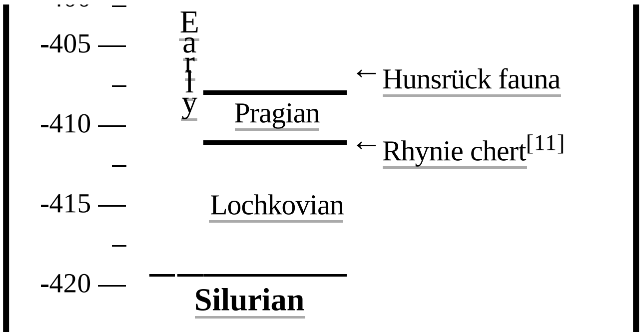
Late Devonian world



A restored *Tiktaalik*



During the Late Devonian, the continents were arranged differently from today, with a supercontinent, Gondwana, covering much of the Southern Hemisphere. The continent of Siberia occupied the Northern Hemisphere, while an equatorial continent, Laurussia (formed by the collision of Baltica and Laurentia), was drifting towards Gondwana, closing the Iapetus Ocean. The Caledonian mountains were also growing across what is now the Scottish Highlands and Scandinavia, while the Appalachians rose over America.[13]



Key events of the Devonian Period.
Axis scale: millions of years ago.

The biota was also very different. Plants, which had been on land in forms similar to mosses, liverworts, and lichens since the Ordovician, had just developed roots, seeds, and water transport systems that allowed them to survive away from places that were constantly wet—and so grew huge forests on the highlands. Several clades had developed a shrubby or tree-like habitat by the Late Givetian, including the cladoxylalean ferns, lepidosigillarioid lycopsids, and aneurophyte and archaeopterid progymnosperms.[14] Fish were also undergoing a huge radiation, and the first tetrapods, such as *Tiktaalik*, were beginning to evolve leg-like structures.

Duration and timing

Extinction rates appear to have been higher than the background rate, for an extended interval covering the last 20–25 million years of the Devonian. During this time, about eight to ten distinct events can be seen, of which two stand out as particularly severe.[15] The Kellwasser event was preceded by a longer period of prolonged biodiversity loss.[16] The fossil record of the first 15 million years of the Carboniferous period which followed is largely void of terrestrial animal fossils, likely related to losses during the end-Devonian Hangenberg event. This period is known as Romer's gap.[10][17]

The Kellwasser event

The Kellwasser event, named for its *locus typicus*, the Kellwassertal in Lower Saxony, Germany, is the term given to the extinction pulse that occurred near the Frasnian–Famennian boundary. Most references to the "Late Devonian extinction" are in fact referring to the Kellwasser, which was the first event to be detected based on marine invertebrate record. There may in fact have been two closely spaced events here, as shown by the presence of two distinct anoxic shale layers.

The Hangenberg event

The Hangenberg event is found on or just below the Devonian–Carboniferous boundary and marks the last spike in the period of extinction. It is marked by an anoxic black shale layer and an overlying sandstone deposit.[18] Unlike the Kellwasser event, the Hangenberg event affected both marine and terrestrial habitats.[10]

Causes

Since the Kellwasser-related extinctions occurred over such a long time, it is difficult to assign a single cause, and indeed to separate cause from effect. The sedimentary record shows that the late Devonian was a time of environmental change, which directly affected organisms and caused extinction. What caused these changes is somewhat more open to debate.

From the end of the Middle Devonian, into the Late Devonian, several environmental changes can be detected from the sedimentary record. Evidence exists of widespread anoxia in oceanic bottom waters;[14] the rate of carbon burial shot up,[14] and benthic organisms were devastated, especially in the tropics, and especially reef communities.[14] Good evidence has been found for high-frequency sea-level changes around the Frasnian–Famennian Kellwasser event, with one sea level rise associated with the onset of anoxic deposits.[19] The Hangenberg event has been associated with sea-level rise followed swiftly by glaciation-related sea-level fall.[18][20]

Possible triggers are as follows:

Bolide impact

Bolide impacts can be dramatic triggers of mass extinctions. An asteroid impact was proposed as the prime cause of this faunal turnover.[2][21] The impact that created the Siljan Ring either was just before the Kellwasser event or coincided with it.[22] Most impact craters, such as the Kellwasser-aged Alamo and the Hangenberg-aged Woodleigh, cannot generally be dated with sufficient precision to link them to the event; others dated precisely are not contemporaneous with the extinction.[1] Although some minor features of meteoric impact have been observed in places (iridium anomalies and microspherules), these were probably caused by other factors.[23][24]

Plant evolution

During the Devonian, land plants underwent a hugely significant phase of evolution. Their maximum height went from 30 cm at the start of the Devonian, to 30 m[25] at the end of the period. This increase in height was made possible by the evolution of advanced vascular systems, which permitted the growth of complex branching and rooting systems.[14] In conjunction with this, the development of seeds permitted reproduction and dispersal in areas which were not waterlogged, allowing plants to colonise previously inhospitable inland and upland areas.[14] The two factors combined to greatly magnify the role of plants on the global scale. In particular, *Archaeopteris* forests expanded rapidly during the closing stages of the Devonian.

