All About

Devonian Period and Events

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Devonian

The **Devonian** is a geologic period and system of the Paleozoic Era spanning from 416 to 359.2 million years ago (ICS, 2004, chart). It is named after Devon, England, where rocks from this period were first studied.

During the Devonian Period the pectoral and pelvic fins of lobe-finned fish evolved into legs as they started to walk on land as tetrapods around 397 Ma. Various terrestrial arthropods also became well-established.

The first seed-bearing plants spread across dry land, forming huge forests. In the oceans, primitive sharks became more numerous than in the Silurian and the late Ordovician, and the first ray finned and lobe-finned bony fish evolved. The first ammonite mollusks appeared, and trilobites, the mollusc-like brachiopods, as well as great coral reefs were still common. The Late Devonian extinction severely affected marine life.

The paleogeography was dominated by the supercontinent of Gondwana to the south, the continent of Siberia to the north, and the early formation of the small supercontinent of Euramerica in between.

History

The period is named after Devon, a county in southwestern England, where Devonian outcrops are common. While the rock beds that define the start and end of the period are well identified, the exact dates are uncertain. According to the International Commission on Stratigraphy (Ogg, 2004), the Devonian extends from the end of the Silurian Period 416.0 ± 2.8 Mya, to the beginning of the Carboniferous Period 359.9 ± 2.5 Mya (in North America, the beginning of the Mississippian subperiod of the Carboniferous) (ICS 2004).

In nineteenth-century texts the Devonian has been called the "Old Red Age", after the red and brown terrestrial deposits known in the United Kingdom as the Old Red Sandstone in which early fossil discoveries were found. Another common term is "Age of the Fishes", referring to the evolution of several major groups of fish that took place during the period. Older literature on the Anglo-Welsh basin divides it into the Downtonian,

Dittonian, Breconian and Farlovian stages, the latter three of which are place in the Devonian.

The Devonian has also erroneously been characterized as a "greenhouse age", due to sampling bias: most of the early Devonian-age discoveries came from the strata of western Europe and eastern North America, which at the time straddled the Equator as part of the supercontinent of Euramerica where fossil signatures of widespread reefs indicate tropical climates that were warm and moderately humid but in fact the climate in the Devonian differed greatly between epochs and geographic regions. For example, during the Early Devonian, arid conditions were prevalent through much of the world including Siberia, Australia, North America, and China, but Africa and South America had a warm temperate climate. In the Late Devonian, by contrast, arid conditions were less prevalent across the world and temperate climates were more common.

Subdivisions

The Devonian Period is formally broken into Early, Middle, and Late subdivisions. The rocks corresponding to these epochs are referred to as belonging to the Lower, Middle and Upper parts of the Devonian System.

The Early Devonian lasts from 416 ± 2.8 million years ago to 397.5 ± 2.7 million years ago and begins with the Lochkovian stage, which lasts until the Pragian. This spans from 411.2 million years ago million years ago to 407 ± 2.8 million years ago, and is followed by the Emsian, which lasts until the Middle Devonian begins, 397.5± 2.7 million years ago. The Middle Devonian comprises two subdivisions, the Eifelian giving way to the Givetian 391.8± 2.7 million years ago. During this time the armoured jawless ostracoderm fish were declining in diversity; the jawed fish were thriving and increasing in diversity in both the oceans and freshwater. The shallow, warm, oxygen-depleted waters of Devonian inland lakes, surrounded by primitive plants, provided the environment necessary for certain early fish to develop essential characteristics such as well developed lungs, and the ability to crawl out of the water and onto the land for short periods of time.

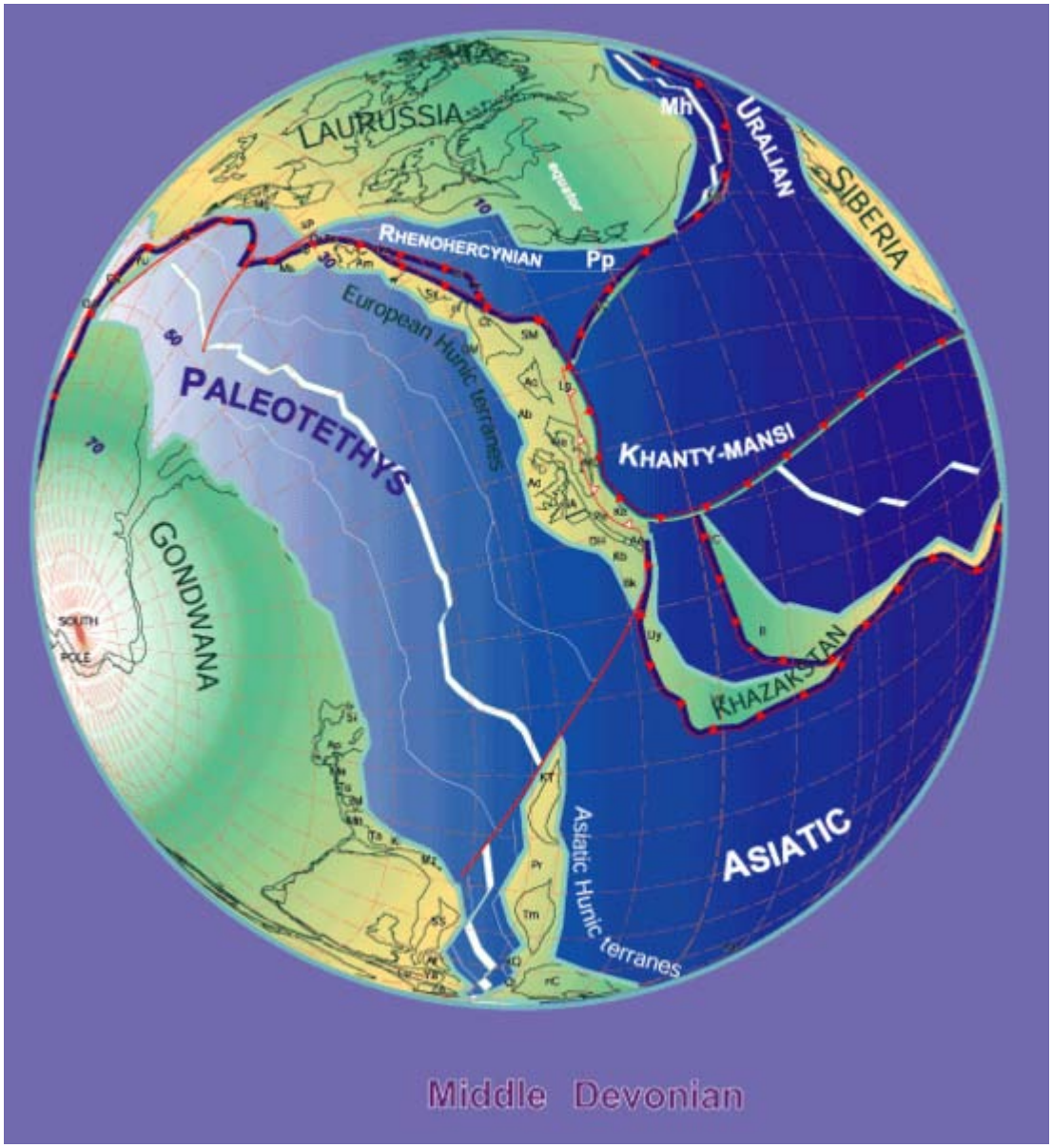
Finally, the Late Devonian starts with the Frasnian, 385.3 ± 2.6 million years ago to 374.5 ± 2.6 million years ago, during which the first forests were taking shape on land. The first tetrapods appear in the fossil record in the ensuing Famennian subdivision, the beginning and end of which are marked with extinction events. This lasted until the end of the Devonian, 359.2± 2.5 million years ago.

Climate

The Devonian was a relatively warm period, and probably lacked any glaciers. Reconstruction of tropical sea surface temperature from conodont apatite implies an average value of 30 °C (86 °F) in the Early Devonian. CO_2 levels dropped steeply throughout the Devonian period as the burial of the newly-evolved forests drew carbon

out of the atmosphere into sediments; this may be reflected by a Mid-Devonian cooling of around 5 °C (9 °F). The Late Devonian warmed to levels equivalent to the Early Devonian; while there is no corresponding increase in CO_2 concentrations, continental weathering increases (as predicted by warmer temperatures); further, a range of evidence, such as plant distribution, points to Late Devonian warming. The climate would have affected the dominant organisms in reefs; microbes would have been the main reef-forming organisms in warm periods, with corals and stromatoporoid sponges taking the dominant role in cooler times. The warming at the end of the Devonian may even have contributed to the extinction of the stromatoporoids.

Paleogeography



The Paleo-Tethys Ocean opened during the Devonian

The Devonian period was a time of great tectonic activity, as Euramerica and Gondwanaland drew closer together.

The continent Euramerica (or Laurussia) was created in the early Devonian by the collision of Laurentia and Baltica, which rotated into the natural dry zone along the Tropic of Capricorn, which is formed as much in Paleozoic times as nowadays by the convergence of two great air-masses, the Hadley cell and the Ferrel cell. In these near-deserts, the Old Red Sandstone sedimentary beds formed, made red by the oxidized iron (hematite) characteristic of drought conditions.

Near the equator, the plate of Euramerica and Gondwana were starting to meet, beginning the early stages of assembling Pangaea. This activity further raised the northern Appalachian Mountains and formed the Caledonian Mountains in Great Britain and Scandinavia.

The west coast of Devonian North America, by contrast, was a passive margin with deep silty embayments, river deltas and estuaries, in today's Idaho and Nevada; an approaching volcanic island arc reached the steep slope of the continental shelf in Late Devonian times and began to uplift deep water deposits, a collision that was the prelude to the mountain-building episode of Mississippian times called the Antler orogeny.

Sea levels were high worldwide, and much of the land lay submerged under shallow seas, where tropical reef organisms lived. The deep, enormous Panthalassa (the "universal ocean") covered the rest of the planet. Other minor oceans were Paleo-Tethys, Proto-Tethys, Rheic Ocean, and Ural Ocean (which was closed during the collision with Siberia and Baltica).

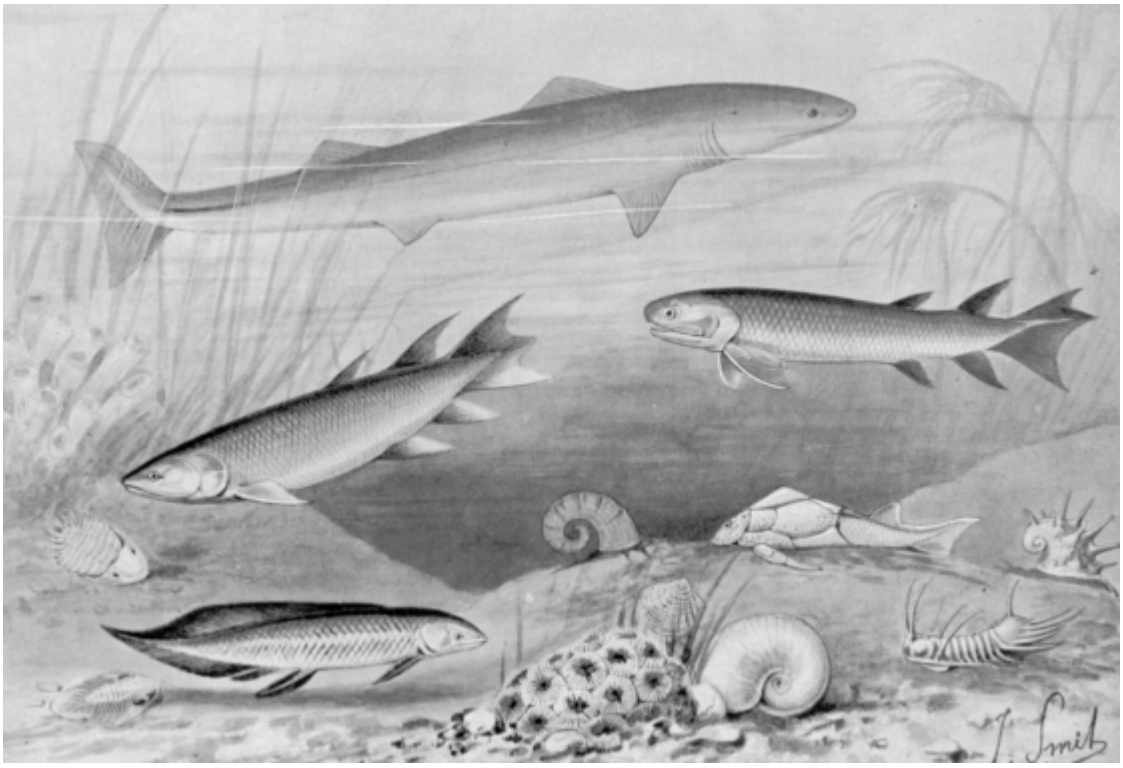
Biota

Marine biota

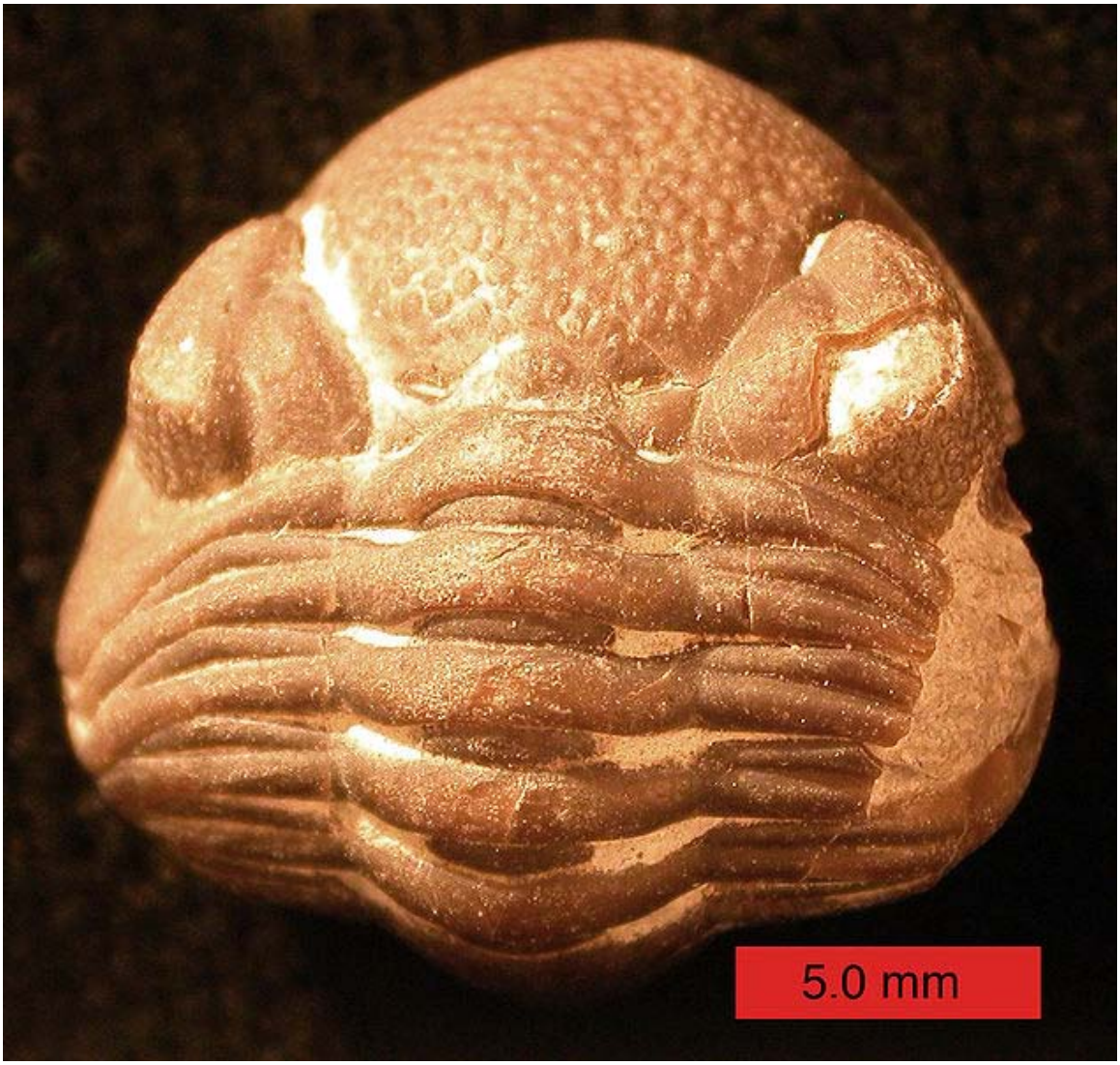
Sea levels in the Devonian were generally high. Marine faunas continued to be dominated by bryozoa, diverse and abundant brachiopods, the enigmatic hederelloids, microconchids and corals. Lily-like crinoids were abundant, and trilobites were still fairly common. Among vertebrates, jaw-less armored fish (ostracoderms) declined in diversity, while the jawed fish (gnathostomes) simultaneously increased in both the sea and fresh water. Armored placoderms were numerous during the lower stages of the Devonian Period and became extinct in the Late Devonian, perhaps because of competition for food against the other fish species. Early cartilaginous (Chondrichthyes) and bony fishes (Osteichthyes) also become diverse and played a large role within the Devonian seas. The first abundant genus of shark, *Cladoselache*, appeared in the oceans during the Devonian period. The great diversity of fish around at the time, have led to the Devonian being given the name "The Age of Fish" in popular culture.

The first ammonites also appeared during or slightly before the early Devonian period around 400 Mya.

Dunkleosteus, one of the largest armoured fishes to ever roam the planet, lived during the late Devonian.



Early shark Cladoselache, several lobe-finned fishes, including *Eusthenopteron* , and the placoderm *Bothriolepis* on a painting from 1905.

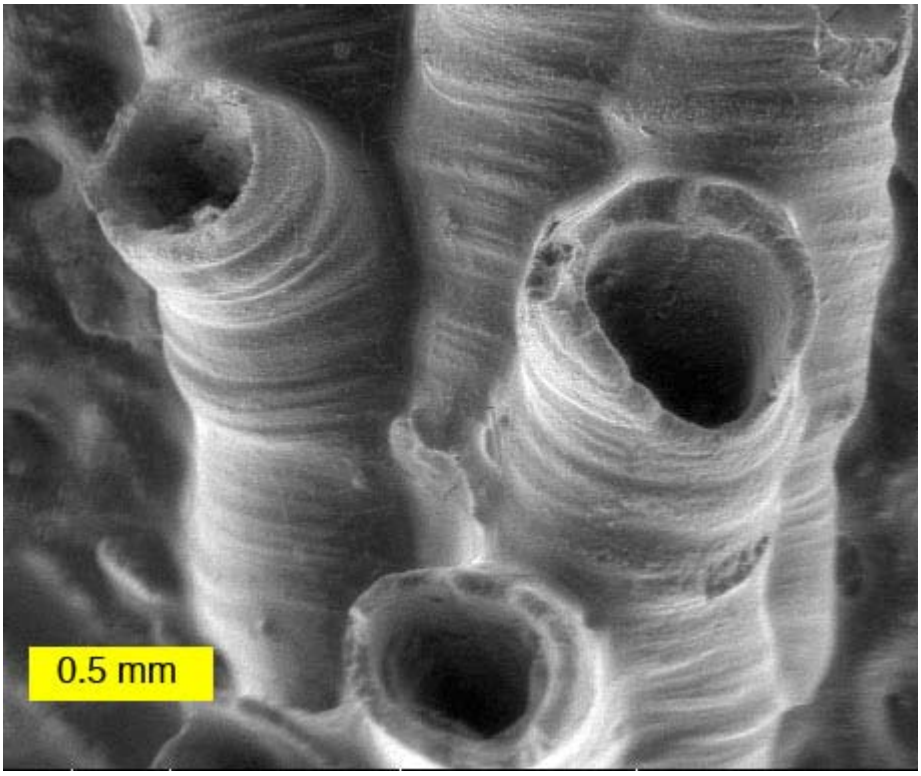


Phacopid trilobite from the Devonian of Ohio. Scale bar is 5.0 mm.

The common tabulate coral *Aulopora* from the Middle Devonian of Ohio; view of colony origin encrusting a brachiopod valve.

Reefs

A now dry barrier reef, located in present day Kimberley Basin of northwest Australia, once extended a thousand kilometers, fringing a Devonian continent. Reefs in general are built by various carbonate-secreting organisms that have the ability to erect wave-resistant frameworks close to sea level. The main contributors of the Devonian reefs were unlike modern reefs, which are constructed mainly by corals and calcareous algae. They were composed of calcareous algae and coral-like stromatoporoids, and tabulate and rugose corals, in that order of importance.



SEM image of a hederelloid from the Devonian of Michigan (largest tube diameter is 0.75 mm).

A Devonian spiriferid brachiopod from Ohio which served as a host substrate for a colony of hederelloids. The specimen is 5 cm wide.

Terrestrial biota

By the Devonian Period, life was well underway in its colonization of the land. The moss forests and bacterial and algal mats of the Silurian were joined early in the period by primitive rooted plants that created the first stable soils and harbored arthropods like mites, scorpions and myriapods (although arthropods appeared on land much earlier than in the Early Devonian and the existence of fossils such as *Climactichnites* suggest that land arthropods may have appeared as early as the Cambrian period). Also the first possible fossils of insects appeared around 416 Mya in the Early Devonian. The first tetrapods evolving from lobe-finned fish, appeared in the coastal water no later than middle Devonian, and give rise to the first Amphibians.

The greening of land

The Devonian period marks the beginning of extensive land colonization by plants. With large herbivorous land-animals not yet being present, large forests could grow and shape the landscape.