Effect on weathering

These tall trees required deep rooting systems to acquire water and nutrients, and provide anchorage. These systems broke up the upper layers of bedrock and stabilized a deep layer of soil, which would have been of the order of metres thick. In contrast, early Devonian plants bore only rhizoids and rhizomes that could penetrate no more than a few centimeters. The mobilization of a large portion of soil had a huge effect: soil promotes weathering, the chemical breakdown of rocks, releasing ions which are nutrients for plants and algae.[14] The relatively sudden input of nutrients into river water may have caused eutrophication and subsequent anoxia. For example, during an algal bloom, organic material formed at the surface can sink at such a rate that decomposing organisms use up all available oxygen by decaying them, creating anoxic conditions and suffocating bottom-dwelling fish. The fossil reefs of the Frasnian were dominated by stromatolites and (to a lesser degree) corals—organisms which only thrive in low-nutrient conditions. Therefore, the postulated influx of high levels of nutrients may have caused an extinction.[14] Anoxic conditions correlate better with biotic crises than phases of cooling, suggesting anoxia may have played the dominant role in extinction.[23]

Effect on CO_2

The "greening" of the continents occurred during the Devonian. The covering of the planet's continents with massive photosynthesizing land plants in the first forests may have reduced CO_2 levels in the atmosphere. Since CO_2 is a greenhouse gas, reduced levels might have helped produce a chillier climate. Evidence such as glacial deposits in northern Brazil (near the Devonian South Pole) suggests widespread glaciation at the end of the Devonian, as a broad continental mass covered the polar region. A cause of the extinctions may have been an episode of global cooling, following the mild climate of the Devonian period. The Hangenberg event has also been linked to glaciation in the tropics equivalent to that of the Pleistocene ice age.[18]

The weathering of silicate rocks also draws down CO_2 from the atmosphere. This acted together with the burial of organic matter to decrease atmospheric CO_2 concentrations from about 15 to three times present levels. Carbon in the form of plant matter would be produced on prodigious scales, and given the right conditions, could be stored and buried, eventually producing vast coal measures (e.g. in China) which locked the carbon out of the atmosphere and into the lithosphere.[26] This reduction in atmospheric CO_2 would have caused global cooling and resulted in at least one period of late Devonian glaciation (and subsequent sea level fall),[27] probably fluctuating in intensity alongside the 40ka Milankovic cycle. The continued drawdown of organic carbon eventually pulled the Earth out of its Greenhouse Earth state into the Icehouse that continued throughout the Carboniferous and Permian.

Magmatism

Magmatism was suggested as a cause of the Late Devonian extinction in 2002.[28] The end of the Devonian Period had extremely widespread trap magmatism and rifting in the Russian and Siberian platforms, which were situated above the hot mantle plumes and suggested as a cause of the Frasnian / Famennian and end-Devonian extinctions.[29] The Viluy and Pripyat-Dnieper-Donets large igneous provinces were suggested to correlate with the Frasnian / Famennian extinction and the Kola and Timan-Pechora magmatism was suggested to correspond to the end Devonian-Carboniferous extinction.[29]

Most recently, scientists have confirmed a correlation between Viluy traps (in the Vilyuysk region) on the Siberian Craton and the Kellwasser extinction by $^{40}Ar/^{39}Ar$ dating.[30][31]

The Viluy Large igneous province covers most of the present day north-eastern margin of the Siberian Platform. The triple-junction rift system was formed during the Devonian Period; the Viluy rift is the western remaining branch of the system and two other branches form the modern margin of the Siberian Platform. Volcanic rocks are covered with post Late Devonian–Early Carboniferous sediments.[32] Volcanic rocks, dyke belts, and sills that cover more than 320,000 km^2, and a gigantic amount of magmatic material (more than 1 million km^3) formed in the Viluy branch.[32]

Ages show that the two volcanic phase hypotheses are well supported and the weighted mean ages of each volcanic phase are 376.7 ± 3.4 and 364.4 ± 3.4 Ma, or 373.4 ± 2.1 and 363.2 ± 2.0 Ma, which the first volcanic phase is in agreement with the age of 372.2 ± 3.2 Ma proposed for the Kellwasser event. However, the second volcanic phase is slightly older than Hangenberg event which place at 358.9 ± 1.2 Ma.[31] Viluy magmatism may have injected enough CO_2 and SO_2 into the atmosphere to have generated a destabilised greenhouse and ecosystem, causing rapid global cooling, sea-level falls and marine anoxia occur during Kellwasser black shale deposition.[33][34][35][36]

Other suggestions

Other mechanisms put forward to explain the extinctions include tectonic-driven climate change, sea-level change, and oceanic overturning. These have all been discounted because they are unable to explain the duration, selectivity, and periodicity of the extinctions.[23] Another overlooked contributor could be the now extinct Cerberean Caldera which was active in the Late Devonian period and thought to have undergone a super eruption approximately 374 Million years ago.[a][38] Remains of this caldera can be found in the modern day state of Victoria, Australia.