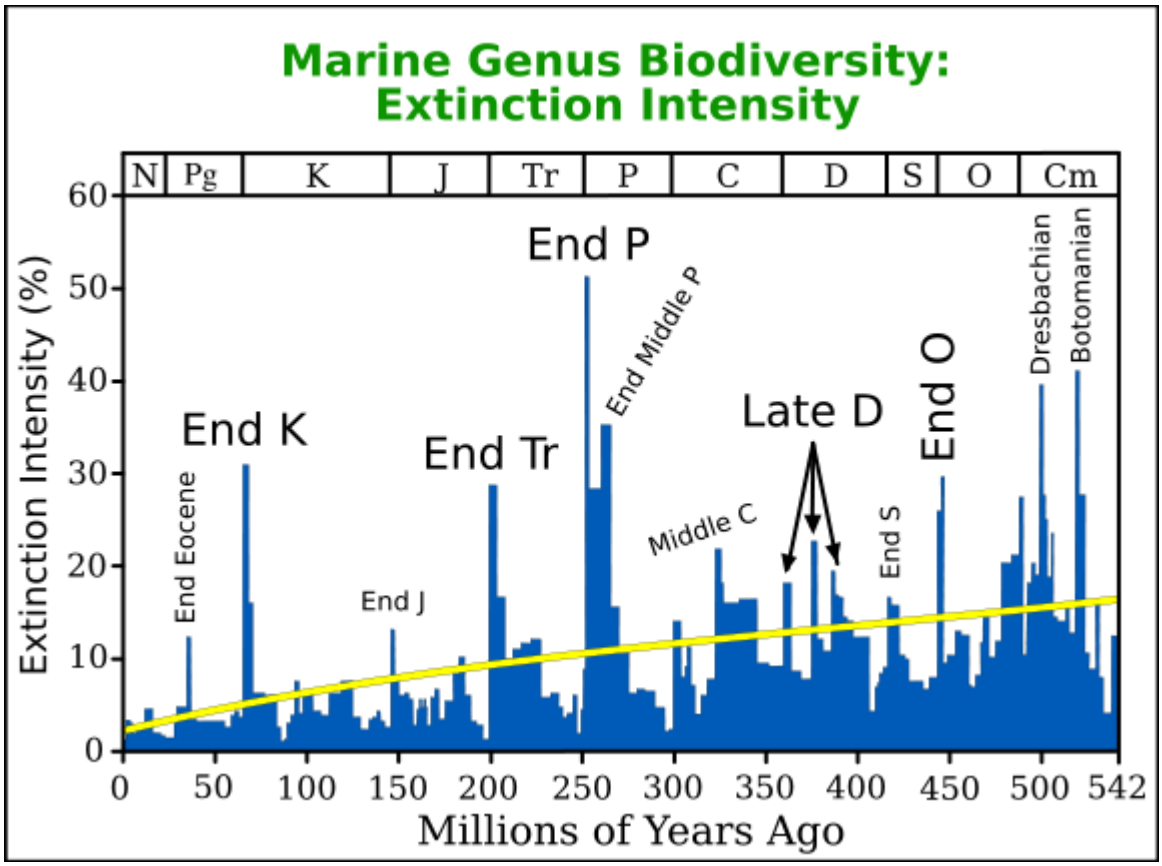
Early Devonian plants did not have roots or leaves like the plants most common today, and many had no vascular tissue at all. They probably spread largely by vegetative growth, and did not grow much more than a few centimeters tall. By far the greatest land organism was *Prototaxites*, the fruiting body of an enormous fungus that stood more than 8 meters tall, towering over the low, carpet-like vegetation. By Middle Devonian, shrub-like forests of primitive plants existed: lycophytes, horsetails, ferns, and progymnosperms had evolved. Most of these plants had true roots and leaves, and many were quite tall. The earliest known trees, from the genus *Wattieza*, appeared in the Late Devonian around 380 Ma. In the Late Devonian, the tree-like ancestral fern *Archaeopteris* and the giant cladoxylopsid trees grew with true wood. These are the oldest known trees of the world's first forests. By the end of the Devonian, the first seed-forming plants had appeared. This rapid appearance of so many plant groups and growth forms has been called the "Devonian Explosion".

The 'greening' of the continents acted as a carbon dioxide sink, and atmospheric levels of this greenhouse gas may have dropped. This may have cooled the climate and led to a massive extinction event.

Animals and the first soils

Primitive arthropods co-evolved with this diversified terrestrial vegetation structure. The evolving co-dependence of insects and seed-plants that characterizes a recognizably modern world had its genesis in the Late Devonian. The development of soils and plant root systems probably led to changes in the speed and pattern of erosion and sediment deposition. The rapid evolution of a terrestrial ecosystem containing copious animals opened the way for the first vertebrates to seek out a terrestrial living. By the end of the Devonian, arthropods were solidly established on the land.

Late Devonian extinction



The Late Devonian is characterised by three episodes of extinction ("Late D")

A major extinction occurred at the beginning of the last phase of the Devonian period, the Famennian faunal stage, (the Frasnian-Famennian boundary), about 364 Mya, when all the fossil agnathan fishes, save for the psammosteid heterostracans, suddenly disappeared. A second strong pulse closed the Devonian period. The Late Devonian extinction was one of five major extinction events in the history of the Earth's biota, more drastic than the familiar extinction event that closed the Cretaceous.

The Devonian extinction crisis primarily affected the marine community, and selectively affected shallow warm-water organisms rather than cool-water organisms. The most

important group to be affected by this extinction event were the reef-builders of the great Devonian reef-systems .

Amongst the severely affected marine groups were the brachiopods, trilobites, ammonites, conodonts, and acritarchs, as well as jawless fish, and all placoderms. Land plants as well as freshwater species, such as our tetrapod ancestors, were relatively unaffected by the Late Devonian extinction event.

The reasons for the Late Devonian extinctions are still unknown, and all explanations remain speculative. Canadian paleontologist Digby McLaren suggested in 1969 that the Devonian extinction events were caused by an asteroid impact. However, while there were Late Devonian collision events, little evidence supports the existence of a Devonian crater large enough.

Chapter- 2

Late Devonian Extinction

The **Late Devonian extinction** was one of five major extinction events in the history of the Earth's biota. A major extinction 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 364 million years ago, when nearly all of the fossil agnathan fishes suddenly disappeared. A second strong pulse closed the Devonian period. Overall, 19% of all families and 50% of all genera went extinct.

Although it is clear that there was a massive loss of biodiversity towards the end of the Devonian, the extent of time during which these events took place is uncertain, with estimates ranging from 500,000 to 15 million years, the latter being the full length of the Famennian. Nor is it clear whether it concerned two sharp mass extinctions or a series of smaller extinctions, though the latest research suggests multiple causes and a series of distinct extinction pulses through an interval of some three million years. 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.

By the late Devonian, the land had been colonized by plants, insects, and amphibians. In the oceans, there were massive reefs built by corals and stromatoporoids on land. Euramerica and Gondwana were beginning to converge into what would become Pangea. The extinction seems to have only affected marine life. Hard-hit groups include brachiopods, trilobites, and reef-building organisms; the latter almost completely disappeared, with coral reefs only returning upon the evolution of modern corals during the Mesozoic. The causes of these extinctions are unclear. Leading theories 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. Some statistical analysis suggests that the decrease in diversity was caused more by a decrease in speciation than by an increase in extinctions.

The Late Devonian world

The world was a very different place in the late Devonian. The continents were arranged differently, 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. The Caledonian mountains were also growing across what is now the Scottish highlands and Scandinavia, while the Appalachians rose over America; these mountain belts were the equivalent of the Himalaya today.

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 consequently formed huge forests on the highlands. Several different clades had developed a shrubby or tree-like habit by the Late Givetian, including the cladoxylalean ferns, lepidosigillarioid lycopsids, and aneurophyte and archaeopterid progymnosperms. Fish were also undergoing a huge radiation, and the first tetrapods were beginning to evolve leg-like structures.

Duration and timing of the extinction events

Extinction rates appear to be higher than the background rate for an extended period lasting the last 20-25 million years of the Devonian. During this period, about eight to ten distinct events can be seen, of which two stand out as particularly severe. Each of these two major events was preceded by a longer period of prolonged biodiversity loss. The fossil record of following first 15 million years of the Carboniferous is largely void of terrestrial animal fossils. This period is known as the Romer's gap.

The Kellwasser event

The Kellwasser event is the term given to the extinction pulse that occurs near the Frasnian/Famennian boundary. There may in fact have been two closely spaced events here.

The Hangenberg event

The Hangenberg event sits on or just below the Devonian/Carboniferous boundary and marks the final spike in the period of extinction.

Effects of the events

The extinction events are 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 Devonian extinction crisis primarily affected the marine community, and selectively affected shallow warm-water organisms over cool-water organisms. The most important

group to be affected by this extinction 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 reef system collapse was so severe that major reef-building (effected by new families of carbonate-excreting organisms, the modern scleractinian or "stony" corals) did not recover until the Mesozoic era;

Further taxa to be severely affected include the brachiopods, trilobites, ammonites, conodonts, and acritarchs, as well as jawless fish, and all placoderms. Freshwater species, including our tetrapod ancestors, and land plants were relatively unscathed.

The surviving taxa show morphological trends through the event. Trilobites evolve smaller eyes in the run up to the Kellwasser event, with eye size increasing again afterwards. This suggests that 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. It is thought that the brims serve a respiratory purpose, and that the increasing anoxia of waters led to an increase in their brim area in response.

The shape of conodonts' feeding apparatus varied with $\delta^{18}O$ and thus seawater temperature; this may relate to them occupying different trophic levels as nutrient input changed.

As with all extinction events, specialist taxa occupying small niches were harder hit than generalists.

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 percent of all the *families* of marine animals (largely invertebrates) were eliminated. The family is a large unit, and to lose such a large number signifies a profound 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 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.

Causes of the extinction

Since the "extinction" occurred over such a long time period, it is difficult to assign a single cause, and indeed to separate cause from effect. The sedimentological 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.

Major environmental changes

From the end of the Middle Devonian, into the Late Devonian, several environmental changes can be detected from the sedimentary record. There is evidence of widespread anoxia in oceanic bottom waters; the rate of carbon burial shot up, and benthic organisms were decimated, especially in the tropics, and especially reef communities. There is good evidence for high-frequency sea level changes around the Frasnian/Famennian boundary, with one sea level rise associated with the onset of anoxic deposits.

Possible triggers

Bolide impact

Bolide impacts can be dramatic triggers of mass extinctions. It has been posited that an asteroid impact was the prime cause of this faunal turnover, but no secure evidence of a specific extraterrestrial impact has been identified in this case. Impact craters, such as the Alamo and Woodleigh, can generally not be dated with sufficient precision to link them to the event; those dated precisely are not contemporaneous with the extinction. Although some minor features of meteoric impact have been observed in places (iridium anomalies and microspherules), these were probably caused by other factors.

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 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. 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. 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 stabilised a deep layer of soil, which would have been on the order of metres thick. In contrast, early Devonian plants bore only rhizoids and rhizomes that could penetrate no more than a couple of centimetres. The mobilisation of a large portion of soil had a huge effect; soil promotes weathering, the chemical breakdown of rocks, releasing ions which act as nutrients to plants and algae. 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, just as phosphate run-off from Australian farmers is causing unmeasurable damage to the great barrier reef today. Anoxic conditions correlate better with biotic crises than phases of cooling, suggesting that anoxia may have played the dominant role in extinction.

Effect on CO_2

The "greening" of the continents occurred during Devonian time. The covering of the planet's continents with massive photosynthesizing land plants in the first forests may have reduced carbon dioxide 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 (located near the Devonian south pole) suggest widespread glaciation at the end of the Devonian, as a large 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 weathering of silicate rocks also draws down carbon dioxide from the atmosphere. This acted in concert with the burial of organic matter to decrease atmospheric carbon dioxide concentrations from ~15 to ~3 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. 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), 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.

Other suggestions

Other mechanisms that have been put forwards 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.

Chapter- 3

Devonian Impact Craters

Alamo bolide impact

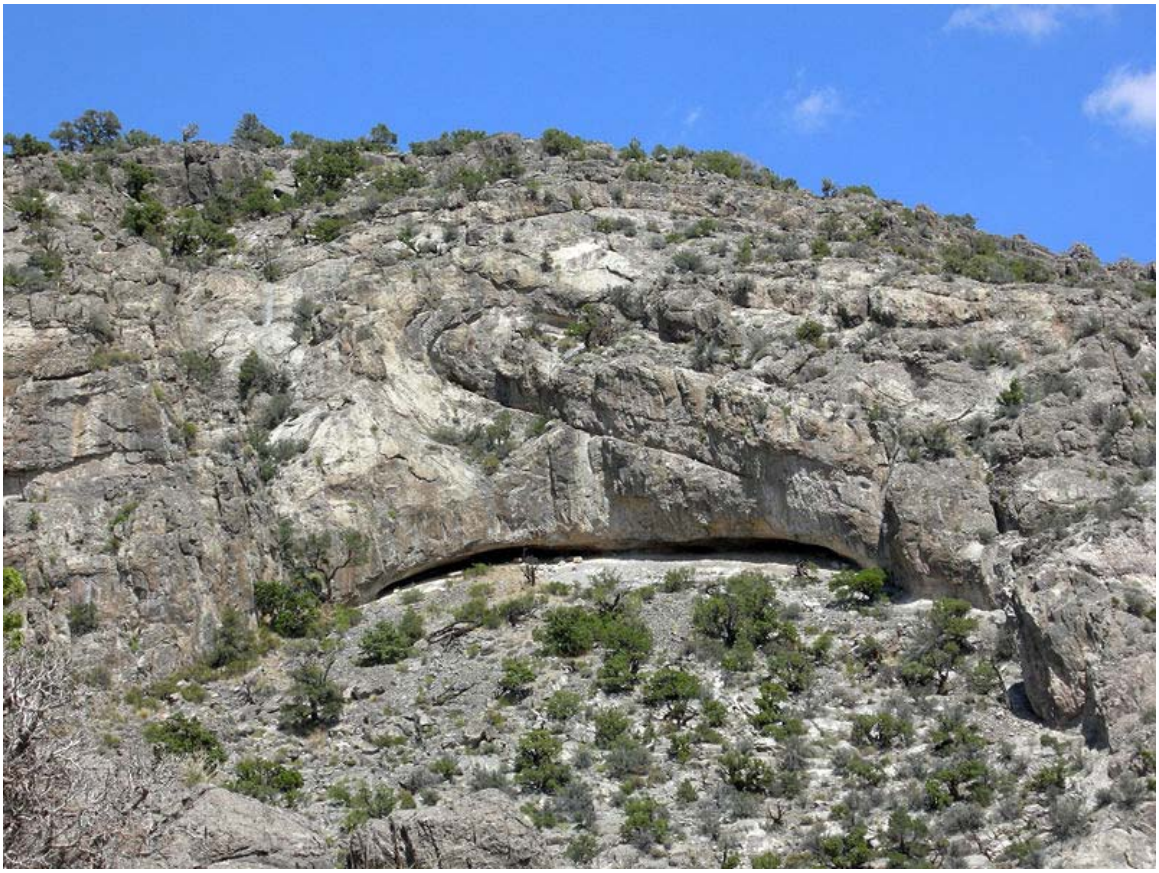
Landscape showing Alamo impact breccia (arrow) near Hancock Summit, Pahranagat Range, Nevada.

The **Alamo bolide impact** occurred 367 million years ago, when one or more hypervelocity objects from space slammed into shallow marine waters at a site that is

now the Devonian Guilmette Formation of the Worthington Mountains and Schell Creek Range of southeastern Nevada; the event is named for breccias of metamorphosed crushed rock deposits, found as far as the town of Alamo, Nevada (the "Alamo Breccia"). This catastrophic impact event resulted in what is one of the best-exposed and has become the most accurately dated impact events; it occurred within the Frasnian age of the Devonian at about 367 Ma, a moment in time that was about 3.5 Ma prior to the Frasnian/Famennian extinction events, which it is unlikely to have affected.

Alamo impact breccia near Hancock Summit, Pahranagat Range, Nevada.

The actual impact site has not yet been significantly documented—even its precise diameter and its internal structural features are not yet clear enough to make speculations on the mass and trajectory genuinely useful. The "tectonic overprint", the subsequent geologic modifications since the event, have distorted the picture; the distribution of the breccia has been compressed and skewed by west-to-east thrust faults across the area. Insufficient detail does not permit a precise reconstruction of the Devonian paleogeography, beyond the fact that it was a "wet-target" impact in a reef front where carbonates were being built up in marine shallows.



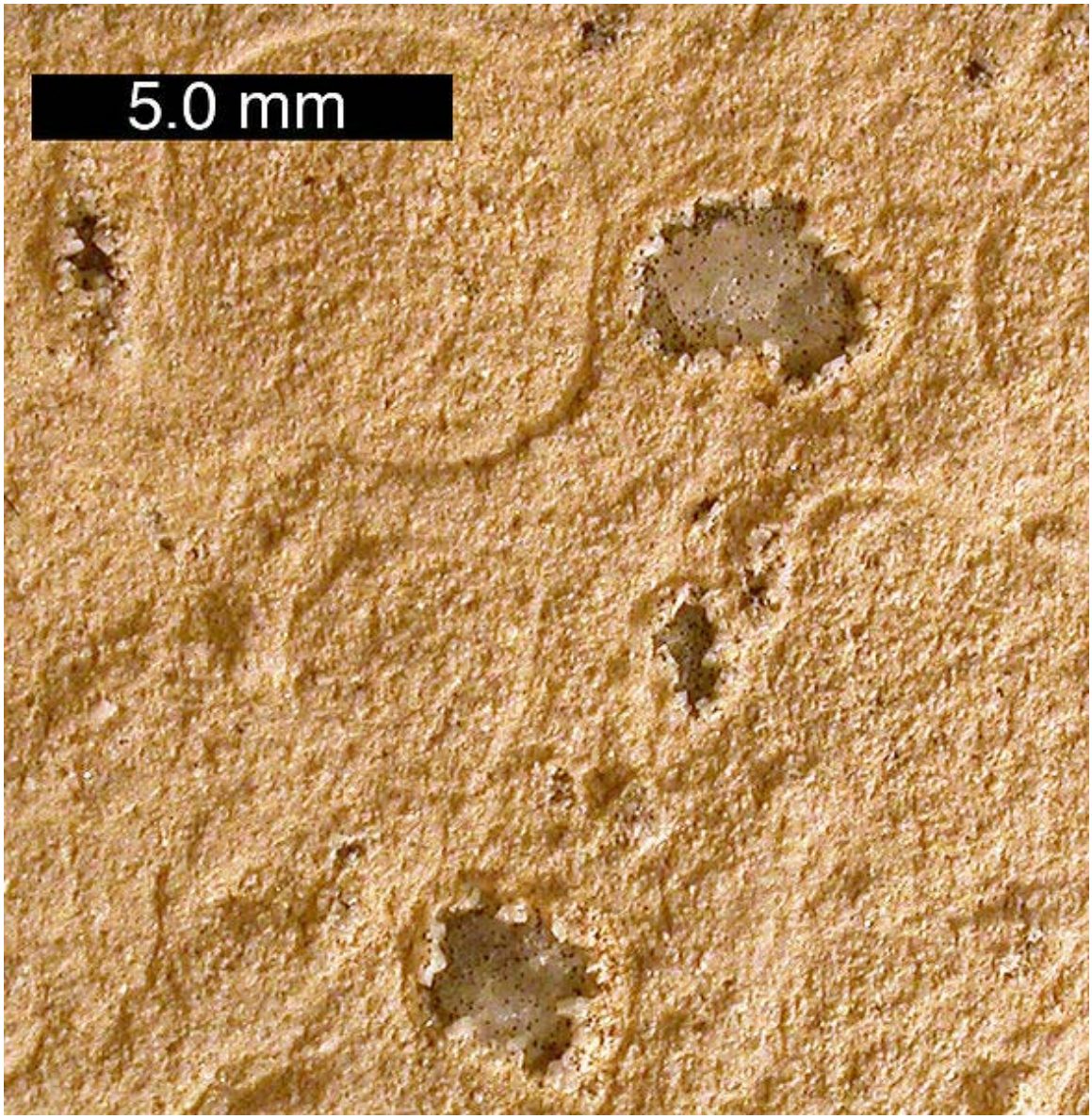
Distorted limestones from the Alamo impact in the Irish Range, Nevada.

Close-up of Alamo impact breccia near Hancock Summit, Pahranagat Range, Nevada.

Alamo impact breccia near Hancock Summit, Pahranagat Range, Nevada.

The impact site contains megabreccia of gigantic displaced blocks, together with several attributes familiar from other impact sites: shocked quartz, elevated iridium levels, and spherical lapilli. John E. Warme, one of the geologists who first recognized the geologic anomalies as the results of a bolide, estimates that the total volume of limestone reef deposits and bedrock that was smashed, deformed, partially melted or shifted during the Alamo event at 1,000 cubic kilometers. "Ensuing tsunamis rearranged much of the debris" he adds.

Top of the Alamo impact breccia near Hancock Summit, Pahranagat Range, Nevada.



Calcitic spherules ("spherical lapilli") from the Alamo bolide impact deposits in the Irish Range, Nevada. Scale bar is 5.0 mm.

After initial resistance from the Geological Society of America, the first paper published concerning the Alamo Breccia was co-authored by John Warme, Brian Ackman, Yarmanto, and Alan Chamberlain in the 1993 *Nevada Petroleum Society Field Conference Guidebook*.

Brent crater

The **Brent crater** is an impact crater located north of Cedar Lake in Algonquin Provincial Park in the Nipissing District of Ontario, Canada. It is 3.8 km in diameter and the age is estimated to be 396 ± 20 million years (Middle Devonian).

A sign, erected at the site by the Archeological and Historic Sites Board, Archives of Ontario, reads:

The Brent Crater: First recognized in 1951 from aerial photographs, the crater is a circular depression about two miles in diameter formed in Precambrian crystalline rocks. Geophysical and diamond drilling investigations show that the crater has a present depth of about 1,400 feet but is partly filled with sedimentary rocks with a thickness of 900 feet. The rocks beneath the crater floor are thoroughly fragmented over a depth of 2,000 feet. Like the similar New Quebec (Chubb) crater, the Brent crater is attributed to the high speed impact of a giant meteorite. It is calculated that the impact released energy equaling 250 megatons of TNT and occurred about 450 million years ago when this area was probably covered by a shallow sea.

There is an observation tower on the rim of the crater. The old wooden tower was demolished in July 2007, because it was not safe to use due to its age. A new tower has been built on a hill directly across the Brent Road from the demolished tower. The new tower on the hill offers a much better panorama of the entire crater. Parking will also be increased as part of the new tower improvements. There is a hiking trail leading to the crater floor. There are two small lakes, Gilmour and Tecumseh, located in the crater. Unlike most Algonquin Park lakes, which are usually acidic, the water in these lakes contains bicarbonate; this is thought to be a result of some sedimentary deposits of limestone escaping removal by glaciers in the lower parts of the crater.

The crater lies in the Ottawa-Bonnechere Graben, a 452 million year old rift valley.

The crater was named after the nearby village of Brent.

Elbow crater

Elbow is a meteorite crater in Saskatchewan, Canada.

It is 8 kilometers (5 mi) in diameter with an age estimated to be 395 ± 25 million years (during the Devonian Period). The crater is not exposed at the surface.

Flynn Creek crater

Flynn Creek crater, is an impact crater situated in Jackson County, approximately 8 km south of Gainesboro, Tennessee, USA. It was formed approximately 360 million years ago as a shallow, saucer-shaped crater, 3.8 km in diameter and about 150 m deep. A large central hill, highly deformed rim strata, and a breccia lens 40 m in thickness were produced during formation. Over 2 km^2 of flat lying Middle and Upper Paleozoic limestone and dolomite were brecciated and mixed to a depth of 200 m, and at least half of the breccia was ejected from the crater. The remaining breccia contains fragments ranging in size from small grains to megabreccia blocks 100 m in length. Undisturbed strata lie 100 m below the original crater floor.

In the middle of the crater, a sequence of steeply-dipping, folded, faulted, and brecciated Middle Ordovician limestone and dolomite has been uplifted 100 m to form a large central hill. Knox strata in the central uplift are raised 350 m above their normal position and locally contain shatter cones.

In the rim surrounding the crater, Ordovician limestone has been uplifted 10 m to 50 m, and is moderately to tightly folded into doubly plunging anticlines and synclines that have axes concentric to the crater walls. In parts of the rim, folds have resulted in radial shortening as great as 35%. Faulting is common in the rim strata and is usually concentric to the crater walls.

In the southeastern rim, a large thrust block forms the crater wall and has been moved out from the crater and uplifed about 50 m. The thrust block partly overrides a tilted rim graben that has down-dropped about 100 m and moved toward the crater. Overlying this graben is a layer of breccia which is apparently the remains of an ejecta blanket that once surrounded the crater.

Post-crater erosion removed the ejecta, except for that overlying the graben, and lowered the regional ground surface less than 30 m. Within a few million years of the cratering event the entire structure was covered with shale deposits from the early Late Devonian Chattanooga Sea, creating one of the best-preserved ancient impact structures presently known. Subsequent erosion along Flynn Creek drainage has exposed a large extent of the structure. Karst development in the immediate area has created numerous caves associated with impact features, including the only cave known to occur in the central uplift of an impact structure, Hawkins Impact Cave.

Flynn Creek crater facts

- ~3830m diameter
- ~200m depth (minus breccia lens)
- ~20m max pre-impact relief
- ~15m max depth of water at time of impact
- ~40m avg breccia thickness

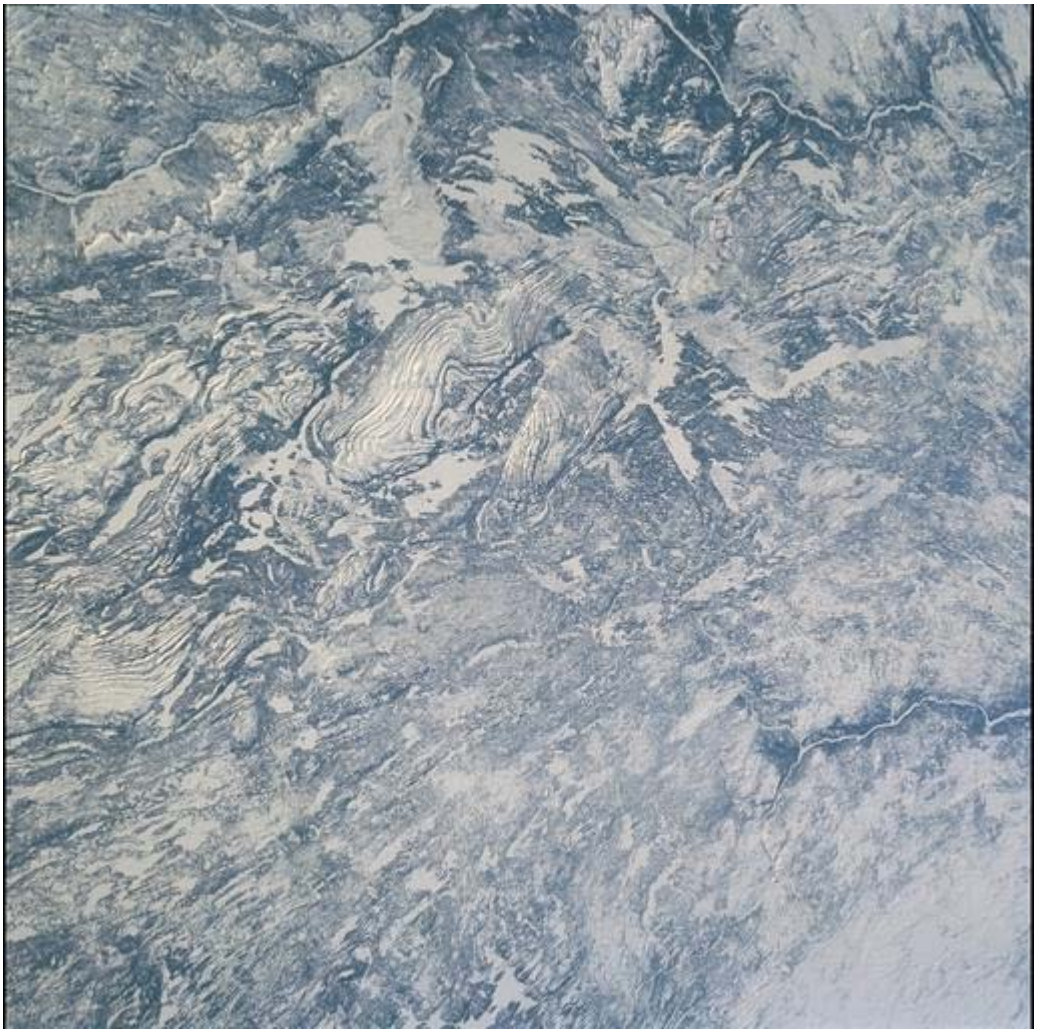
- ~140m avg breccia depth below crater floor
- ~35% max radial shortening of rim strata
- ~90-190m range for bolide diameter
- roughly polygonal shape
- lateral zone of disturbance averages 1000 m in extent from crater wall
- lowermost size limit for complex craters with central uplifts
- 1700 m of sediments overlying crystalline basement in area
- estimated length of time for initial crater formation: <60 seconds
- conodonts found in immediate crater infill indicate marine environment
- central uplift is composed of strata which have been structurally uplifted 300 m above normal position
- 11.2-72 km/s--max velocity range for terrestrial impacting bodies
- 25 km/s--total vaporization of stony bolides

Kaluga crater

Kaluga is a meteorite crater in Russia.

It is 15 km in diameter and the age is estimated to be 380 ± 5 million years old (Upper Devonian). The crater is not exposed at the surface.

La Moinerie crater



Lac La Moinerie, Quebec, Canada, as seen from Earth orbit. Image courtesy NASA.

La Moinerie is a impact crater in Quebec, Canada. It is 8 km in diameter and the age is estimated to be 400 ± 50 million years (Silurian or Devonian). The crater is exposed to the surface and filled with water, forming Lac La Moinerie. Glaciers have eroded many of La Moinerie crater's original physical features, including much of the central uplift.

Nicholson crater

Nicholson is a meteorite crater in the Northwest Territories, Canada.

It is 12.5 km in diameter and the age is estimated to be less than 400 million years (Devonian or earlier). The crater is not exposed at the surface.

Woodleigh crater

Woodleigh is a large meteorite impact crater (astrobleme) in Western Australia, centered on Woodleigh Station east of Shark Bay. A team of four scientists at the Geological Survey of Western Australia and the Australian National University, led by Arthur J. Mory, announced the discovery in the April 15, 2000 issue of *Earth and Planetary Science Letters*.

The crater is not exposed at the surface and therefore its size is uncertain. The original discovery team believe it may be up to 120 kilometres in diameter, but others argue it may be much smaller, with one study suggesting a diameter closer to 60 kilometres. The larger estimate, if correct, would make this the fourth largest confirmed impact structure in the world, and imply a bolide (asteroid or comet) about 5–6 kilometres in diameter.

The central uplift, interpreted to be 20 kilometres in diameter, was first intersected by drilling activities in the late 1970s; however its significance as an impact structure was only realised in 1997 during a gravity survey. In 1999 a new core sample was taken. The thin veins of melted glass, breccia, and shocked quartz found would have formed under pressures 100,000 times greater than atmospheric pressure at sea level, or between 10 and 100 times greater than those generated by volcanic or earthquake activity. Only a large impact could have generated such conditions.

The Woodleigh impact event, originally thought to have occurred between the Late Triassic and Late Permian, is now thought to date from 364 ± 8 million years (Late Devonian). This time corresponds approximately to a minor extinction event when around 40% of species disappeared. There is evidence for other large impact events at around the same time, so if the extinction is related to impact, perhaps more than one crater was involved.

Of the two dozen or more impact craters known in Australia, the three largest are Woodleigh, Acraman, and Tookoonooka.

The proximity to Shark Bay and its orientation suggest the bay is the incipient part of the track of the Woodleigh impact. Most of the track, which is cut off at the edge of the continental shelf, would be lost after the break-up of Gondwana.

Chapter- 4

Panther Mountain

Panther Mountain	
 Panther from the west, along Route 28 near Highmount	
Elevation	~3,720 feet (~1,134 m)
Prominence	980 feet (300 m)
Listing	Catskill 3500 Club
Location	
Location	Shandaken, New York, USA
Range	Catskills
Coordinates	42°03′23″N 74°23′42″W / 42.05639°N 74.395°WCoordinates: 42°03′23″N 74°23′42″W / 42.05639°N 74.395°W
Topo map	USGS Shandaken
Climbing	
Easiest route	trail

Panther Mountain is one of the Catskill High Peaks, located in the Town of Shandaken in Ulster County, New York. At approximately 3,720 feet (1,135 m) in elevation, it is the 18th highest in the range. A combination of factors has led geologists to believe the mountain is on the site of an ancient meteorite impact crater.

Its proximity to Slide Mountain, the highest Catskill peak, the relatively short distance required to climb the mountain from the south and the excellent views available from the mountain and nearby Giant Ledge have made Panther one of the most popular hikes in the range. Aspiring members of the Catskill Mountain 3500 Club must climb it twice, at least once during winter.

Name

The origin of the name is unknown. Panthers may once have been seen in the area; but are not resident in the Catskills today.

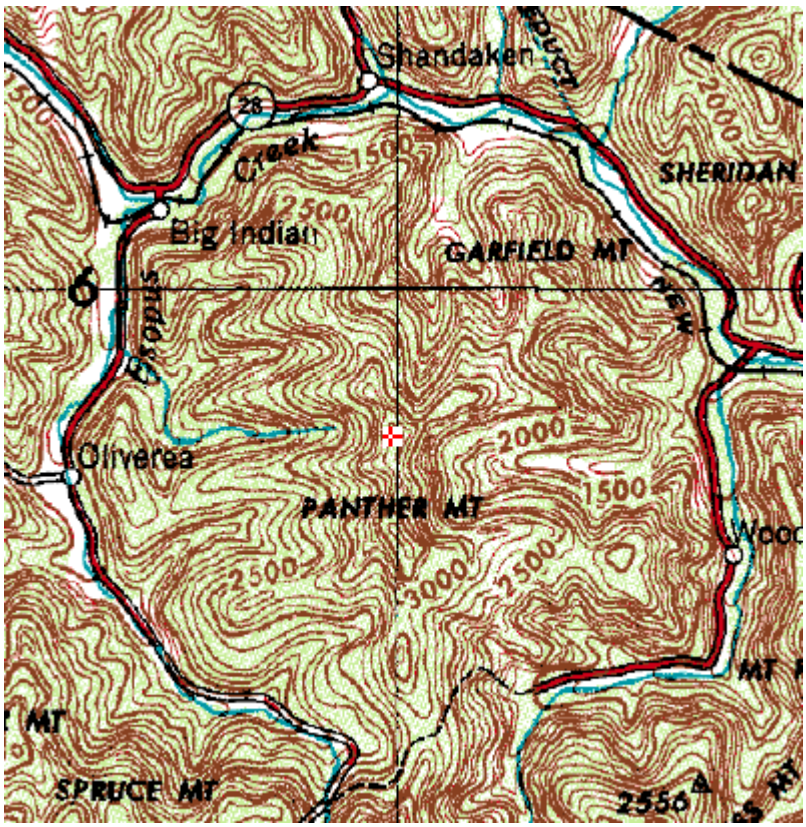
Geography

The mountain takes the shape of a longitudinal ridge in the center of the rough circle mostly formed by Esopus and Woodland creeks. Slide's north ridge begins right where the Panther/Giant Ledge ridge ends. Two named tributaries of Woodland, its Dougherty Branch and Panther Kill, rise on the mountain's western slopes.

Three of the valleys around the edge of the mountain have earned separate names of their own. Going clockwise from the southwest, they are Little Peck Hollow, Hatchery Hollow and Fox Hollow. The ridge aside the Daugherty Branch is called Fork Ridge.

The mountain rises gradually from the north, with many false summits. The drop to the south, to the col with Giant Ledge, is much sharper.

The entire area has long been a part of New York's Forest Preserve. Today it is within the Slide Mountain Wilderness Area, part of the Catskill Park, managed by the state Department of Environmental Conservation.



The nearly-complete circle made by Esopus and Woodland creeks around Panther gives a rough indication where the crater walls were.

Natural history

Geology

The circular pattern made by the two creeks surrounding Panther Mountain suggest that it might have a different origin from other Catskill peaks. Most mountains' drainage basins show a more dendritic (tree-like) pattern rather than the rosette made by Esopus and Woodland creeks around the mountain.

In the 1940s, geologist George Chadwick noticed this dome structure, and concluded that it might be the result of gas pushing up from below. The Dome Gas Company drilled a 6,000 feet (1.8 km) well into the structure. This well produced roughly 50,000 cubic feet (150 m^3) of natural gas a day, but since that was not profitable, the effort was abandoned.

In the early 1970s, another geologist, Yngvar Isachsen of the New York State Geological Survey at the New York State Museum in Albany, wondered if the stream pattern

indicated an impact crater buried beneath the surface. Since it wasn't his primary task at the Geological Survey, Isachsen did most of his research into the crater question in his own time. He found, when looking at the bed of Esopus Creek, that much of the exposed sandstone and shale showed an unusually closely spaced fracture pattern — every foot (30 cm) instead of every meter (3.3 ft), as is seen elsewhere in the Catskills. He reasoned that if a crater wall lay beneath, the debris from the impact and the sedimentary rock already in the area would have settled more compactly and been more prone to sagging and fracturing over time.

It wasn't until his later years, in the early 1990s, that Isachsen was able to devote more time to the crater question. Since the walls of a newly-formed impact crater are often unable to support themselves, landslides occur and build up a mound of rock and soil in the center. This results in a lower density of rock and thus slightly reduced gravitational pull, which can be measured. Isachsen took a gravimeter along on two hikes up the mountain and took regular readings. As he had expected, the gravity in the area was slightly lower than other mountains of comparable elevation in the Catskills, adding more weight to the crater theory.

To prove his hypothesis, Isachsen needed to drill deep into the rock under the mountain and find direct mineral evidence of a meteorite strike, but this was beyond his resources. Then he discovered that drill cuttings from the earlier gas well were archived at the New York State Geological Survey museum. These cuttings were examined carefully, during which graduate students working for him found microscopic iron spherules — to him irrefutable evidence of an impact crater.

However, questions from crater specialists at a conference in Budapest sent him back to look more closely at the cuttings. One attendee pointed out that he hadn't ruled out the possibility that the spherules had merely been deposited by a passing meteorite or comet. In October 1999, closer examination of tiny quartz crystals in the samples turned up shock lamellae, which could only have resulted from impact. A group of Canadian specialists confirmed the finding.

The impact is estimated to have occurred 375 million years ago, during the Devonian period, when much of what is now the Catskills was either river delta or a shallow sea. The crater lies 2,640 feet (800 m) below the surface, is 6 miles (10 km) wide, and lies directly under the mountain. The meteorite that struck is believed to have been roughly one-half mile (1 km) wide, striking with a force equivalent to 11 trillion tons (9.9 trillion tonnes) of TNT.

Isachsen believes it is possible that there may be significant hydrocarbon deposits, often associated with ancient buried impact craters, very deep beneath the mountain.

In 2004, the European Space Agency's Mars Express probe found an analogous circular plateau in the Solis Planum region of the Thaumasia Planum area of Mars. While it has not yet eroded as Panther has, both are an example of inverted relief.

Forests

Panther's forests are for the most part typical of the Catskills, with beech-birch-maple northern hardwood forests on its lower slopes giving way to boreal forests of balsam fir and red spruce above 3,500 feet (1,100 m) on the mountain. While the lower slopes were logged in the 19th century, particularly for Eastern hemlock bark and its tannin, the upper mountain remains in first growth. According to Catskill forest historian Michael Kudish, there is a rare virgin spruce grove near the summit. There are also two open areas visible from the summit on a knob known as Beech Flat, one of about two acres (8,000 m²) at 2,740 feet (835 m) and another of 5–7 acres (2–3 ha) at 2,848 feet (868 m), are totally natural, resulting from the absence of soil in those areas.

Human history

It is not known who first climbed Panther, due to the sketchy records kept by early inhabitants of the area. Farming, Kudish found, went much lower on Panther (1,613 feet (492 m) on average) than it did elsewhere in the Catskills, due to the steep slopes at the mountain's base. Later logging climbed to a higher elevation, particularly near the hamlets of Big Indian and Phoenicia due to nearby train stations (Garfield Mountain's summit does not appear to be in first growth).

The proximity of the railroad led to another common Catskill industry of the time, bluestone quarrying. Kudish has found several along the northern edge of the mountain and suspects there may be more.

The Fox Hollow-Panther-Giant Ledge Trail across the mountain used by hikers to reach the summit today was cut in 1935, based on a contemporary Conservation Department pamphlet. The Fox Hollow Lean-To was built the next year.

Approaches

Panther is traversed by the blue-blazed Fox Hollow-Panther-Giant Ledge Trail (GP), which runs north-south from Fox Hollow down to a junction with the yellow-blazed Phoenicia-East Branch (P-EB) Trail 0.5 mile (1 km) south of Giant Ledge. The vast majority of attempts on the mountain use this route.

The shorter southern approach is much more popular due not only to its brevity but the excellent views available from Giant Ledge. The northern approach, however, is not without some views of its own. Sometimes the entire 7.5-mile (12 km) GP trail, plus the route to the Giant Ledge trailhead or Woodland Valley State Campground, will be hiked as an overnight backpack, with one of the designated campsites along the trail being use, and cars parked at both ends.

Panther and Giant Ledge from near the summit of Slide

Southern route

Hikers typically park at the trailhead lot, 2,100 feet (641 m) in elevation, where Ulster County Route 47 bends sharply about three-quarters of a mile (1.3 km) north of Winnisook Lake, midway up or down the hill between it and Big Indian Hollow. Here the P-EB leaves the road again and leads southeast uphill 0.7 mile (1.1 km) and 500 vertical feet (150 m) to the GP in the level area between the ledge and Slide's north ridge. The former route of the P-EB, now closed, leads downhill to the southwest to its former route across the Winnisook Club.

Turning north on the GP, the trail remains level, passing an official campsite and some muddy spots until it reaches the base of Giant Ledge 0.6 mile (1 km) later, where a good, reliable spring can be found via a short side trail. A climb of 0.15 mile (240 m) up the steep, rocky south slope of the ledge, sometimes assisted by rock steps, levels out at 3,200 feet (975 m), where the trail stays close to the east side. There are many viewpoints from the cliff tops here that take in the nearby Burroughs Range (Slide, Wittenberg and Cornell) to the south; the valley of Woodland Creek below with a small area of Ashokan Reservoir; and the Devil's Path to the northeast. There are more campsites, often likely to be taken early on good summer weekends.

The Devil's Path from Panther's summit.

The trail remains on the ledge for 0.3 mile (500 m), then drops down again more gently on the north slope. Not too long after reaching level ground, the 720-foot (219 m) climb up Panther proper begins. At first the trail gently switches back up some rocky stretches of the mountain's south slope, then at 0.75-mile (1.21 km) from the ledge, a short side trail leads to an excellent viewpoint over the Burroughs Range at about 3,300 feet (1,000 m). Another 0.2 mile (400 m) further, the trail passes a grassy area that has been home to a less reliable spring in the past. Not too far beyond, in the middle of two steep, rocky chutes, the trail passes the sign marking 3,500 feet (1,067 m) in elevation, above which open fires are forbidden and camping is only permitted in winter, due to the fragile high-montane environment. The trail levels off gently but there is still almost 0.5 mile (1 km) to the small ledge with a view to the northeast that marks the summit.