Effects

The extinction events were accompanied by widespread oceanic anoxia; that is, a lack of oxygen, prohibiting decay and allowing the preservation of organic matter. This, combined with the ability of porous reef rocks to hold oil, has led to Devonian rocks being an important source of oil, especially in the USA.

Biological impact

The Kellwasser event and most other Later Devonian pulses primarily affected the marine community, and had a greater effect on shallow warm-water organisms than on cool-water organisms. The most important group to be affected by the Kellwasser event were the reef-builders of the great Devonian reef-systems, including the stromatoporoids, and the rugose and tabulate corals. Reefs of the later Devonian were dominated by sponges and calcifying bacteria, producing structures such as oncolites and stromatolites. The collapse of the reef system was so stark that bigger reef-building by new families of carbonate-secreting organisms, the modern scleractinian or "stony" corals, did not recover until the Mesozoic era.

Further taxa to be starkly affected include the brachiopods, trilobites, ammonites, conodonts, and acritarchs. Both graptolites and cystoids disappeared during this event. The surviving taxa show morphological trends through the event. Trilobites evolved smaller eyes in the run-up to the Kellwasser event, with eye size increasing again afterwards. This suggests vision was less important around the event, perhaps due to increasing water depth or turbidity. The brims of trilobites (i.e. the rims of their heads) also expanded across this period. The brims are thought to have served a respiratory purpose, and the increasing anoxia of waters led to an increase in their brim area in response. The shape of conodonts' feeding apparatus varied with the oxygen isotope ratio, and thus with the sea water temperature; this may relate to them occupying different trophic levels as nutrient input changed.[34] As with most extinction events, specialist taxa occupying small niches were harder hit than generalists.[2]

The Hangenberg event affected both marine and freshwater communities. This mass extinction affected ammonites and trilobites, as well as jawed vertebrates, including tetrapod ancestors.[10][39] The Hangenberg is linked to the extinction of 44% of high-level vertebrate clades, including all placoderms and most sarcopterygians, and the complete turnover of the vertebrate biota.[10] 97% of vertebrate species disappeared, with only smaller forms surviving. After the event only sharks less than a meter and most fishes and tetrapods less than 10 centimeters remained, and it would take 40 million years before they started to increase in size again.[40] This led to the establishment of the modern vertebrate fauna in the Carboniferous, consisting mostly of actinopterygians, chondrichthyans, and tetrapods. Romer's gap, a

15 million-year hiatus in the early Carboniferous tetrapod record, has been linked to this event.[10] Also, the poor Famennian record for marine invertebrates suggests that some of the losses attributed to the Kellwasser event likely actually occurred during the Hangenberg extinction.[10][41]

Magnitude

The late Devonian crash in biodiversity was more drastic than the familiar extinction event that closed the Cretaceous. A recent survey (McGhee 1996) estimates that 22% of all the 'families' of marine animals (largely invertebrates) were eliminated. The family is a great unit, and to lose so many signifies a deep loss of ecosystem diversity. On a smaller scale, 57% of genera and at least 75% of species did not survive into the Carboniferous. These latter estimates[b] need to be treated with a degree of caution, as the estimates of species loss depend on surveys of Devonian marine taxa that are perhaps not well enough known to assess their true rate of losses, so it is difficult to estimate the effects of differential preservation and sampling biases during the Devonian.

See also

- Evolutionary history of plants

Notes

a. Though a super eruption on its own would have devastating effects in the long term, the Late Devonian extinction was caused by a series of events which contributed to the extinction.[37]
b. The species estimate is the toughest to assess and most likely to be adjusted.

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External links

- Late Devonian mass extinctions (http://www.devoniantimes.org/opportunity/massExtinction.html) at The Devonian Times. An excellent overview.
- Devonian Mass Extinction (https://web.archive.org/web/20061028130757/http://hannover.park.org/Canada/Museum/extinction/devmass.html)
- BBC "The Extinction files" (https://www.bbc.co.uk/education/darwin/exfiles/devonian.htm) "The Late Devonian Extinction"
- "Understanding Late Devonian and Permian-Triassic Biotic and Climatic Events: Towards an Integrated Approach (http://gsa.confex.com/gsa/2003AM/finalprogram/session_8723.htm)": a Geological Society of America conference in 2003 reflects current approaches
- PBS: Deep Time (https://www.pbs.org/wgbh/evolution/change/deeptime/devonian.html)