Via this route, it is 3.2 miles (5.1 km) to the summit. Total vertical gain is 1,920 feet (585 m); net is 1,720 feet (524 m), due to the presence of Giant Ledge along the trail. However, some more experienced hikers sometimes bushwhack around the base of the ledge to save themselves this extra vertical if they do not want to take in the views.

Northern route

The GP trail's northern end begins at a small parking area at the end of Fox Hollow Road, 1.5 mile (2.5 km) south of NY 28 at 1,420 feet (433 m) in elevation. At 0.4 mile (640 m) from that trailhead, a short side trail leads to the Fox Hollow lean-to and a reliable spring.

The trail then begins to climb the long ridge of Panther, finally reaching the first (3,480-foot; 1,061 m) of two false summits after 2.7 miles (4.3 km). A short descent follows, then another climb to the second false summit 0.6 mile (1 km) to the south. Along the

way there is an excellent view of the peaks to the west: Balsam, Fir and Big Indian. It is another 1.2 mile (1.9 km) and a steeper climb to the actual summit.

Total distance via this route is 4.9 miles (7.9 km). Total vertical ascent is 2,450 feet (747 m).

Chapter- 5

Devonian Life

Aglaophyton

Aglaophyton
Fossil range: Early Devonian

Reconstruction of *Aglaophyton*, illustrating bifurcating axes with terminal sporangia, and rhizoids.

Scientific classification	
Kingdom:	Plantae
Division:	unspecified
Class:	unspecified
Order:	unspecified
Family:	unspecified
Genus:	***Aglaophyton***
Species:	***A. major***

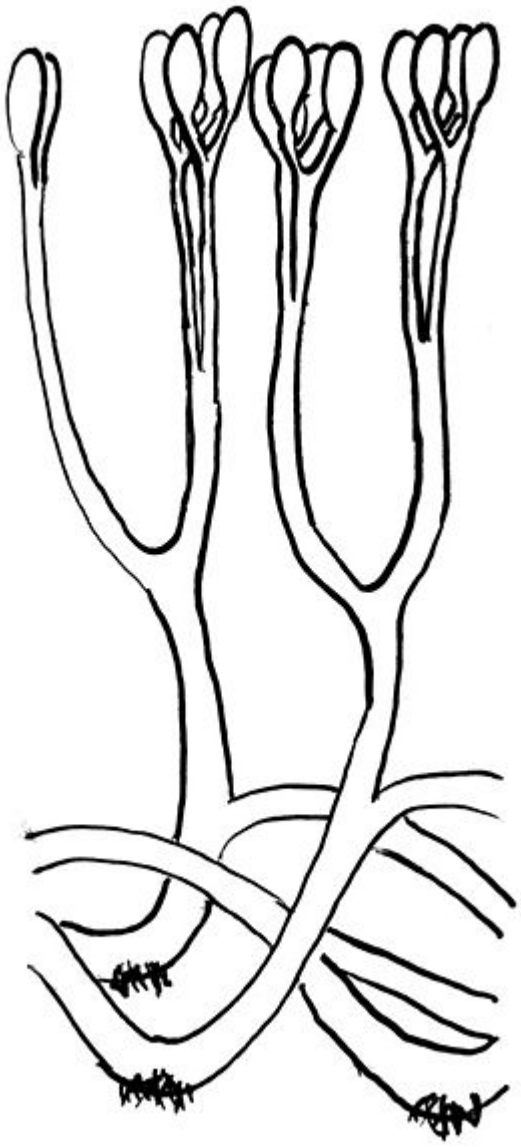
Binomial name

Aglaophyton major

Synonyms

Rhynia major

Aglaophyton major was the sporophyte generation of diplohaplontic, pre-vascular, axial, free-sporing land plant of the Lower Devonian that had anatomical features intermediate between those of the bryophytes and vascular plants or tracheophytes.



A. major was first described by Kidston and Lang in 1920 as the new species *Rhynia major*. The species is known only from the Rhynie chert in Aberdeenshire, Scotland, where it grew in the vicinity of a silica-rich hot spring, together with a number of associated vascular plants such as a smaller species *Rhynia gwynne-vaughanii* which may be interpreted as a representative of the ancestors of modern vascular plants and *Asteroxylon mackei*, which was an ancestor of modern clubmosses (Lycopsida).

Description

Aglaophyton major

The stems of *Aglaophyton* were round in cross-section, smooth, unornamented, and up to about 6mm in diameter. Kidston and Lang interpreted the plant as growing upright, to about 50 cm in height, but Edwards has re-interpreted it as having prostrate habit, with shorter aerial axes of about 15 cm height. The axes branched dichotomously, the aerial axes branching at a comparatively wide angle of up to 90^{o}, and were terminated with elliptical, thick-walled sporangia containing many identical spores (isospores) bearing trilete marks. The spores may therefore be interpreted as meiospores, the product of meiotic divisions, and thus the plants described by Edwards and Kidston and Lang were diploid, sporophytes. The plant was originally interpreted as a tracheophyte, because the stem has a simple central vascular cylinder or protostele , but more recent interpretations in the light of additional data indicated that *Rhynia major* had water-conducting tissue lacking the secondary thickening bars seen in the xylem of *Rhynia gwynne-vaughanii*, more like the water-conducting system (hydrome) of moss sporophytes. Edwards demoted the species to the status of a non-vascular plant and re-named it *Aglaophyton major*.

Aglaophyton is among the first plants known to have had a mycorrhizal relationship with fungi , which formed arbuscules in a well-defined zone in the cortex of its stems. *Aglaophyton* lacked roots, and like other rootless land plants of the Silurian and early

Devonian may have relied on mycorrhizal fungi for acquisition of water and nutrients from the soil.

The male gametophyte of the species has been formally described, which was assigned to a new form taxon *Lyonophyton rhyniensis*, but is now properly referred to as an *Aglaophyton* gametophyte. The Rhynie chert bears many examples of male and female gametophytes, which are loosely similar in their construction to the sporophyte phase, down to bearing rhizoids.

Archaeopteris

Archaeopteris
Fossil range: Late Devonian - Early Carboniferous

Archaeopteris hibernica

Scientific classification	
Kingdom:	Plantae
Division:	†Progymnospermophyta
Order:	Archaeopteridales
Family:	Archaeopteridaceae
Genus:	***Archaeopteris*** Dawson (1871)

Species

- ***A. fissilis***
- ***A. halliana***
- ***A. hibernica***
- ***A. macilenta***
- ***A. obtusa***

Archaeopteris is an extinct genus of tree-like plants with fern-like leaves. A useful index fossil, this tree is found in strata dating from the Upper Devonian to Lower Carboniferous, and has a global distribution.

Until the 2007 discovery of *Wattieza*, many scientists considered *Archaeopteris* to be the earliest known tree. Bearing buds, reinforced branch joints, and branched trunks similar to today's timber, it is more reminiscent of modern seed-bearing trees than other spore bearing taxa; It combines characteristics of woody trees and herbaceous ferns, and belongs to a group of extinct plants sometimes called the progymnosperms, plants with gymnosperm-like wood but that produce spores rather than seeds.

Anatomy

The trees of this genus were small to medium in size with leafy foliage reminiscent of some conifers. The large fronds were thickly set with fan-shaped leaflets on stems that inclined sharply upward. They typically grew to 10 m in height. Some species are large, with trunks that exceeded 1.5 m in diameter. The veining branches diverged dichotomously. There was also intermediate feathering at each frond node or axes.

Leafy shoots occurred in opposite arrangement in a single plane. The leaflets, or pinnules, overlapped one another and were subcircular to wedge-shaped. On fertile branches, the leaves were replaced by spore capsules.

Other modern adaptations

Aside from its woody trunk, *Archaeopteris* possessed other modern adaptations to light interception and perhaps to seasonality as well. The large umbrella of fronds seems to have been quite optimized for light interception at the canopy level. In some species, the pinnules were shaped and oriented to avoid shading one another. There is evidence that whole fronds were shed together as single units, perhaps seasonally like modern deciduous foliage or like trees in the cypress family Cupressaceae.

The plant had nodal zones that would have been important sites for the subsequent development of lateral roots and branches. Some branches were latent and adventitious, similar to those produced by living trees that eventually develop into roots. Before this time, shallow, rhizomatous roots had been the norm, but with *Archaeopteris*, deeper root systems were being developed that could support ever higher growth.

Habitat

Evidence indicates that *Archaeopteris* preferred wet soils, growing close to river systems and in flood plain woodlands. It would have formed a significant part of the canopy vegetation of early forests. Speaking of the first appearance of *Archaeopteris* on the world-scene, Stephen Scheckler, a professor of biology and geological sciences at Virginia Polytechnic Institute, says, "When [Archaeopteris] appears, it very quickly became the dominant tree all over the Earth. On all of the land areas that were habitable, they all had this tree".

Scheckler believes that *Archaeopteris* had a major role in transforming its environment. "Its litter fed the streams and was a major factor in the evolution of freshwater fishes, whose numbers and varieties exploded in that time, and influenced the evolution of other marine ecosystems. It was the first plant to produce an extensive root system, so had a profound impact on soil chemistry. And once these ecosystem changes happened, they were changed for all time. It was a one-time thing."

Looking roughly like a top-heavy Christmas tree, *Archaeopteris* may have played a part in the transformation of Earth's climate during the Devonian before becoming extinct within a short period of time at the beginning of the Carboniferous period.

Relationship to conifers

Because *Archaeopteris* reproduced by releasing spores rather than by producing seeds, paleobotanists suspect that modern trees come from a sibling line of plants they call the "progymnosperms". *Archaeopteris* is more like an ancient cousin than a direct ancestor.

Discovery and classification

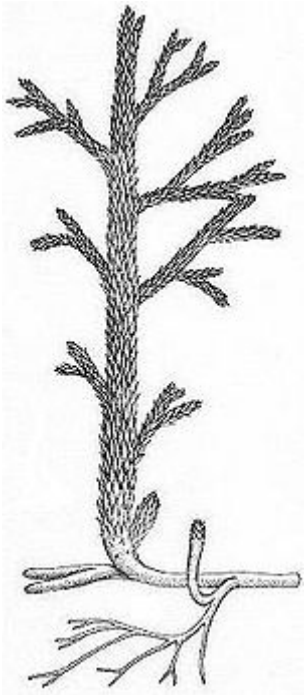
Archaeopteris was originally classified as a fern, and it remained classified so for over 100 years. In 1911, Russian paleontologist Mikhail Dimitrievich Zalessky described a new type of petrified wood from the Donetz Basin in Russia. He called the wood *Callixylon*, though he did not find any structures other than the trunk. The similarity to conifer wood was recognized. It was also noted that ferns of the genus *Archaeopteris* were often found associated with fossils of *Callixylon*.

In the 1960s, paleontologist Charles B. Beck was able to demonstrate that the fossil wood known as *Callixylon* and the leaves known as *Archaeopteris* were actually part of the same plant. It was a plant with a mixture of characteristics not seen in any living plant, a link between true gymnosperms and ferns.

The genus *Archaeopteris* is placed in the order Archaeopteridales and family Archaeopteridaceae. The name is similar to that of the first known feathered bird, *Archaeopteryx*, but in this case refers to the feather-like nature of the plant's fronds.

Asteroxylon

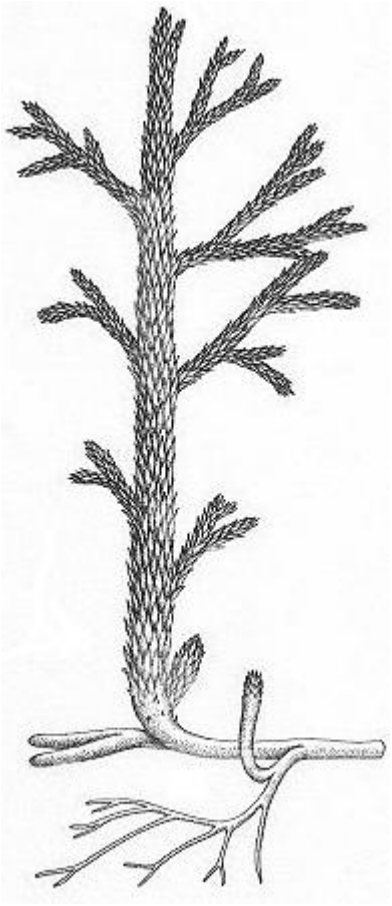
Asteroxylon
Fossil range: Early Devonian



Scientific classification

Kingdom:	Plantae
Division:	Lycopodiophyta
Class:	Lycopodiopsida
Order:	Drepanophycales
Family:	Asteroxylaceae
Genus:	*Asteroxylon* Kidston & Lang 1920
Species:	*Asteroxylon mackiei* Kidston & Lang (Type species)

Asteroxylon ("star-shaped xylem") is an extinct genus of plants of the Division Lycopodiophyta known from anatomically preserved specimens in an Early Devonian deposit of chert at Rhynie, Aberdeenshire in North-East Scotland that has been dated at 396 +/- 8million years old . *Asteroxylon* is probably a stem group to the Drepanophycaceae.



Description

Asteroxylon is a terrestrial genus of vascular plant which flourished in the Early Devonian period. Dichotomously branching stems, which reached 12 mm in diameter and 40 cm in length, were erect, rising from a ground-running organ, from which also protruded underground "rhizoids" or "roots": these reached a depth of up to 20 cm below the surface. An actinostelic vascular bundle occupied the centre of the axes, with tracheids being of primitive annular or helical type (so-called G-type). "Leaves" – not true leaves, but protrusions – were of the form of unbranched strap-shaped enations up to 5 mm long; a single vascular trace branched from the main bundle in the centre of the stem to terminate at the base of each enation. Enations and axes bore stomata.

Asteroxylon differs from externally similar genera of the same period, *Drepanophycus* and *Baragwanathia*, as the vascular thread proceeding well into the leaf in these genera.

Cladoxylopsid

Cladoxylopsida Fossil range: Middle Devonian

Wattieza
Scientific classification
Kingdom: Plantae
Division: Pteridophyta
Class: **Cladoxylopsida**

The **cladoxylopsids** are a group of plants known only as fossils that are thought to be ancestors of ferns and horsetails.

They had a central trunk, from the top of which several lateral branches were attached. Fossils of these plants originate in the Devonian and Carboniferous periods, mostly just as stems.

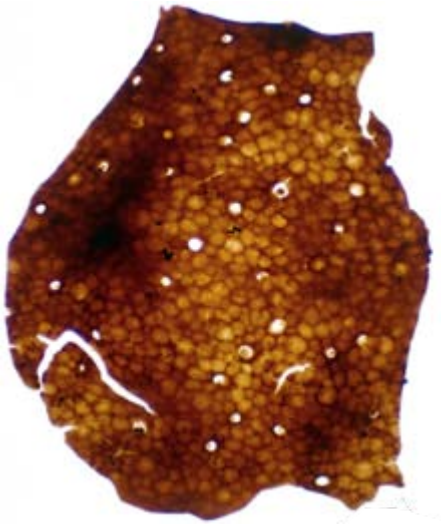
Taxonomy is still uncertain, the major taxon being *Cladoxylopsida* which includes two orders, *Cladoxylales* and *Hyeniales*

Intact fossils of the Middle Devonian cladoxylopsid *Wattieza* show it to have been a tree, the earliest identified in the fossil record as of 2007.

Cosmochlaina

Cosmochlaina Fossil range: 424–410 Ma
PreЄ
Є
O
S
D
C

P
T
J
K
Pg
N
Upper Silurian – lowermost Devonian



Cuticle of Cosmochlaina, retrieved from the Burgsvik beds by acid maceration. Cells about 12 µm in diameter.

Scientific classification

Kingdom:	Plantae (?)
Phylum:	Nematophyta
Class:	†Nematophytina
Order:	†Nematophytales
Family:	†Nematothalaceae Strother 1993
Genus:	***Cosmochlaina*** Edwards 1986

Species

- *C. verruculosus*

  (May be a typo, in Taylor 1988)

- *C. verrucosa* (Type)
- *C. maculata*
- *C. physema*
- *C. Versiformis*

(All defined by EDWARDS 1986)

Cosmochlaina (from Greek: kosmos=ornament; xlaina=wrapper/cloak) is a form genus of nematophyte – an early (Siluran – Devonian) plant known only from fossil cuticles, often found in association with tubular structures. Where *Nematothallus* is sometimes used to relate only to tube-like structures, *Cosmochlaina* refers to the cuticle fragments. The form genus was put forwards by Dianne Edwards, and is diagnosed by inwards-pointing flanges and randomly oriented pseudo-cellular units. Projections on the outer surface are always present, and sometimes also appear on the inner surface; however, the surface of the cuticle itself is always smooth. The holes in the cuticle are often covered by round flaps, loosely attached along a side.

It has been suggested that the pores of Cosmochlaina represent broken-off rhizoids, on the basis that the rotting and maceration of extant liverworts produces a similar perforated texture. However, the status of this form genus in any one kingdom is not secure; members could, for example, represent arthropod cuticle. Alternatively, different species may in fact represent different parts of the same organism.

Drepanophycus spinaeformis

Drepanophycus spinaeformis	
Scientific classification	
Kingdom:	Plantae
Division:	Lycopodiophyta
Class:	Lycopodiopsida
Order:	Drepanophycales
Family:	Drepanophycaceae
Genus:	*Drepanophycus*
Species:	***D. spinaeformis*** †
Binomial name	
Drepanophycus spinaeformis Göppert	

Drepanophycus spinaeformis is an extinct species of small Lycopodium-like plant which lived 410 to 390 million years ago in the early Devonian period of the Paleozoic era. First discovered in Scotland, *D. spinaeformis* remains have since been recovered in Russia (around Lake Shunet in the republic of Khakassia), in the Yunnan province of the People's Republic of China, and in Egypt. They were among the earliest land plants.

Description

The plants grew to approximately 80 cm in height and are notably differentiated from other plants in the *Drepanophycus* genus by their thicker stems. Foliage is described as firm and spiny, though recovered fossils rarely retain leaf detail. The stomata of *D. spinaeformis* look similar to that of *Lycopodium japonicum*. They both consist of two large guard cells and pore, and are anomocytic. There were two small guard cells surrounded by two large similarly shaped subsidiary cells (paracytic) deriving from a pronounced elliptical cuticular ledge on the surface of the guard cells surrounding a thickened circumporal area.

Nematothallus

Nematothallus
Fossil range: Ludfordian–Downtonian
PreЄ
Є
O
S
D
C
P
T
J
K
Pg
N

Scientific classification

Kingdom: Plantae (?)

Phylum: Nematophyta

Class: †Nematophytina Strother 1993

Order: †Nematophytales Lang 1937

Family: **†Nematothalaceae** Strother 1993

Genus: ***Nematothallus*** Lang 1937

Species

N. pseudo-vasculosa Lang 1937

N. radiata Lang 1937

N. lobata Strother 1988

N. thaiti Strother 1988

Nematothallus is a form genus comprising cuticle-like fossils.

History of research

Nematothallus was first described by Lang in 1937 , who envisioned it being an early thallose land plant with tubular features and sporophytes, covered by a cuticle which preserved impressions of the underlying cells. He had found abundant disaggregated remains of all three features, none of which were connected to another, leaving his reconstruction of the phytodebris as parts of a single organism highly conjectural.

Further work failed to draw together all aspects of the organism: Edwards (1982) and Edwards and Rose (1984) both provided thorough descriptions of the cuticular aspects of the plants, while Pratt *et al.* (1978) and Niklas and Smocovitis (1983) focused on the anatomy of the tubes. Indeed, some workers suggested that the name *Nematothallus* should only apply to the tubes, until Strother (1993) found more complete specimens, with tubes attached to the cuticle. He attempted to unite and formalise the genus, and extended it to include banded tubes, which are instead referred to as nematoclasts (Graham & Gray 2001).

It is possible that *Nematothallus* consisted of two layers of cuticle, although fossils giving this impression may in fact represent two layers which happened to overlap one another and become stuck. It is not readily established what the cuticle represents. Lang (1945) had it as an epidermal layer, similar to the waxy cuticle of plants today, covering a parenchymatous layer. Alternatively, Edwards (1982) proposed that the inner tissue of *Nematothallus* comprised stringy tubes, with the cellular patterning produced by their ends.

The genus was later formalised by Strother, who discovered better preserved and more complete specimens in Pennsylvania, America – which appear to show tubes connected to the rims of cuticle. *Nematothallus* is widespread from the late Silurian, but similar cuticle is reported from the Caradoc epoch (late Ordovician, 450 million years ago). It is, however, difficult to distinguish *Nematothallus* cuticle from that of arthropods.

Further work by Edwards and Rose has identified oval-shaped growths in places on the cuticles of a limited number of *Nematothallus* fragments, which develop into holes – whose purpose is unknown. Since they are not found in all *Nematothallus* individuals, it is unlikely that they were involved in gas exchange – perhaps they were involved in the release of spores? One fossil gives the impression, which may well be an illusion, of spores being trapped between two layers of cuticle.

Habitat

Nematothallus was originally recovered from the Red Downtonian near the base of the Old Red Sandstone, between the clearly marine Ludlow deposits beneath it, and the unambiguously terrestrial Lower Old Red Sandstone. Further samples came from

elsewhere in the Lower Old Red Sandstone (St Maughams Group, lowermost Devonian), where the co-occur with plant spores. Additional, older material occurs with *Hostinella*, *Cooksonia* and *Steganotheca* in the Ludlow (upper Ludfordian) Whitcliffe formation.

Affinity

There is a possibility that the genus represents a lichen, rather than a plant – although this is not yet supported by firm evidence. The biochemistry of the organism is not inconsistent with an algal affinity, but Edwards (1982) considers it unlikely that algae would be preserved as coalified impressions. However, Edwards does note that the surface patterning could have been produced in a similar fashion to surface layers in green algae – that is, by the ends of tightly packed filaments causing indentation on the surface layer. (Just because they were formed in the same way doesn't mean they were formed by green algae, though.)

Ornatifilum

Ornatifilum
Fossil range: Late Silurian (Wenlock) - Early Devonian (Lochkovian)

An *Ornatifilum*-like fossil, identical to those described by Sherwood-Pike and Gray (1985). 250 μm long.

O. lornensis from the Silurian of Kerrera, Scotland. 200 µm long.

Scientific classification	
Kingdom:	?Fungi
Phylum:	?Ascomycetes
Genus:	***Ornatifilum*** Burgess & Edwards 1991

Species

- *O. granulatum* (type)

  BURGESS & EDWARDS 1991

- *O. lornensis*

  WELLMAN 1995

Ornatifilum (Latin *ornatis* + *filum*, Ornamented filament) is an artificial form genus, which is used to categorise any small, branched filaments with external ornamentation. It has been applied to microfossils of Devonian age with possible fungal affinities; two "species" have been described, and further Silurian fossils closely resemble it. These Silurian specimens hint that the organisms may have been fungal, placing them among the oldest representatives of this kingdom.

Background

The form genus *Ornatifilum* was erected by Burgess and Edwards in 1991 to describe tubular fossils retrieved by acid maceration from the late Silurian. It was originally intended as a form genus, to facilitate stratigraphy and environmental reconstruction; the fossils do not display enough features to classify them confidently, even at a kingdom level.

The organisms comprise tubes of around 10 µm diameter, with an ornamented, granular surface texture. These fossils were compared to late Silurian (Ludlow epoch) fossils

retrieved from the Burgsvik beds by Sherwood-Pike and Gray, and the genus was used when similar fossils were recovered from the Scottish island of Kerrera by Charles Wellman ten years later. Similar, unornamented filaments are known from the USA.

O. granulatum

The type species of the genus consists of flattened filaments - perhaps an artefact resulting from post-burial pressure. Their branching is typically at obtuse angles; the irregularly sized grana, which ornament their surfaces, are concentrated at branching points. They are often found as individuals, but sometimes group together into "wefts", as Wellman has termed them. The filaments are septate, with the septa looking like "pinch points" where the tube is slightly constricted - like a twisted balloon. No sign of perforation was visible in the septa; perforate spores are only found in red algae and fungi, but their absence does not preclude their presence in one of these groups: indeed the perforations are difficult to see or image. There are no other diagnostic features of this species that allow classification in any group. Surface ornamentation is a common convergent feature, found for example in liverwort rhizoids and some fungi, so does not help in classification. The specimens recovered are most common in near-shore environments; however, they are never abundant.

O. lornensis

This species has a more complex appearance than *O. granatum*. For a start, its surface ornament - which covers most of the surface uniformly - takes an array of forms, with "grana, coni, spinae verrucae and occasionally plia" present. Further, side-branches and the flask-shaped protuberances occasionally protrude from the tubes, on which the ornament is larger (2.5 μm rather than ~1 μm). Such branching typically occurs in pairs across the main thread.

Sherwood-Pike and Gray's "fungus"

Ornatifilum is compared extensively to microfossil remains recovered from the Ludlow of Gotland by Sherwood-Pike and Gray. These fossils, which have never been formally described, had less prominent grana, but the vase-shaped protrubences are very similar to those exhibited by *O. lornensis*.

These fossils allow a classification to be suggested. Firstly, they possess punctate spores, which as mentioned earlier restricts their affinities to the red algae and fungi. Further circumstantial evidence made a fungal affinity look more likely: firstly, they were found in association with fungal spores; further, a "1:1 correlation" was observed with trilete spores diagnostic of land plants. Whilst such spores could easily have been blown or washed into the sea, Sherwood-Pike and Gray consider this correlation to imply a terrestrial habit of the fossils; as the red algæ are solely marine, this would only leave the fungi - dominantly terrestrial today, but with high diversity in marine settings too - as a

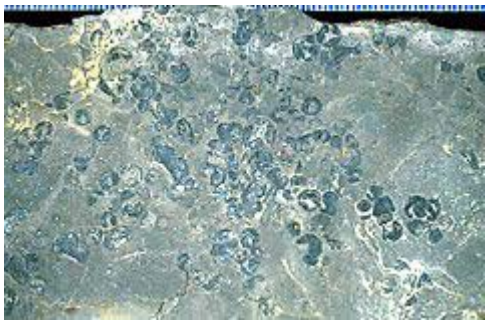
possible home. Further suggesting a fungal connection, the fossils were found in association with spores that could be assigned to the ascomycetous fungi.

Other early fungi

A rich diversity of fungi is known from the lower Devonian Rhynie chert, but the previous record is absent. Since fungi don't biomineralise, they do not readily enter the fossil record; aside from *Ornatifilum*, there are only two other claims of early fungi. One from the Ordovician has been dismissed on the grounds that it lacks any distinctly fungal features, and is held by many to be contamination; the position of a "probable" Proterozoic fungus is still not established, and it may represent a stem group fungus. If the case for *Ornatifilum*'s fungal affinity were affirmed, that would make it the oldest known fossil fungus - although, since the fungi form a sister group to the animals, the two lineages must have diverged before the first animal lineages, which are known from fossils as early as the Ediacaran.

Protosalvinia

Protosalvinia
Fossil range: Late Devonian



A fossil of *Protosalvinia furcata* from Devonian shale of Kentucky, USA.

Scientific classification	
Kingdom:	Plantae
Phylum:	*incertae sedis*
Genus:	†***Protosalvinia***

Species
Protosalvinia arnoldii †
Protosalvinia braziliensis †
Protosalvinia furcata †
Protosalvinia ravenna †

Synonyms
Foerstia

Protosalvinia is a prehistoric plant found commonly in shale from shoreline habitats of the Upper Devonian period. The name *Protosalvinia* is a misnomer. The name literally means *early Salvinia*, and was given in the erroneous belief that the fossils were an earlier form of the living aquatic fern *Salvinia*. It is no longer believed that the fossils come from a fern, but deciding exactly what the fossils represent is still a matter of debate. This is surprising when one considers how much is known about the fossils.

The most likely interpretation of *Protosalvinia* is that it represents either a fossil liverwort or brown alga, although no definitive brown algae have been identified from before the Tertiary period, and examination of the spore structure shows no features in common with living groups of brown algae. The living plant was a thallus with short dichotomous branching. The branches in the largest species were as much as one centimeter across. In some fossils, the branching lobes lie flat, but in others the tips of the branches are curled up over the fossil, giving it a round outline. Embedded in the tissues of the thallus are chambers in which spores (200 micrometre diameter) were produced by meiosis.

Microscope slide mount of *Protosalvinia sp.* showing bifurcating thallus.

Because *Protosalvinia* is usually preserved as a compression fossil, it can be difficult to determine whether its anatomy is more like a plant or an alga. Some biochemical evidence favors interpretation as an alga. Lignin and cutin have been found in the thalli, and sporopollenin in the spore walls. [:64] The grouping of the spores found in the thallus favors interpretation as a plant. The absence of any stomata on the surface is inconclusive, as all bryophytes lack stomata on the main body of the plant.

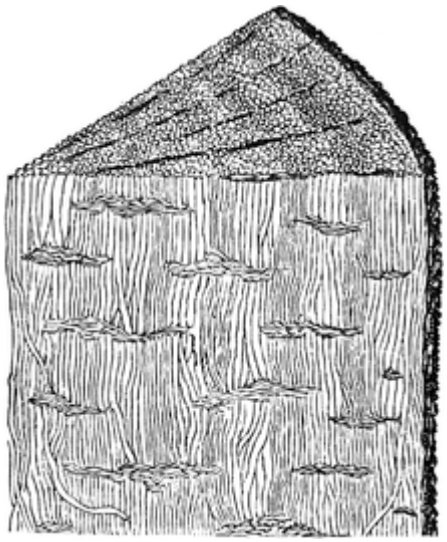
However, the tips of *Protosalvinia* branches show evidence of conceptacle-like dips. [:64]

Protosalvinia is found in association with conodont elements.

For the present, the relationships of *Protosalvinia* remain uncertain.

Prototaxites

Prototaxites
Fossil range: 420–370 Ma
Late Silurian to Upper Devonian



An 1888 illustration of *Prototaxites* in section.

Scientific classification	
Kingdom:	Incertae sedis
Genus:	***Prototaxites*** Dawson, 1859

Species

- *P. loganii*

  DAWSON 1859

- *P. southworthii*

  ARNOLD 1952

Synonyms

- *Nematophycus*
- *Nematophyton*

The genus ***Prototaxites*** describes terrestrial organisms known only from fossils dating from the Silu-Devonian, approximately 420 to 370 million years ago. *Prototaxites* formed large trunk-like structures up to 1 metre (3 ft) wide, reaching 8 metres (26 ft) in

height, made up of interwoven tubes just 50 micrometres (0.0020 in) in diameter. Whilst traditionally very difficult to assign to an extant group of organisms, current opinion is converging to a fungal placement for the genus. It might have had an algal symbiont, which would make it a lichen rather than a fungus in the strict sense.

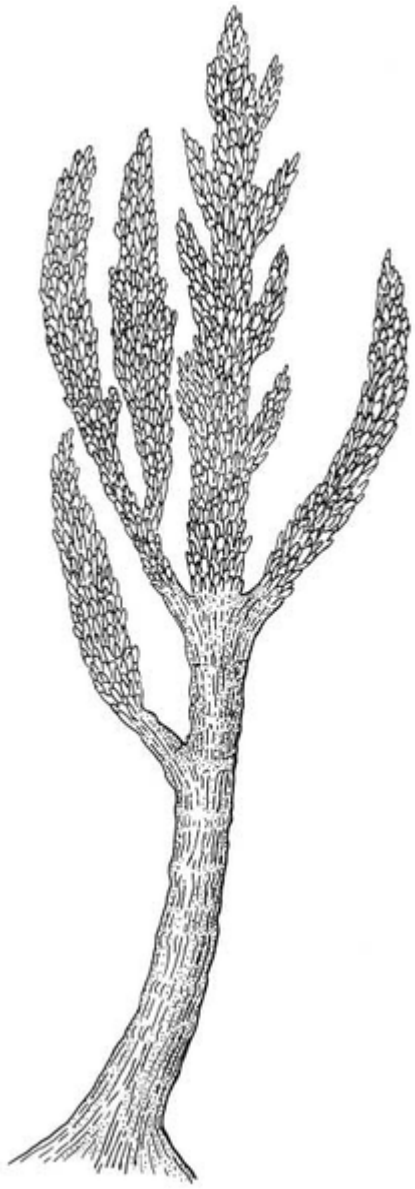
An opposing view has been presented that *Prototaxites* was not a fungus but consisted of enrolled liverwort mats with associated cyanobacteria and fungal tubular elements.

Morphology

With a diameter of up to a meter, and a height reaching 8 m, *Prototaxites* fossils are by far the largest from its period of existence. Viewed from afar, the fossils take the form of tree-trunks, spreading slightly near their base in a fashion that suggests a connection to unpreserved root-like structures. Infilled casts which may represent the "roots" of *Prototaxites* are common in early Devonian strata. Concentric growth rings, sometimes containing embedded plant material, suggest that the organism grew sporadically by the addition of external layers. It is probable that the preserved "trunks" represent the fruiting body, or "sporophore", of a fungus, which would have been fuelled by a net ("mycelium") of dispersed filaments ("hyphae"). On a microscopic scale, the fossils consist of narrow tube-like structures, which weave around one another. These come in two types: skeletal "tubes", 20–50 μm across, have thick (2–6 μm) walls and are undivided for their length, and generative "filaments", which are thinner (5–10 μm diameter) and branch frequently; these mesh together to form the organism's matrix. These thinner filaments are septate – that is to say, they bear internal walls. These septa are perforate - i.e. they contain a pore, a trait only present in the modern red algae and fungi.

The similarity of these tubes to structures in early plant *Nematothallus* has led to suggestions that the latter may represent leaves of *Nematothallus*. Unfortunately for this hypothesis, the two have never been found in connection, although this may be a consequence of their detachment after the organisms' death.

History of research



Dawson's 1888 reconstruction of a conifer-like *Prototaxites*

First collected in 1843, it was not until 14 years later that John William Dawson, a Canadian scientist, studied *Prototaxites* fossils, which he described as partially rotten giant conifers, containing the remains of the fungi which had been decomposing them. This concept was not disputed until 1872, when a rival scientist named Carruthers poured ridicule on the idea. Such was his fervour that he rebuked the name *Prototaxites* (loosely translated as "first yew") and insisted that the name ***Nematophycus*** ("stringy alga ") be adopted, a move strongly against scientific convention. Dawson fought adamantly to defend his original interpretation until studies of the microstructure made it clear that his position was untenable, whence he promptly attempted to rename the genus himself (to ***Nematophyton***, "stringy plant"), denying with great clout that he'd ever considered it to be a tree. Despite these political attempts to re-name the genus, the rules of botanical

nomenclature mean that the name "*Prototaxites*", however inappropriate in meaning, remains in use today.

Despite the overwhelming evidence that the organism grew on land, Carruthers' interpretation that it was a giant marine alga was challenged just the once, in 1919, when Church suggested that Carruthers had been too quick to rule out the possibility of the fungi. The lack of any characters diagnostic of any extant group made the presentation of a firm hypothesis difficult, and so the fossil remained an enigmatic mystery and subject of debate. It was not until 2001, after 20 years of research, that Francis Hueber, of Washington's National Museum of Natural History, published a long-awaited paper which attempted to put *Prototaxites* in its place. The paper deduced, based on its morphology, that *Prototaxites* was a fungus.

This idea was faced with disbelief, denial and strong scepticism, but further evidence is emerging to support it. In 2007, isotopic analyses by a team including Hueber and Kevin Boyce of the University of Chicago concluded that *Prototaxites* was a giant fungus. They detected a highly variable range of values of carbon isotope ratios in a range of *Prototaxites* specimens; autotrophs (organisms such as plants and algae, that make a living via photosynthesis) living at the same time draw on the same (atmospheric) source of carbon; as organisms of the same type share the same chemical machinery, they reflect this atmospheric composition with a constant carbon isotope trace. The inconsistent ratio observed in *Prototaxites* appears to show that the organism did not survive by photosynthesis, and Boyce's team deduce that the organism fed on a range of substrates, such as the remains of whichever other organisms were nearby.

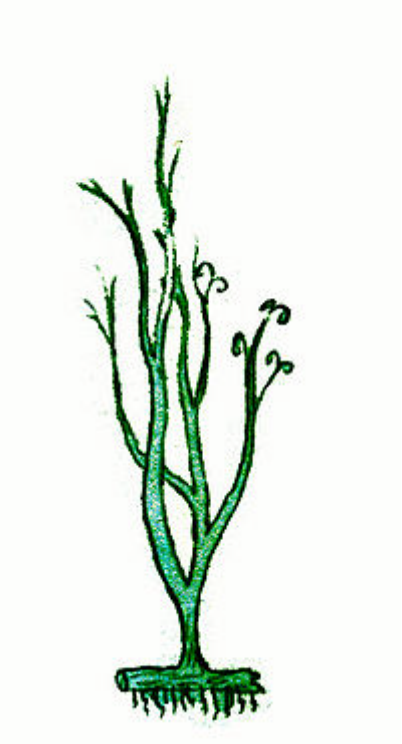
Ecological context

This organism would have been the tallest living thing in its day by far; the plant *Cooksonia* (pictured in navigational box below) only reached 1 m, and itself towered over the "moss forests"; invertebrates were the only other land-dwelling life. *Prototaxites* became extinct as shrubs and vascular trees rose to prominence. The organism could have used its raised platform for spore dispersal, or, if *Prototaxites* really did form leaves, in competition for light. The University of Chicago research team has it reconstructed as a branchless, columnal structure. The presence of bio-molecules often associated with the algae may suggest that the organism was covered by symbiotic (or parasitic) algae, or even that it was an alga itself.

Prototaxites mycelia (strands) have been fossilised invading the tissue of vascular plants; in turn, there is evidence of animals inhabiting *Prototaxites*: mazes of tubes have been found within some specimens, with the fungus re-growing into the voids, leading to speculation that the organisms' extinction may have been caused by such activity; however, evidence of arthropod borings in *Prototaxites* has been found from the early and late Devonian, suggesting the organism survived the duress of boring for many millions of years. Intriguingly, *Prototaxites* is bored long before plants developed a structurally equivalent woody stem, and it is possible that the borers transferred to plants when these evolved.

Psilophyton

Psilophyton
Fossil range: Devonian



Psilophyton princeps

Scientific classification

Kingdom: Plantae
Division: Trimerophytophyta
Genus: ***Psilophyton*** †

Psilophyton is a fossil genus which currently contains seven species known mostly from compression, impression and some permineralized anatomy. Most specimens come from northern Maine, Gaspé Bay in Quebec, New Brunswick and the Czech Republic. *P. princeps*, *P. forbesii*, *P. dapsile*, *P. charientos*, *P. dawsonii*, *P. microspinosum*, *P. kräuselii* and *P. crenulatum* are the currently accepted members of the genus Psilophyton. Variation within the genus is significant. . The average specimen was 60 cm or more tall.

Pteridospermatophyta

Pteridospermatophyta
Fossil range: Carboniferous-Permian

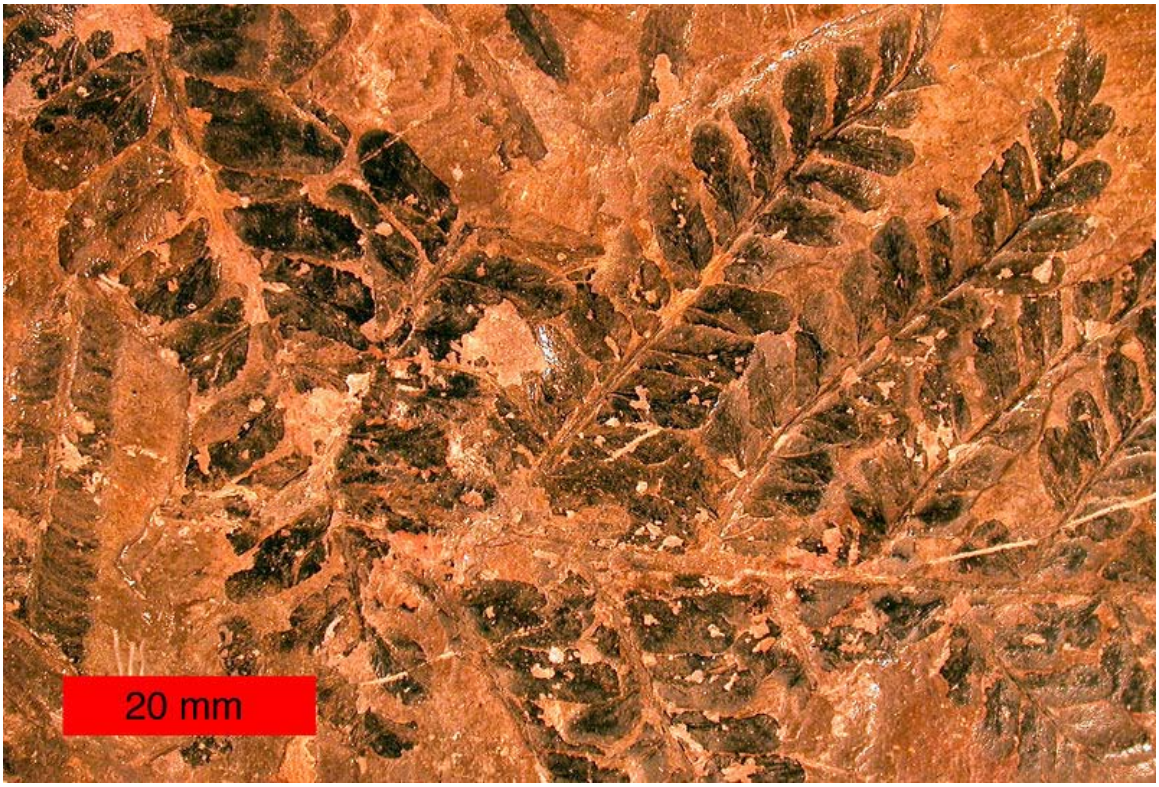
Fossil seed fern leaves from the Late Carboniferous of northeastern Ohio.

Scientific classification	
Domain:	Eukaryota
(unranked):	Archaeplastida
Kingdom:	Plantae

Orders

- Arberiales (= "Glossopteridales")
- Calamopityales
- Callistophytales
- Corystospermales
- Gigantopteridaceae
- Leptostrobales
- Lyginopteridales
- Medullosales
- Peltaspermales

The term **Pteridospermatophyta** (or "**seed ferns**") refers to several distinct groups of extinct seed plants (spermatophytes). The oldest fossil evidence of plants of this type is of late Devonian age, and they flourished particularly during the Carboniferous and Permian periods. Pteridosperms declined during the Mesozoic Era and had mostly disappeared by the end of the Cretaceous Period, though some fossil pteridosperm-like plants seem to have survived into Eocene times in Tasmania.



The concept of the pteridosperms goes back to the late 19th century when palaeobotanists came to realise that many Carboniferous fossils resembling fern fronds had anatomical features more reminiscent of the modern-day seed plants the cycads. The German palaeobotanist Henry Potonié coined the term "Cycadofilices" for such fossils, suggesting that they were a group of non-seed plants intermediate between the ferns and cycads. Shortly afterwards, the British palaeobotanists Frank Oliver and Dukinfield Henry Scott (with the assistance of Oliver's student at the time Marie Stopes) made the critical discovery that some of these fronds (*Lyginopteris*) were associated with seeds (*Lagenostoma*) that had identical and very distinctive glandular hairs, and concluded that the fronds and seeds belonged to the same plants. Soon, additional evidence came to light suggesting that seeds were also attached to the Carboniferous fern-like fronds *Dicksonites*, *Neuropteris* and *Aneimites*. Initially it was still thought that they were intermediate between the ferns and cycads, and especially in the English-speaking world they were referred to as "seed ferns" or "pteridosperms". Today, most palaeobotanists regard them as being only distantly related to ferns and that these names are misleading, but the names have nevertheless "stuck". Nowadays, four orders of Palaeozoic seed plants tend to be referred to as pteridosperms: Lyginopteridales, Medullosales, Callistophytales and Peltaspermales.

Their discovery attracted considerable attention at the time as the pteridosperms were the first extinct group of vascular plants to be identified solely from the fossil record. In the 19th century the Carboniferous Period was often referred to as the "Age of Ferns" but these discoveries during the first decade of the 20th century made it clear that the "Age of Pteridosperms" was perhaps a better description.

Later during the 20th century, the concept of pteridosperms was expanded to include various Mesozoic groups of seed plants with fern-like fronds, such as the Corystospermales and Leptostrobales. Some palaeobotanists also included seed plant groups with entire leaves such as the glossopterids (Arberiales) and Gigantopteridales, which was clearly stretching the concept. In the context of modern phylogenetic models, the groups often referred to as pteridosperms appear to be liberally spread across a range of clades and many palaeobotanists today would regard pteridosperms as little more than a paraphyletic 'grade-group'. One of the few characters that may unify the group is that the ovules were borne in a cupule, but this has not been confirmed for all "pteridosperm" groups.

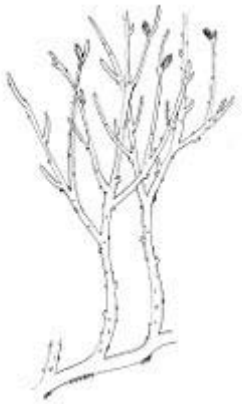
So, does the concept of pteridosperms have any value today? Many palaeobotanists still use the term in an informal sense for the seed plants that are not angiosperms, coniferoids (conifers or cordaites), ginkgophytes or cycadophytes (cycads or bennettites). This is particularly useful for extinct seed plant groups, whose systematic relationships remain speculative; we can call them pteridosperms with no implications being made as to their systematic affinities. Also, from a purely curatorial or collecting perspective the term pteridosperms is a useful shorthand for describing the fern-like fronds that were probably produced by seed plants, which are commonly found in many Palaeozoic and Mesozoic fossil floras

The following Orders of seed plants are often referred to as pteridosperms:

- Arberiales (= "Glossopteridales")
- Calamopityales
- Callistophytales
- Corystospermales
- Gigantopteridales
- Leptostrobales
- Lyginopteridales
- Medullosales
- Peltaspermales

Rhynia

Rhynia
Fossil range: Early Devonian



Reconstruction of *Rhynia gwynne-vaughanii*, redrawn after

Scientific classification

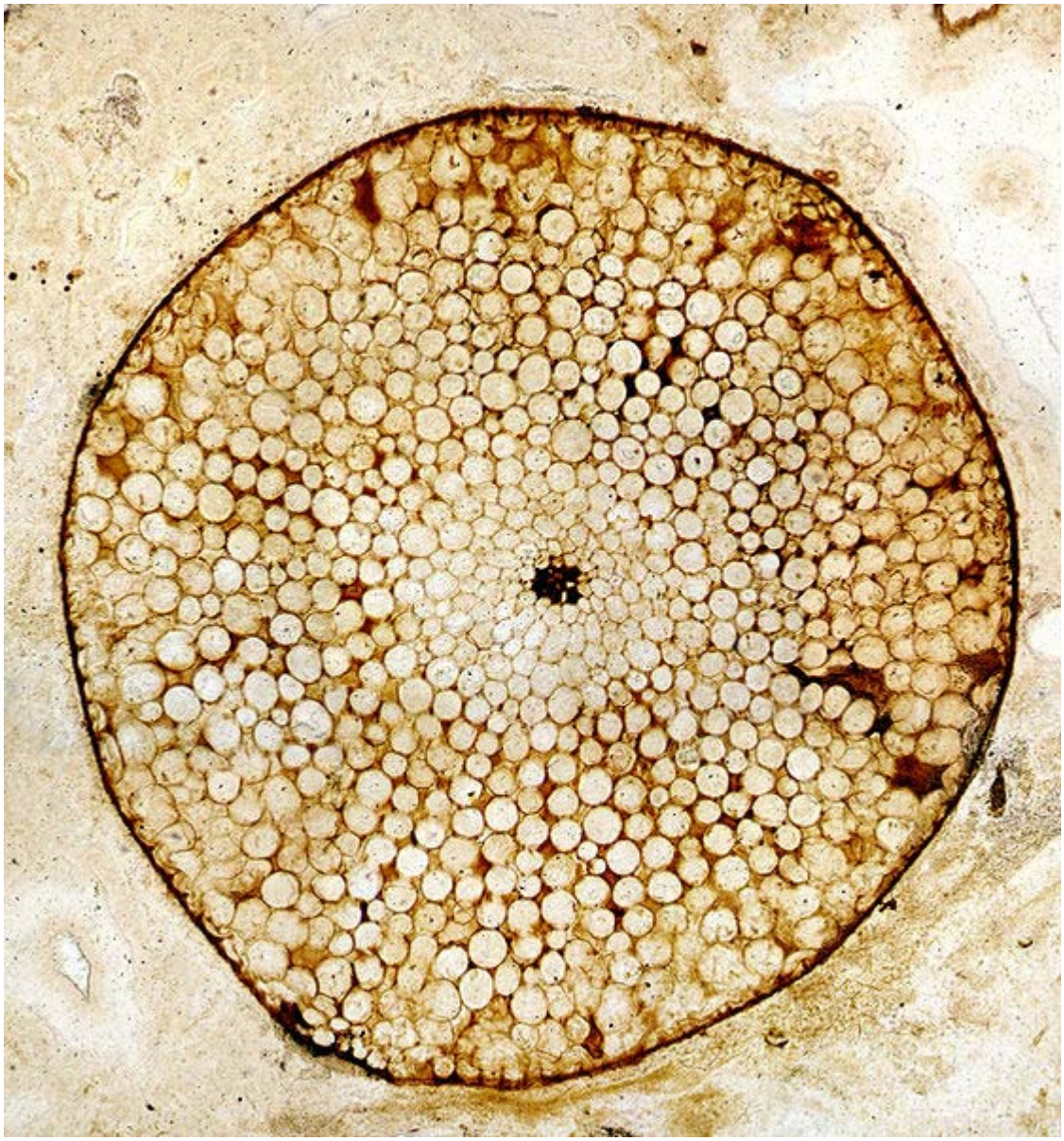
Kingdom:	Plantae
Division:	Rhyniophyta
Class:	Rhyniopsida
Order:	Rhyniales
Family:	Rhyniaceae
Genus:	***Rhynia*** Kidston & Lang (1917)
Species:	***R. gwynne-vaughanii***

Binomial name

Rhynia gwynne-vaughanii Kidston & Lang (1917)

Rhynia gwynne-vaughanii was the sporophyte generation of a vascular, axial, free-sporing diplohaplontic embryophytic land plant of the Lower Devonian that had anatomical features more advanced than those of the bryophytes, and was basal to modern vascular plants or eutracheophytes.

R. gwynne-vaughanii was first described as a new species by Kidston and Lang in 1917. The species is known only from the Rhynie chert in Aberdeenshire, Scotland, where it grew in the vicinity of a silica-rich hot spring. *Rhynia* was a vascular plant, and grew in association with other vascular plants such as *Asteroxylon mackei*, a probable ancestor of modern clubmosses (Lycopsida), and with pre-vascular plants such as *Aglaophyton major*, which is interpreted as basal to true vascular plants.



A transverse section of a stem of *Rhynia gwynne-vaughanii*, Lower Devonian, Rhynie chert

Rhynia is thought to have had deciduous lateral branches, which it used to disperse laterally over the substrate and stands of the plant may therefore have been clonal populations.

Evidence of the gametophyte generation of *Rhynia* has been described in the form of crowded tufts of diminutive stems only a few mm in height, with the form genus name *Remyophyton delicatum*. Like those of *Aglaophyton major*, *Horneophyton lignieri* and *Nothia aphylla* the gametophytes of *Rhynia* are dioicous, bearing male and female gametangia (antheridia and archegonia) on different axes. A significant finding is that the

axes were vascular, unlike almost all of the gametophytes of modern pteridophytes except for that of Psilotum.

Spongiophyton

Spongiophyton was a thallose fossil of the early to mid Devonian, which is notoriously difficult to classify.

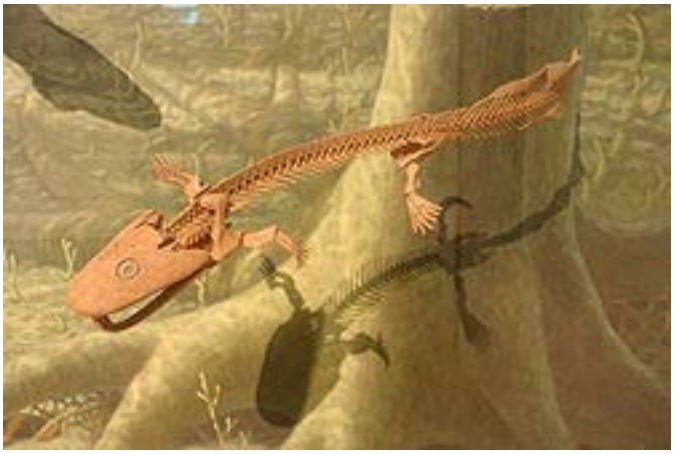
Spongiophyton displayed dichotomous branching, and a flattened/elliptical cross section with a thick (20–80 μm) upper cuticular surface. It is also perforated with pores resembling those of some liverworts. It probably grew on the banks of rivers. *Spongiophyton* has been mistakenly interpreted as tree resin and lycopod cuticle, and was later identified as the cuticle of a thalloid plant. It has most recently been interpreted on morphological and isotopic grounds as a lichen - which would make it the earliest known representative of this group.

The significance of the isotopic data has, however, been called into question. Jahren *et al.* argued that mosses and liverworts had a $\delta^{13}C$ signature of under −26‰, and lichens were exclusively > −26‰. But in deducing this they relied solely on their own data, neglecting to include published datasets or bryophytes from a wide range of habitats. They also failed to take into account any adjustment necessary to overcome post-burial alteration of the $\delta^{13}C$, or to compensate for the different isotopic composition of the early Devonian atmosphere. Repeating Jahren's experiments with these factors taken into account shows that most major groups' $\delta^{13}C$ values overlap significantly, and do not provide a statistically significant case for the inclusion of *Spongiophyton* in any group.

Chapter- 6

Devonian Animals

Acanthostega

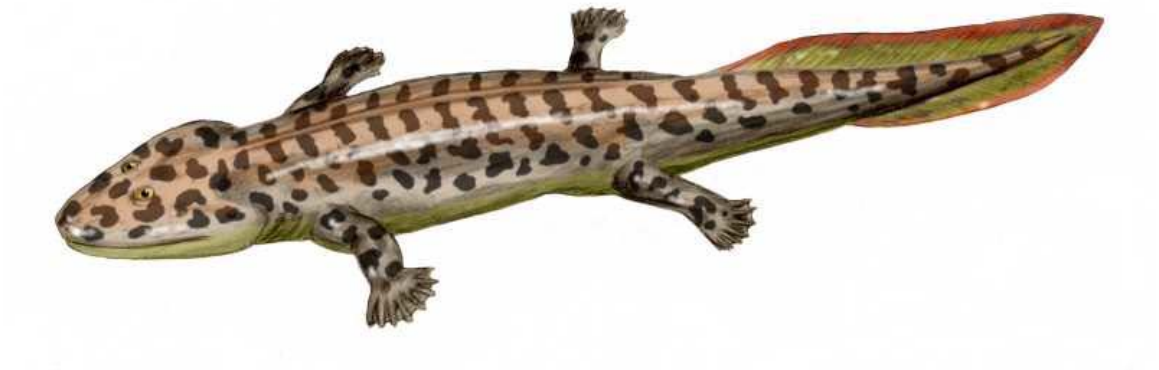
Acanthostega **Fossil range: 365 Ma** **Late Devonian**	
	
Acanthostega gunnari skeleton reconstruction	
Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Amphibia
Order:	Ichthyostegalia
Family:	Acanthostegidae
Gemus:	**Acanthostega**
Binomial name	
Acanthostega gunnari Jarvik, 1952	

Acanthostega (meaning **Spiny Roof**) is an extinct labyrinthodont genus, among the first vertebrate animals to have recognizable limbs. It appeared in the Upper Devonian

(Famennian) about 365 million years ago, and was anatomically intermediate between lobe-finned fishes and the first tetrapods fully capable of coming onto land.

Description

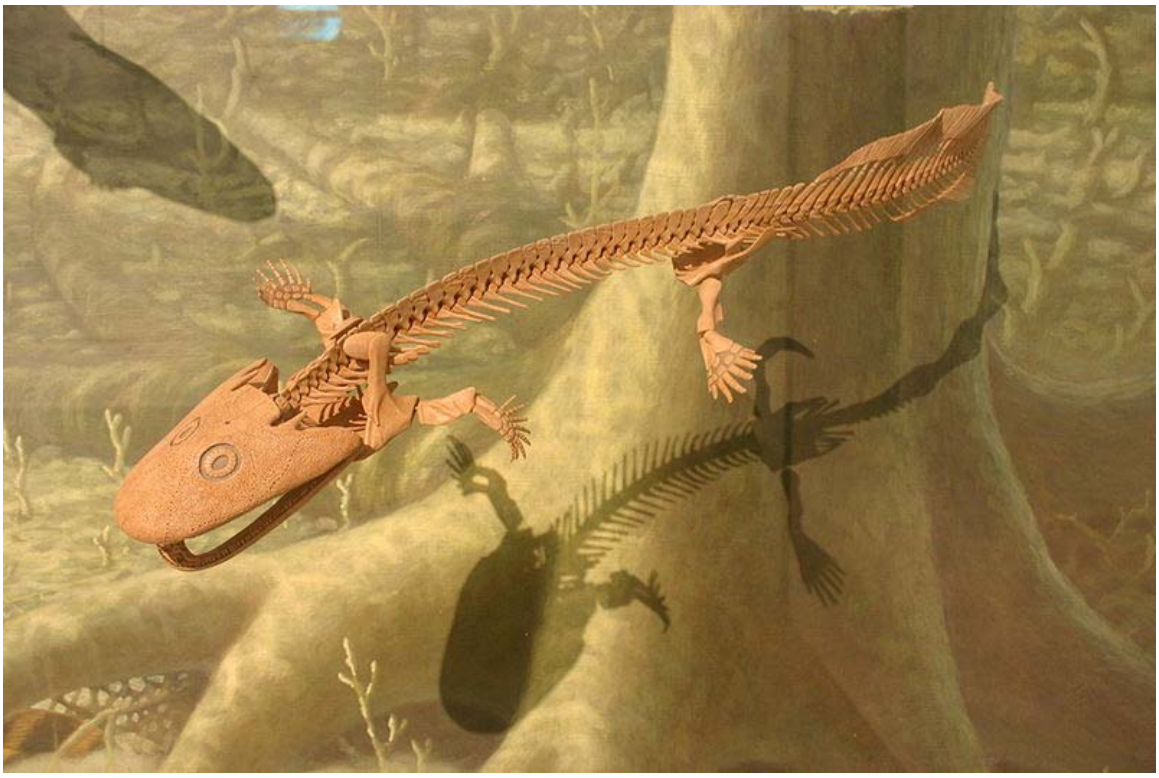
Skull of *Acanthostega gunnari*.



Restoration

It had eight digits on each hand (the number of digits on the feet is unclear) linked by webbing, it lacked wrists, and was generally poorly adapted to come onto land. *Acanthostega* also had a remarkably fish-like shoulder and forelimb. The front foot of *Acanthostega* could not bend forward at the elbow, and thus could not be brought into a weight bearing position, appearing to be more suitable for paddling or for holding on to aquatic plants. It had lungs, but its ribs were too short to give support to its chest cavity

out of water, and it also had gills which were internal and covered like those of fish, not external and naked like those of some modern amphibians which are almost wholly aquatic. Acanthostega is the first tetrapod to show the shift in locomotory dominance from the pectoral to pelvic girdle. There are many morphological changes that allowed the pelvic girdle of Acanthostega to become a weight-bearing structure. In more ancestral states the two sides of the girdle were not attached. In Acanthostega there in contact between the two dies and fusion of the girdle with the sacral rib of the vertebral column. These fusions would have made the pelvic region more powerful and equipped to counter the force of gravity when not supported by the buoyancy of and aquatic environment.



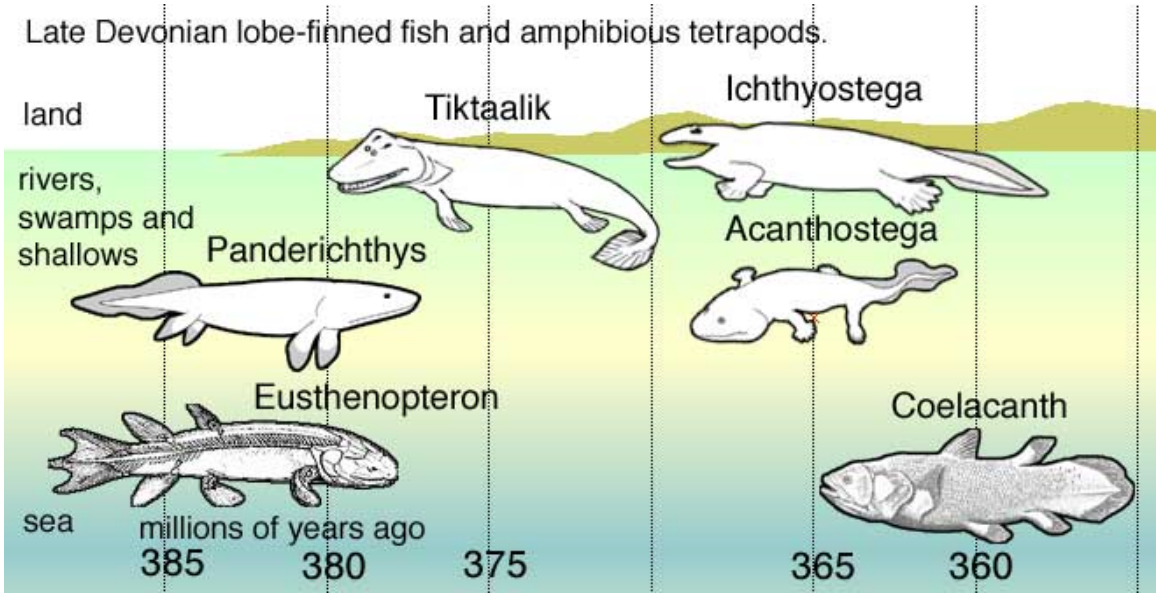
Therefore, paleontologists surmise that it probably lived in shallow, weed-choked swamps, the legs having evolved for some other purpose than walking on land. Jennifer A. Clack interprets this as showing that this was primarily an aquatic creature descended from fish that had never left the sea, and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

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

Discovery

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

Related species



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

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

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

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

Aciculopoda

Aciculopoda mapesi **Fossil range: Famennian**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Crustacea
Class:	Malacostraca
Order:	Decapoda
Suborder:	Dendrobranchiata
Superfamily:	Penaeoidea
Family:	**Aciculopodidae** Feldmann & Schweitzer, 2010
Genus:	***Aciculopoda*** Feldmann & Schweitzer, 2010
Species:	***A. mapesi***
Binomial name	
Aciculopoda mapesi Feldmann & Schweitzer, 2010	

Aciculopoda is an extinct prawn which existed in what is now Oklahoma approximately 360 million years ago. It was described in 2010 on the basis of a single fossil from Oklahoma. The single species, ***Aciculopoda mapesi***, was named by Rodney Feldmann and Carrie Schweitzer in honour of Royal Mapes, a paleontologist who discovered the type specimen. It is only the third unambiguous fossil decapod from before the Mesozoic.

Discovery

The fossil was discovered in the Woodford Shale, exposed at the Ryan Quarry, in Pontotoc County, Oklahoma. The Woodford Shale is a dark-colored siliceous shale which outcrops to the north-east and the south-west of the Arbuckle Mountains in Oklahoma. It contains "radiolarians, conodonts, sponge spicules, ammonoid and nautiloid cephalopods, inarticulate brachiopods [...] and small phyllocarid arthropods", and spans the Devonian–Carboniferous boundary. The strata which produced *Aciculopoda* are thought on the basis of conodont biostratigraphy to be from the Famennian.

Description

The holotype of *Aciculopoda mapesi* is housed at the United States National Museum as lot USNM 540766. The animal is 68.8 mm (2.71 in) long, of which the anterior 31 mm (1.2 in) is the cephalothorax. The pleon (abdomen) is around 62 mm (2.4 in) long, along its curved dorsal margin, and about 9 mm (0.35 in) deep at its base. The cuticle is missing from the pleon, exposing the well-preserved muscles beneath.

Etymology

The genus name *Aciculopoda* derives from the Latin roots *acicula* ("needle") and "*poda*" ("foot"), referring to the sharp spines on the pereiopods. The specific epithet commemorates Royal Mapes, who discovered the specimen and has published widely on fossil crustaceans.

Interpretation

The only unambiguous decapod fossil older than *Aciculopoda* is *Palaeopalaemon newberryi*, found in Devonian sediments in Ohio. (The assignment of *Imocaris* to the Decapoda is the subject of some debate.) The fact that both *Aciculopoda* and *Palaeopalaemon* were discovered in the United States led Feldmann & Schweitzer to suggest that their common ancestor, the most recent common ancestor of the Decapoda may also have originated in the ancient continent Laurentia.

Acutiramus

Acutiramus
Fossil range: Late Silurian–Early Devonian

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Chelicerata
Class:	Merostomata
Family:	Pterygotidae
Genus:	***Acutiramus*** Ruedemann, 1935

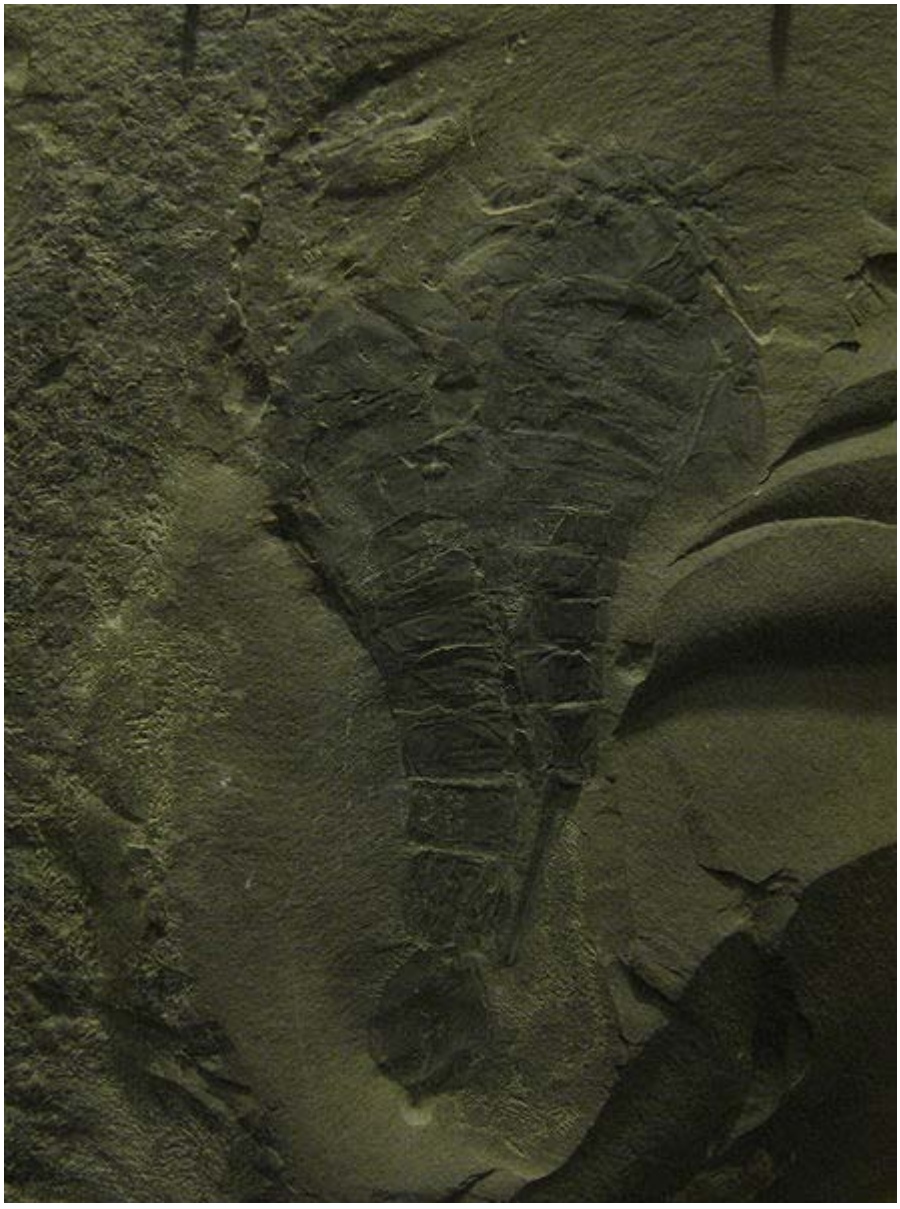
Species

- *A. bohemicus* Barrande, 1872
- *A. buffaloensis* Pohlman, 1881
- *A. cummingsi*
- *A. macrophthalmus*

Acutiramus is an extinct genus of eurypterid which lived in the Late Silurian (Ludlow) to Early Devonian.

Acutiramus was one of the largest eurypterids with pincers 5 cm and length about 2 m. It was related to another large eurypterid, *Pterygotus*.

Description



Eurypterids *Acutiramus buffaloensis* and *Eurypterus remipes* on display at Schiele Museum of Natural History, Gastonia, North Carolina

Pterygotidae, which lived from the Ordovician to Devonian Eras, were characterized by small to large exoskeletons with semilunar scales. The telson, (tail) was expanded, or flatter than it was tall. Pterygotidae also had chelicerae (claws in front of the mouth) that were large and long, with strong, well developed teeth on the claws. Their walking legs were small and slender, without spines.

Acutiramus is distinguishable from other Pterygotidae by the distal margin of the chelae, where the final tooth is at an acute angle to the rest of the claw (hence the name *Acutiramus*, or "acute arm"). The large tooth in the center of the claw is distally inclined, which is to say it points forwards. The prosoma (head) is subquadrate, with compound eyes located at the edge of the front corners. The telson has a low row of knobs running down its center.

Species

- ***Acutiramus*** Ruedemann, 1935
  - *Acutiramus bohemicus* (Barrande, 1872) — Silurian, Czech Republic
    - = *Pterygotus* comes Barrande, 1872 — Silurian, Czech Republic
    - = *Pterygotus mediocris* Barrande, 1872 — Silurian, Czech Republic
    - = *Pterygotus blahai* Semper, 1898 — Silurian, Czech Republic
    - = *Pterygotus fissus* Seemann, 1906 — Silurian, Czech Republic
  - *Acutiramus cummingsi* (Grote & Pitt, 1875) — Silurian USA & Canada
    - = *Pterygotus acuticaudatus* Pohlman, 1882 — Silurian, USA
    - = *Pterygotus buffaloensis* Pohlman, 1881 — Silurian, USA
    - = *Pterygotus quadraticaudatus* Pohlman, 1882 — Silurian, USA
  - *Acutiramus floweri* Kjellesvig-Waering & Caster, 1955 — Silurian, USA
  - *Acutiramus macrophthalmus* (Hall, 1859) — Silurian USA & Canada
    - = *Pterygotus osborni* Hall, 1859 — Silurian , USA
    - = *Pterygotus cobbi* var. juvenis Clarke & Ruedemann, 1912 — Silurian, USA
  - *Acutiramus perneri* Chlupáč, 1994 — Devonian, Czech Republic
  - *Acutiramus perryensis* Leutze, 1958 — Silurian, USA
  - *Acutiramus suwanneensis* Kjellesvig-Waering, 1955 — Silurian?, USA

Agoniatitida

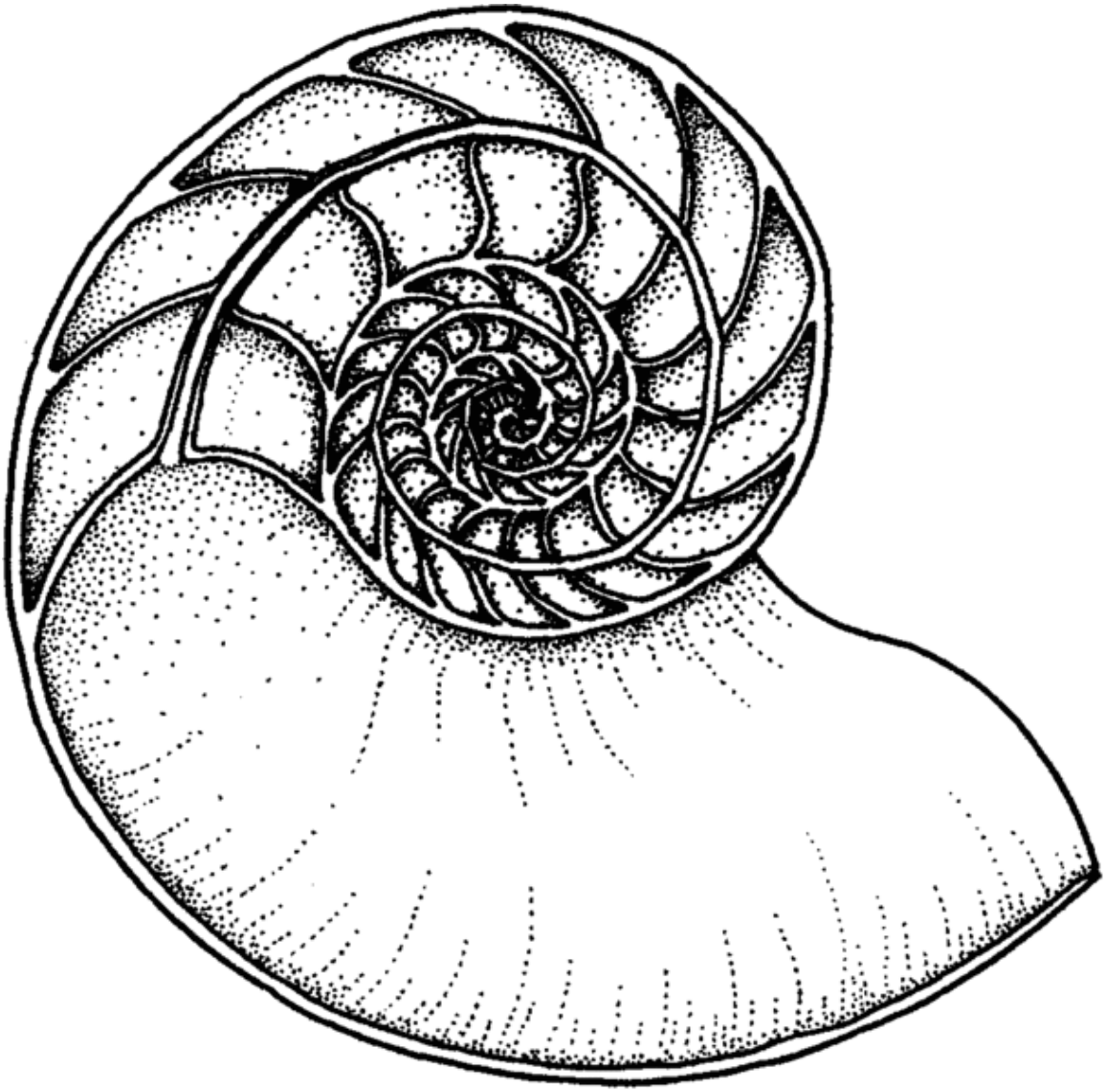
Agoniatitida **Fossil range: L-M Devonian**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	Ammonoidea
Order:	**Agoniatitida** Ruzhencev, 1957

Agoniatitida, also known as the **Anarcestida**, is the ancestral order within the cephalopod Subclass Ammonoidea, that lived in what would become Africa, Asia, Australia, Europe, and North America during the Devonian from about 410—385 mya, existing for approximately 25 million years.

Taxonomic Nomenclature

The Order Agoniatitida, named by Ruzhencev, 1957, is a subjective synonym for the Order Anarcestida, named by Miller and Furnish, 1954. Accordingly the name Anarcerstida is based on the family Anarcestidae (ex Anarcestinae) of Steinmann 1890. That of Agoniatiida is based on the family Agnoniatidae of Holzapfel, 1899.

Saunders, Work, and Nikolaeva, 1999, refer to the Anarcestida, with Agoniatina a suborder, maintaining the priority as found in the Treatise. Shevyrev, 2006 on the other hand follows Ruzhencev, 1957 and used Agonititida.



An image showing the siphuncle, the tube which connects the current living shell to the previous ones.

Morphology

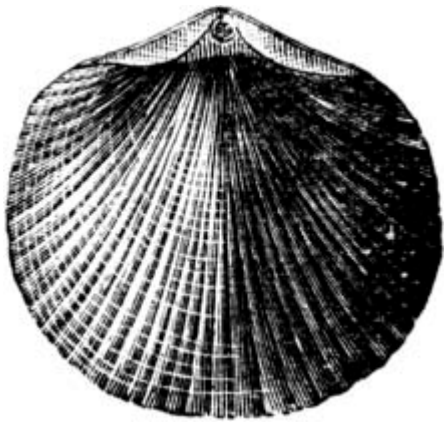
Agoniatitida are primitive ammonoids with a ventral retrochoanitic siphuncle (septal necks point to the rear) reflective of their nautiloid ancestors.and goniatitic sutures with a variable number of lobes. Shells vary from discoidal to globular. Coiling may be loose with whorls barely touching or tight with a dorsal impression.

Fossil distribution

Fossils were restricted to the strata of the Zlichovian to Famennian ages.

Atrypa

Atrypa
Fossil range: Late Ordovician - Carboniferous



Atrypa reticularis

Scientific classification	
Kingdom:	Animalia
Phylum:	Brachiopoda
Order:	Atrypida
Genus:	***Atrypa***

Atrypa aka **lamp shell** is an extinct genus of brachiopod that lived from the Late Ordovician (444 million years ago) to the Carboniferous (318 million years ago) and occurs abundantly as fossils in marine rocks. It has a wide distribution on all the continents except Antarctica.

The genus has distinctive concentric growth lines and is unusual in that in some Devonian beds there are numerous remains of the pedicle valve, but extremely few of the brachial valve.

Dawsonoceratidae

Dawsonoceratidae Fossil range: ?UOrd-?M Dev
Scientific classification
Kingdom: Animalia
Phylum: Mollusca
Class: Cephalopoda
Subclass: Orthoceratoidea
Order: Orthocerida
Family: Dawsonoceratidae Flower (1946)

Dawsonoceratidae is an extinct family of orthoconic nautiloid cephalopods that lived in what would be North America and Europe from the Late Ordovician through the Middle Devonian from about 480–390 mya, existing for approximately 90 million years.

Taxonomic Position

Dawsonoceratidae was named by Flower (1962) and included in the Michelinoceratida. It was assigned to the Orthocerida by Walter Sweet in Teichert et al 1964 as part of the Orthocerataceae. The type genus is *Dawsonoceras*, named by Hyatt in 1883.

Morphology

Dawsonoceratidae are michelinocerids (Orthocerida) with the internal pattern of the Michelinoceratidae except that the siphuncle segments, which are generally tubular, are constricted at the septal foremina (the openings through with the siphuncular tissues pass). This feature is also found in Silurian *Kionoceras*, but less developed. Septal necks are short and generally recumbent. The type genus, *Dawsonoceras* and its close relative *Dawsonocerina* are further characterized by having orthoconic shells with conspicuous annulations, covered by transverse, scalloped or festooned lirae which in some are also longitudinal. Annulations consist of narrow encircling ribs that may be somewhat oblique, separated by generally wider areas in between

Genera

The Dawsonoceratidae comprise six known genera, *Dawsonoceras*, the type, *Anaspyroceras*, *Calocyrtocerina*, *Dawsonocerina*, *Metaspyroceras*, and *Palaeodawsonocerina*.

Anaspyroceras, named by Shimizu and Obata (1935) and *Metaspyroceras*, named by Foeste (1932), were previously included in the orthoceratid subfamily Leuroceratinae, which is no longer considered a valid taxon, and reassigned to the Dawsonoceratidae. *Anaspyroceras* and *Metaspyroceras* differ from Flowers definition of the Dawsonoceratidae in that the septal necks are othochoanitic rather than recumbent and siphuncle segments are without noted constrictions. *Calocyrtocerina*, named by Chen (1981) was originally included in the Paraphragmitidae of Flower and Kummel 1950. *Palaeodawsonocerina* started off as *Spyroceras senckenbergi* Teichert (1932) and redefined by Kroger and Isakar (2006) as the type species of *Paleodawsonocerina* (*P. senckenbergi*)

Dicranurus

Dicranurus
Fossil range: Devonian

Dicranurus monstrosus

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Trilobita
Order:	Lichida Moore, 1959
Family:	Odontopleuridae
Genus:	***Dicranurus***

species

- *D. hamatus*
- *D. elegans*
- *D. monstrosus*

Dicranurus ("Twin head-tail") was a genus of Lower Devonian lichid trilobites that lived in a shallow sea that lay between Euramerica and Gondwanaland, corresponding to modern-day Oklahoma and Morocco, respectively. As such, their fossils are found in Oklahoma and Morocco.

Dicranurus monstrosus fossil

Their bodies averaged about an inch or so, in length, though their large spines made them at least 2 inches in length. It is speculated that such tremendous spines hampered the ability of predators, such as arthrodire placoderms, to attack them, as well as to help prevent them from sinking into the soft mud of their environment. *Dicranurus* trilobites are distinguished from other lichids by the pair of large, curled, horn-like spines that emanate from behind the glabellum. The genus name refers to these distinctive horns, in fact.

Elginerpeton

Elginerpeton
Fossil range: Late Devonian, 395 Ma

Life restoration of *Elginerpeton*

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Class:	Amphibia
Order:	Ichthyostegalia
Family:	Elginerpetontidae
Genus:	***Elginerpeton***

Binomial name
Elginerpeton pancheni
Ahlberg, 1995

Elginerpeton is a monotypic genus of early tetrapod, the fossils of which were recovered from Scat Craig, Scotland, in rocks dating to the late Devonian Period (Frasnian stage, 395 million years ago). The only known fossil has been given the name *Elginerpeton pancheni*.

Elginerpeton is known from a partial skeleton including a partial shoulder and hip, a femur, tibia (lower hind limb), and jaw fragments. It is estimated to have measured about 1.5 m (5 ft) in length.

Orthoceras

Orthoceras
Fossil range: 488–199.6 Ma
Ordovician - Triassic

Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	Nautiloidea
Order:	Orthocerida
Family:	Orthoceratidae
Genus:	***Orthoceras*** Bruguière, 1789

Species

- ***O. regulare*** SCHLOTHEIM 1820

Orthoceras ("straight horn") is a genus of extinct nautiloid cephalopod. This genus is sometimes called *Orthoceratites*. Note it is sometimes misspelled as *Orthocera*, *Orthocerus* or *Orthoceros* (Sweet 1964:K222).

Orthoceras fossils are common and have a global distribution, occurring in any marine rock, especially limestones.

These are slender, elongate shells with the middle of the body chamber transversely constricted, and a subcentral orthochoanitic siphuncle. The surface is ornamented by a network of fine lirae (Sweet 1964:K224). Many other very similar species are included under the genus *Michelinoceras*.

Monospecific assemblages

Artist's reconstruction of *O. regulare*

These orthocone cephalopods are conspicuous in the fossil record for their occasional but persistent appearances in monospecific assemblages dense enough to be rock-forming.

Based on studies of size distributions of the orthocone shells, some scientists have concluded that these assemblages likely represent post-mating mass deaths, as are common among modern cephalopods (though not modern nautiloids) and indeed among many semelparous species. However, such studies have not been entirely convincing and do leave the door open for alternate interpretations. These assemblages, are known mostly from Ordovician rocks but do occur later as well, at least into the Devonian. Well-known examples occur in Morocco, Scandinavia, the Alps, and Iowa (USA).

The Baltic island of Öland off the southern coast of Sweden has many quarries that yield orthocone nautiloids of great beauty. For centuries Öland has supplied greater Europe with material for floors, stairs and grave stones. This hard limestone is durable and the fossil inclusions make it very desirable. Occasionally the chambers of the fossil shells are colored differently. The ground water minerals that percolated the strata during diagenesis determines the color. Greens and browns are most common.

Orthoceras grew to a length of 6 inches (15 centimeters) and fed upon small animals.

History of the name

Originally *Orthoceras* referred to all nautiloids with a straight-shell, called an "orthocone" (Fenton & Fenton 1958:40). But later research on their internal structures,

such as the siphuncle, cameral deposits, and others, showed that these actually belong to a number of groups, even different orders.

In the authoritative Treatise on Invertebrate Paleontology, the name *Orthoceras* is now only used to refer to the type species *O. regulare* (Schlotheim 1820) from the Middle Ordovician of Estonia, Lithuania, Sweden and parts of the former Soviet Union such as Ukraine and Belarus. The genus might include a few related species.

Confusion with *Baculites*

Orthoceras and related orthoconic nautiloid cephalopods are often confused with the superficially similar *Baculites* and related Cretaceous orthoconic ammonoids. Both are long and tubular in form, and both are common items for sale in rock shops (often under each others' names). Both lineages evidently evolved the tubular form independently of one another, and at different times in earth history. *Orthoceras* lived much earlier (Middle Ordovician) than *Baculites* (Late Cretaceous) The two types of fossils can be distinguished by many features, most obvious among which is the suture line: simple in *Orthoceras*, intricately foliated in *Baculites* and related forms.

Mucrospirifer

Mucrospirifer **Fossil range: Devonian**	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Brachiopoda
Class:	Rhynchonellata
Order:	Spiriferida
Family:	Mucrospiriferidae
Genus:	***Mucrospirifer*** Grabau, 1931
Species	

Mucrospirifer is a genus of extinct brachiopod in the class Rhynchonellata (Articulata) and the order Spiriferida. They are sometimes known as "butterfly shells". Like other brachiopods, they were filter feeders. Fossils occur mainly in middle Devonian strata.

The biconvex shell was typically 2.5 cm, but they could grow to 4 cm long. It has a fold, sulcus and costae. It was greatly elongated along the hinge line, which extends outward to form sharp points. This gave them a fin- or wing-like appearance. The apex area (umbo) of the pedicle valve contains a small fold for the pedicle. They lived in muddy marine sediments, and were attached to the sea floor via the pedicle.They sometimes look like two seashells stuck together.

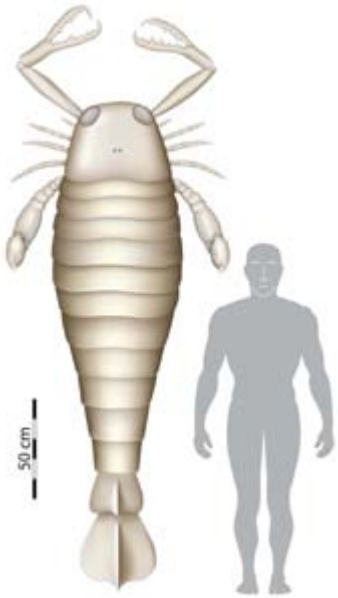
Select species

- *Mucrospirifer albanensis*
- *Mucrospirifer arkonensis*
- *Mucrospirifer bouchardi*
- *Mucrospirifer grabaui*
- *Mucrospirifer medfordsis*
- *Mucrospirifer mucronatus*
- *Mucrospirifer paradoxiformis*
- *Mucrospirifer profundus*
- *Mucrospirifer prolificus*
- *Mucrospirifer refugiensis*
- *Mucrospirifer thedfordensis*

- *Mucrospirifer williamsi*

Jaekelopterus rhenaniae

Jaekelopterus rhenaniae
Fossil range: 390 Ma
Middle Devonian



Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Subphylum:	Chelicerata
Class:	†Eurypterida
Order:	†Pterygotoidea
Family:	†Jaekelopteridae
Genus:	†*Jaekelopterus*
Species:	†***J. rhenaniae***

Binomial name
Jaekelopterus rhenaniae

Jaekelopterus rhenaniae ("Otto Jaekel's wing from the Rhineland") is an extinct species of the Eurypterida (sea scorpions). At an estimated length of 2.5 meters (8.2 feet), it is one of the two largest arthropods ever discovered (the other is a giant millipede-like

animal, *Arthropleura*, although which animal was larger is unclear). The second largest eurypterid known is *Pterygotus*. *Jaekelopterus* lived approximately 390 million years ago. Although called a "sea scorpion", it is speculated to have lived in fresh water rivers and lakes, rather than in saltwater seas. The animal was described by Simon Braddy and Markus Poschmann of the University of Bristol in the journal *Biology Letters* (November 2007); they found a 46 cm chelicera (claw-like mouth part), and estimated the total size of the animal based on the proportions of this claw. When extended, the chelicerae would have added another meter to its length.

The animal's fossilized remains were discovered in the Early Devonian (Emsian) Klerf Formation Lagerstätte of Willwerath near Prüm, Germany.

Ichthyostegidae

Ichthyostega, the nominal genus

The **Ichthyostegidae** is a small family of extinct labyrinthodont amphibian from the Devonian. All members of the family were relatively large animals with primitively polydactyl, paddle-like feet.

Two genera are asigned to the family: the nominal *Ichthyostega* from Greenland and *Hynerpeton* found in Pennsylvania, U.S.A. Bout appear to have been fairly capable on dry land, when compared with the contemporary Acanthostegids.

Walliserops

Walliserops
Fossil range: Devonian

W. trifurcatus

Scientific classification	
Kingdom:	Animalia
Phylum:	Arthropoda
Class:	Trilobita
Order:	Phacopida
Family:	Acastidae
Genus:	***Walliserops***

Type species

W. trifurcatus
Morzadec, 2001

Species

- *W. trifurcatus*
- *W. hammii*
- *W. tridens*

- + 3 undescribed species

Walliserops (named after Prof. O. Walliser of Göttingen) is a genus of spinose phacopid (acastid) trilobite found in Lower to Middle Devonian age rocks from Morocco. All species of *Walliserops* share, and are famous for, the spectacular three-pronged "trident" that rises from the glabella. *Walliserops* is most closely related to the genus *Comura*.

Walliserops was originally erected for a single species, ***W. trifurcatus***. Later, two other species were assigned: ***W. hammii*** & ***W. tridens***. All three currently described species come from the same strata near Foum Zguid in southern Morocco, three as yet un-described species are recorded from other locations.

Early reports of "trident" trilobites and placement within the proposed new genus "*Parabolops*" ("parabola face") - long tridents being placed within "*P. neptunis*", short tridents placed within "*P. hammi*" - were pre-empted by the publication of the detailed analysis of *Walliserops*.

Walliserops trifurcatus

Walliserops hammii

Walliserops tridens

Walliserops n. sp. undescribed species

Departures from bilateral symmetry are an unusual feature within *Walliserops* species, most clearly shown by the curved occipital spine of *W. hammii* taking a noticeable curl to one side. The regular development of these features in multiple specimens suggest a genetically controlled feature of the genus and not mutations or pathology. Most of the exceptions to bilateral symmetry noted (and also the absence of spines on the first two thoracic segments) can be explained by adaptations allowing the trident to be held off the sea floor while walking. Between the species there are variations in the extent of departure from bilateral symmetry: *W. trifurcatus*, with a long trident that is curved away from the seabed, has less obvious departures from bilateral symmetry than *W. hammii*, with a short trident close to the seabed.

The function of the trident itself is poorly understood. With the amount of energy and nutrients expended in growing such a large adornment (probably multiple times as the trilobite shed its skin) its function was clearly important. Although a number of suggestions have been made (e.g. sensory apparatus, disguise or protection), the most satisfactory current explanation is that the trident served as "horns" similar to present day beetles.

Sexual dimorphism was an intriguing prospect (longer trident forms as jousting males) when only two species (or possible dimorphs) were known. With the description of three species from the same location, polymorphism (e.g. caste system in ants and bees) was another prospect but seemed unlikely. Although the presence of horns strongly suggests sexual dimorphism, lack of data on numerous fronts currently prevents firm conclusions from being drawn.

Sexual dimorphism in any trilobite exoskeleton has not yet been satisfactorily

demonstrated and any decision to regard evidence as sexual dimorphism or as subspecific/specific difference(s) will be arbitrary.

— Whittington, 1

Chapter- 7

Devonian Extinctions

Acleistoceras

Acleistoceras **Fossil range: middle Devonian**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	Nautiloidea
Order:	Oncocerida
Family:	Acleistoceratidae
Genus:	***Acleistoceras*** Hyatt 1884

Acleistoceras is a genus of the oncocerid, nautiloid family Acleistoceratidae that lived in the shallow seas that covered much of North America during the Devonian; living from 409—383.7 mya, existing for approximately 25.3 million years.

Taxonomy

Acleistoceras was named by Hyatt (1884) and assigned by Flower (1950) to the newly established Acleistoceratidae which at that time was added to the Oncoceratida. Sepkoski's listing of *Acleistoceras* in the Oncoceratida simply follows Flower (1950) and Teichert & Moore (1964).

Morphology

Acleistoceras has a straight to slightly curved breviconic shell (i.e. is short) with a circular to slightly depressed cross section . The maximum diameter is in the forward part of the phragmocone; the body chamber tapers slightly to a transverse, subtriangular aperture with a well developed hyponomic sinus. The dorsal profile is virtually straight,

the ventral profile is convex, giving it an overall exogastric form. The siphuncle is subventral, composed of broadly expanded segments which gives it a nummuloidal or beaded appearance.

Agoniatitida

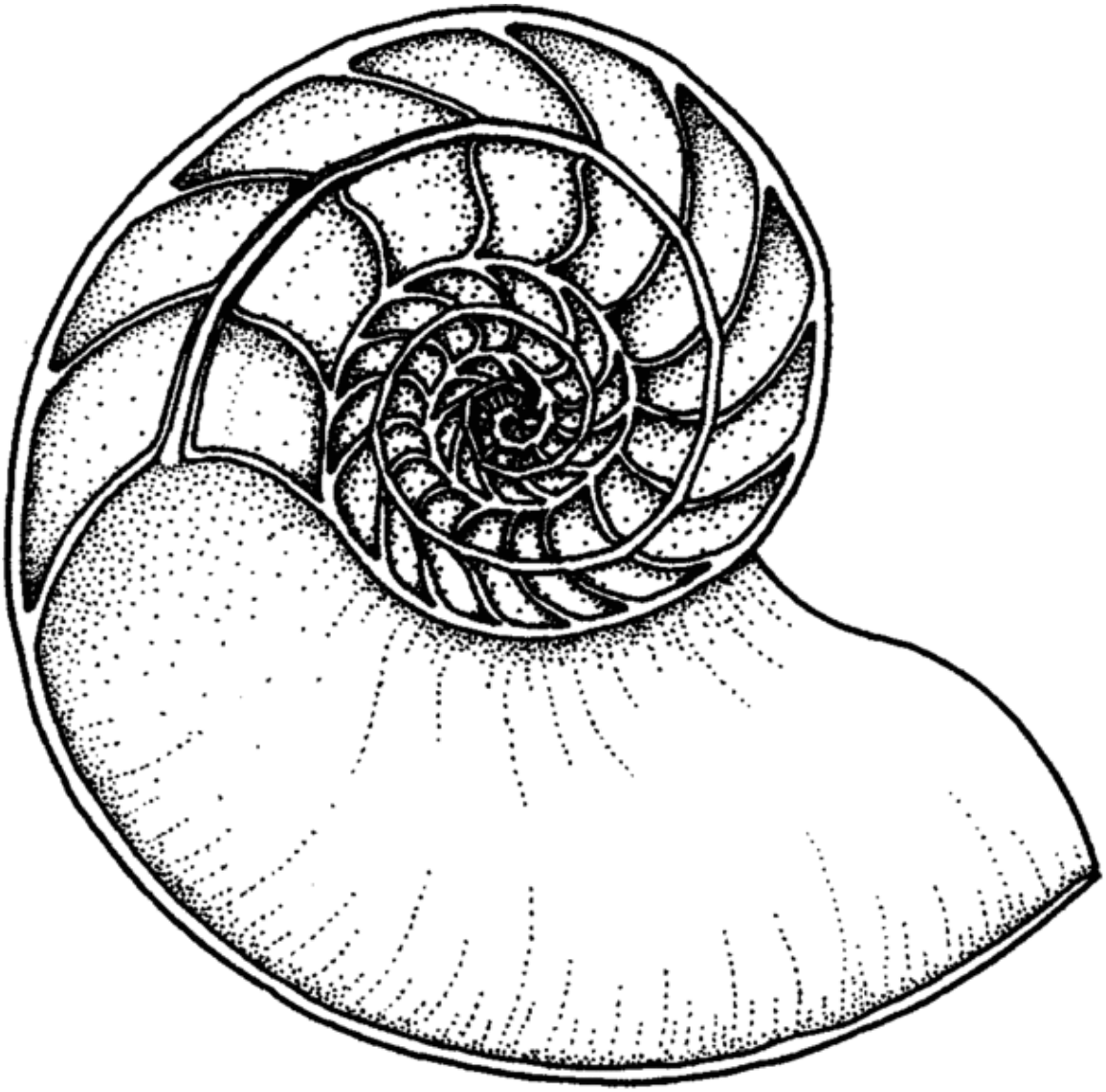
Agoniatitida **Fossil range: L-M Devonian**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	Ammonoidea
Order:	**Agoniatitida** Ruzhencev, 1957

Agoniatitida, also known as the **Anarcestida**, is the ancestral order within the cephalopod Subclass Ammonoidea, that lived in what would become Africa, Asia, Australia, Europe, and North America during the Devonian from about 410—385 mya, existing for approximately 25 million years.

Taxonomic Nomenclature

The Order Agoniatitida, named by Ruzhencev, 1957, is a subjective synonym for the Order Anarcestida, named by Miller and Furnish, 1954. Accordingly the name Anarcerstida is based on the family Anarcestidae (ex Anarcestinae) of Steinmann 1890. That of Agoniatiida is based on the family Agnoniatidae of Holzapfel, 1899.

Saunders, Work, and Nikolaeva, 1999, refer to the Anarcestida, with Agoniatina a suborder, maintaining the priority as found in the Treatise. Shevyrev, 2006 on the other hand follows Ruzhencev, 1957 and used Agonititida.



An image showing the siphuncle, the tube which connects the current living shell to the previous ones.

Morphology

Agoniatitida are primitive ammonoids with a ventral retrochoanitic siphuncle (septal necks point to the rear) reflective of their nautiloid ancestors.and goniatitic sutures with a variable number of lobes. Shells vary from discoidal to globular. Coiling may be loose with whorls barely touching or tight with a dorsal impression.

Fossil distribution

Fossils were restricted to the strata of the Zlichovian to Famennian ages.

Dawsonoceratidae

Dawsonoceratidae Fossil range: ?UOrd-?M Dev
Scientific classification
Kingdom: Animalia
Phylum: Mollusca
Class: Cephalopoda
Subclass: Orthoceratoidea
Order: Orthocerida
Family: Dawsonoceratidae Flower (1946)

Dawsonoceratidae is an extinct family of orthoconic nautiloid cephalopods that lived in what would be North America and Europe from the Late Ordovician through the Middle Devonian from about 480–390 mya, existing for approximately 90 million years.

Taxonomic Position

Dawsonoceratidae was named by Flower (1962) and included in the Michelinoceratida. It was assigned to the Orthocerida by Walter Sweet in Teichert et al 1964 as part of the Orthocerataceae. The type genus is *Dawsonoceras*, named by Hyatt in 1883.

Morphology

Dawsonoceratidae are michelinocerids (Orthocerida) with the internal pattern of the Michelinoceratidae except that the siphuncle segments, which are generally tubular, are constricted at the septal foremina (the openings through with the siphuncular tissues pass). This feature is also found in Silurian *Kionoceras*, but less developed. Septal necks are short and generally recumbent. The type genus, *Dawsonoceras* and its close relative *Dawsonocerina* are further characterized by having orthoconic shells with conspicuous annulations, covered by transverse, scalloped or festooned lirae which in some are also longitudinal. Annulations consist of narrow encircling ribs that may be somewhat oblique, separated by generally wider areas in between

Genera

The Dawsonoceratidae comprise six known genera, *Dawsonoceras*, the type, *Anaspyroceras*, *Calocyrtocerina*, *Dawsonocerina*, *Metaspyroceras*, and *Palaeodawsonocerina*.

Anaspyroceras, named by Shimizu and Obata (1935) and *Metaspyroceras*, named by Foeste (1932), were previously included in the orthoceratid subfamily Leuroceratinae, which is no longer considered a valid taxon, and reassigned to the Dawsonoceratidae. *Anaspyroceras* and *Metaspyroceras* differ from Flowers definition of the Dawsonoceratidae in that the septal necks are othochoanitic rather than recumbent and siphuncle segments are without noted constrictions. *Calocyrtocerina*, named by Chen (1981) was originally included in the Paraphragmitidae of Flower and Kummel 1950. *Palaeodawsonocerina* started off as *Spyroceras senckenbergi* Teichert (1932) and redefined by Kroger and Isakar (2006) as the type species of *Paleodawsonocerina* (*P. senckenbergi*)

Galeaspida

Galeaspida
Fossil range: 430–400 Ma
Mid Silurian to Early Devonian

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	Vertebrata
Class:	**Galeaspida**

Galeaspida ("Helmet shields") is an extinct taxon of jawless marine and freshwater fish. Their name is derived from a Latin word for helmet, *galea*, and refers to their massive bone shield on the head. Galeaspida lived in shallow, fresh water and marine environments during the Silurian and Devonian times (430 to 370 million years ago) of what is now Southern China, Tibet and Vietnam. Their morphology is superficially similar to that of the Heterostraci more than the Osteostraci, as there is currently no evidence that the galeaspids had paired fins. However, the Galeaspida are regarded as being more closely related to the Osteostraci than Heterostraci as the morphology of the braincase is more similar to that of Osteostraci than Heterostraci.

Headshield of *Nochelaspis*

Morphology

The defining characteristic of all galeaspids was a large opening on the dorsal surface of the head shield, which was connected to the pharynx and gill chamber. It may have served both the olfaction and the intake of the respiratory water similar to the nasopharyngeal duct of hagfishes. Galeaspids are also the vertebrates which have the largest number of gills, as some species of the order Polybranchiaspidida (literally "many gills shields") had up to 45 gill openings. The body is covered with minute scales arranged in oblique rows and there is no other fin besides the caudal fin. The mouth and gill openings are situated on the ventral side of the head, which is flat or flattened and suggests that they were bottom-dwellers.

Taxonomy

There are around 76 + described species of galeaspids in at least 53 genera.

If the families Hanyangaspidae and Xiushuiaspidae can be ignored as basal galeaspids, the rest of Galeaspida can be sorted into two main groups: the first being the order

Eugaleaspidiformes, which comprises the genera *Sinogaleaspis*, *Meishanaspis*, and *Anjianspis*, and the family Eugaleaspididae, and the second being the Supraorder Polybranchiaspidida, which comprises the order Polybranchiaspidiformes, which is the sister taxon of the family Zhaotongaspididae and the order Huananaspidiformes, and the family Geraspididae, which is the sister taxon of Polybranchiaspidiformes + Zhaotongaspididae + Huananaspidiformes.

Some experts demote Galeaspida to the rank of subclass, and unite it with Pituriaspida and Osteostraci to form the class Monorhina.

Fossil Record

The oldest known galeaspids, such as those of the genera *Hanyangaspis* and *Dayongaspis*, first appear near the start of the Telychian age, of the latter half of the Llandovery Epoch of the Silurian, about 436 million years ago. During the transition from the Llandovery to the Wenlock, the Eugaleaspids underwent a diversification event. By the time the Wenlock epoch transitioned into the Ludlow Epoch, all of the eugaleaspids, save for the Eugaleaspidae, were extinct. The Eugaleaspidae lived from the Wenlock, and were fairly long-lived, especially the genus *Eugaleaspis*. The last of the Eugaleaspididae disappeared by the end of the Pragian Epoch of the Lower Devonian.

The first genus of Geraspididae, the eponymous *Geraspis*, appears during the middle of the Telychian. The other genera of Polybranchiaspidida appear in the fossil record a little after the beginning of the Lochkovian Epoch, at the start of the Devonian. The vast majority of the supraorder's genera either date from the Pragian epoch, or have their ranges end there. By the time the Emsian epoch starts, only a few genera, such as *Duyunolepis* and *Wumengshanaspis*, survive, with most others already extinct. The last galeaspid is an as of yet undescribed species and genus from the Fammenian epoch of the Late Devonian, found in association with the tetrapod *Sinostega* and the antiarch placoderm *Remigolepis*, in strata from the Northern Chinese province of Ningxia.

Hangenberg event

The **Hangenberg event** was an anoxic period at the end of the Famennian epoch (late Devonian) associated with the Late Devonian extinction, marked by a black shale. It has been proposed that this was related to a rapid sea-level fall due to the last phase of the Devonian Southern Hemisphere glaciation. It has also been suggested that it was linked to an increase in terrestrial plant cover, leading to increased nutrient supply in rivers. This may have led to eutrophication of semi-restricted epicontinental seas and could have stimulated algal blooms.

It is named from the Hangenberg Shale, part of a sequence that straddles the Devonian-Carboniferous boundary, from the Rhenish Massif in Germany.

Schinderhannes bartelsi

Schinderhannes bartelsi **Fossil range: Lower Devonian**

The one known specimen of *Schinderhannes*. Credit: Steinmann Institute/University of Bonn

Scientific classification	
Kingdom:	Animalia
Superphylum:	Ecdysozoa
(unranked):	Panarthropoda
Phylum:	Lobopodia
Class:	† Dinocaridida
Order:	Radiodonta
Family:	Anomalocarididae
Genus:	***Schinderhannes***
Species:	***S. bartelsi***

Binomial name
Schinderhannes bartelsi Kühl, Briggs & Rust, 2009

Schinderhannes bartelsi is an anomalocarid known from one specimen from the lower Devonian Hunsrück Slates. Its discovery was astonishing because previously, anomalocaridids had only been known from exceptionally preserved fossil beds (lagerstatten) from the Cambrian, 100 million years earlier.

Anomalocaridids are organisms such as *Anomalocaris*, thought to be distantly related to the arthropods, which look quite unlike any organism living today—they had a segmented exoskeleton with lateral lobes used for swimming, large compound eyes, and most strikingly a pair of large, claw-like great appendages resembling the tails of shrimp, which are thought to have passed food to a mouth resembling a pineapple ring.

Discovery

The single specimen was discovered in the Eschenbach-Bocksberg Quarry in Bundenbach, and is named after the outlaw Schinderhannes who frequented the area. Its specific epithet *bartelsi* honours Christoph Bartels, a Hunsrück Slate expert. The specimen is now housed in the Naturhistorisches Museum, Mainz.

Morphology

Life restoration

Schinderhannes is about 10 centimetres (3.9 in) long; like other anomalocaridids, it bears a pair of great appendages (very similar to those of *Hurdia*), a radial *Peytoia* 'pineapple-ring' mouth, and large, stalked, compound eyes. It has 12 body segments; large flap-like structures used for swimming protrude from the 11th segment, and from just behind the head.

Ecology

Its preserved guts are typical of predators, and this lifestyle is supported by the raptorial nature of the spiny great appendages and the size of the eyes. The organism clearly swam, propelling itself with the 'flippers' attached to its head, and using its wing-like lobes on the 11th segment to steer. These lobes presumably derived from the lateral lobes

of Cambrian anomalocaridids, ancestors that used lobes along their sides to swim, and lacked the specialisations of *Schinderhannes*.

Significance

The organism allows the classification of early arthropods to be resolved, to some degree. The organism is classified basally to the true arthropods, but is closer to that group than *Anomalocaris*. By analogy, *Schinderhannes* could be thought of as an 'aunt' to the arthropods, and *Anomalocaris* a 'great-aunt'. This suggests that the anomalocaridid group is in fact paraphyletic—that is, that the arthropods are descended from anomalocaridids. It also seems to suggest that the biramous limb of arthropods arose through fusion of anomalocaridid lateral lobes and gills. The fossil has other implications—it shows that the group of early arthropods with short 'great appendages' are not a natural grouping.

The organism's discovery was most significant because of the huge range extension of the anomalocaridids it caused: the group was only previously known from lagerstatte of the lower-to-middle Cambrian, 100 million years before. This underlined the utility of lagerstatte like the Hunsrück slate: these exceptionally preserved fossil horizons may be the only available opportunity to observe non-mineralised forms.

Psammosteidae

Drepanaspis gemuendina and *Tiaraspis subtilis*

The **Psammosteidae** are a family of flattened, benthic jawless vertebrates that lived in marine and estuary environments in Europe, Russia & North America. They arose during the Early Devonian, with the first (and best) known genus, *Drepanaspis* from the Hunsrück lagerstätte. The Psammosteids were the only heterostracans that survived the Upper Frasnian extinction event during the Late Devonian, dying out in the extinction event at the very end of the Devonian.

Many of the Late Devonian genera, such as *Psammolepis*, were among the largest heterostracans ever, growing to be at least 1.5 metres in width.