All About
Silurian Period and Events

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Chapter- 1

Silurian

The **Silurian** is a geologic period and system that extends from the end of the Ordovician Period, about 443.7 ± 1.5 Mya (million years ago), to the beginning of the Devonian Period, about 416.0 ± 2.8 Mya (ICS, 2004, chart). As with other geologic periods, the rock beds that define the period's start and end are well identified, but the exact dates are uncertain by several million years. The base of the Silurian is set at a major extinction event when 60% of marine species were wiped out.

History

The Silurian system was first identified by British geologist Sir Roderick Impey Murchison, who was examining fossil-bearing sedimentary rock strata in south Wales in the early 1830s. He named the sequences for a Celtic tribe of Wales, the Silures, following the convention his friend Adam Sedgwick had established for the Cambrian. In 1835 the two men presented a joint paper, under the title *On the Silurian and Cambrian Systems, Exhibiting the Order in which the Older Sedimentary Strata Succeed each other in England and Wales,* which was the germ of the modern geological time scale. As it was first identified, the "Silurian" series when traced farther afield quickly came to overlap Sedgwick's "Cambrian" sequence, however, provoking furious disagreements that ended the friendship. Charles Lapworth resolved the conflict by defining a new Ordovician system including the contested beds. An early alternative name for the Silurian was *"Gotlandian"* after the strata of the Baltic island of Gotland.

The French geologist Joachim Barrande, building on Murchison's work, used the term *Silurian* in a more comprehensive sense than was justified by subsequent knowledge. He divided the Silurian rocks of Bohemia into eight stages. His interpretation was questioned in 1854 by Edward Forbes, and the later stages of Barrande, F, G and H, have since been shown to be Devonian. Despite these modifications in the original groupings of the strata, it is recognized that Barrande established Bohemia as a classic ground for the study of the earliest fossils.

Subdivisions

Llandovery

The Llandovery epoch lasted from 443.7 ± 1.5 million years ago to 428.2 ± 2.3 million years ago, and is subdivided into three stages: the Rhuddanian, lasting until 439 million years ago, the Aeronian, lasting to 436 million years ago, and the Telychian. The epoch is named for the town of Llandovery in Carmarthenshire, Wales.

Wenlock

The Wenlock, which lasted from 428.2 ± 2.3 million years ago to 422.9 ± 2.5 million years ago, is subdivided into the Sheinwoodian (to 426.2 million years ago) and Homerian ages. It is named after the Wenlock Edge in Shropshire, England. During the Wenlock, the oldest known tracheophytes of the genus *Cooksonia*, appear. The complexity of slightly younger Gondwana plants like *Baragwanathia* indicates either a much longer history for vascular plants, perhaps extending into the early Silurian or even Ordovician.

Ludlow

The Ludlow, lasting from 422.9 ± 2.5 million years ago to 418.7 ± 2.7 million years ago, comprises the Gorstian stage, lasting until 421.3 million years ago, and the Ludfordian stage. It is named for the town of Ludlow in Shropshire, England.

Přídolí

The Pridoli, lasting from 418.7 ± 2.7 million years ago to 416 ± 2.8 million years ago, is the final and shortest epoch of the Silurian. It is named after one locality at natural reserve *Homolka a Přídolí* near the Prague suburb Slivenec in the Czech Republic. *Přídolí* is the old name of a cadastral field area.

Regional stages

In North America a different suite of regional stages is sometimes used:

- Cayugan (Late Silurian - Ludlow)
- Lockportian (middle Silurian: late Wenlock)
- Tonawandan (middle Silurian: early Wenlock)
- Ontarian (Early Silurian: late Llandovery)
- Alexandrian (earliest Silurian: early Llandovery)

Geography

Ordovician-Silurian boundary exposed on Hovedøya, Norway, showing the very marked difference between the light gray Ordovician calcareous sandstone and brown Silurian mudstone. The layers have been inverted (overturned) by the Caledonian orogeny.

With the supercontinent Gondwana covering the equator and much of the southern hemisphere, a large ocean occupied most of the northern half of the globe. The high sea levels of the Silurian and the relatively flat land (with few significant mountain belts) resulted in a number of island chains, and thus a rich diversity of environmental settings.

During the Silurian, Gondwana continued a slow southward drift to high southern latitudes, but there is evidence that the Silurian icecaps were less extensive than those of the late Ordovician glaciation. The southern continents remained united during this period. The melting of icecaps and glaciers contributed to a rise in sea level, recognizable from the fact that Silurian sediments overlie eroded Ordovician sediments, forming an unconformity. The continents of Avalonia, Baltica, and Laurentia drifted together near the equator, starting the formation of a second supercontinent known as Euramerica.

A fossilised piece of Late Silurian sea floor

Amongst the fossils are fragments of the trilobite *Dalmanites*; the coral
Favosites; bryozoans including *Favositella*; straight orthocone shells;
brachiopods including *Atrypa*, *Leptæna* and a rhynchonellid.
Wenlock Epoch, Wenlock Limestone
Dudley, West Midlands

Fossilised Late Silurian shallow sea floor, on display in Bristol City Museum, Bristol, England. From the Wenlock epoch, in the Wenlock limestone, Dudley, West Midlands, England.

When the proto-Europe collided with North America, the collision folded coastal sediments that had been accumulating since the Cambrian off the east coast of North America and the west coast of Europe. This event is the Caledonian orogeny, a spate of mountain building that stretched from New York State through conjoined Europe and Greenland to Norway. At the end of the Silurian, sea levels dropped again, leaving telltale basins of evaporites in a basin extending from Michigan to West Virginia, and the new mountain ranges were rapidly eroded. The Teays River, flowing into the shallow mid-continental sea, eroded Ordovician strata, leaving traces in the Silurian strata of northern Ohio and Indiana.

The vast ocean of Panthalassa covered most of the northern hemisphere. Other minor oceans include two phases of the Tethys— the Proto-Tethys and Paleo-Tethys— the Rheic Ocean, a seaway of the Iapetus Ocean (now in between Avalonia and Laurentia), and the newly formed Ural Ocean.

Climate and sea level

The Silurian period enjoyed relatively stable and warm temperatures, in contrast the extreme glaciations of the Ordovician before it, and the extreme heat of the ensuing Devonian. Sea levels rose from their Hirnantian low throughout the first half of the Silurian; they subsequently fell throughout the rest of the period, although smaller scale patterns are superimposed on this general trend; fifteen high-stands can be identified, and the highest Silurian sea level was probably around 140 m higher than the lowest level reached.

During this period, the Earth entered a long warm greenhouse phase, and warm shallow seas covered much of the equatorial land masses. Early in the Silurian, glaciers retreated back into the South Pole until they almost disappeared in the middle of Silurian. The period witnessed a relative stabilization of the Earth's general climate, ending the previous pattern of erratic climatic fluctuations. Layers of broken shells (called coquina) provide strong evidence of a climate dominated by violent storms generated then as now by warm sea surfaces. Later in the Silurian, the climate cooled slightly, but in the Silurian-Devonian boundary, the climate became warmer.

Perturbations

Marine Genus Biodiversity: Extinction Intensity
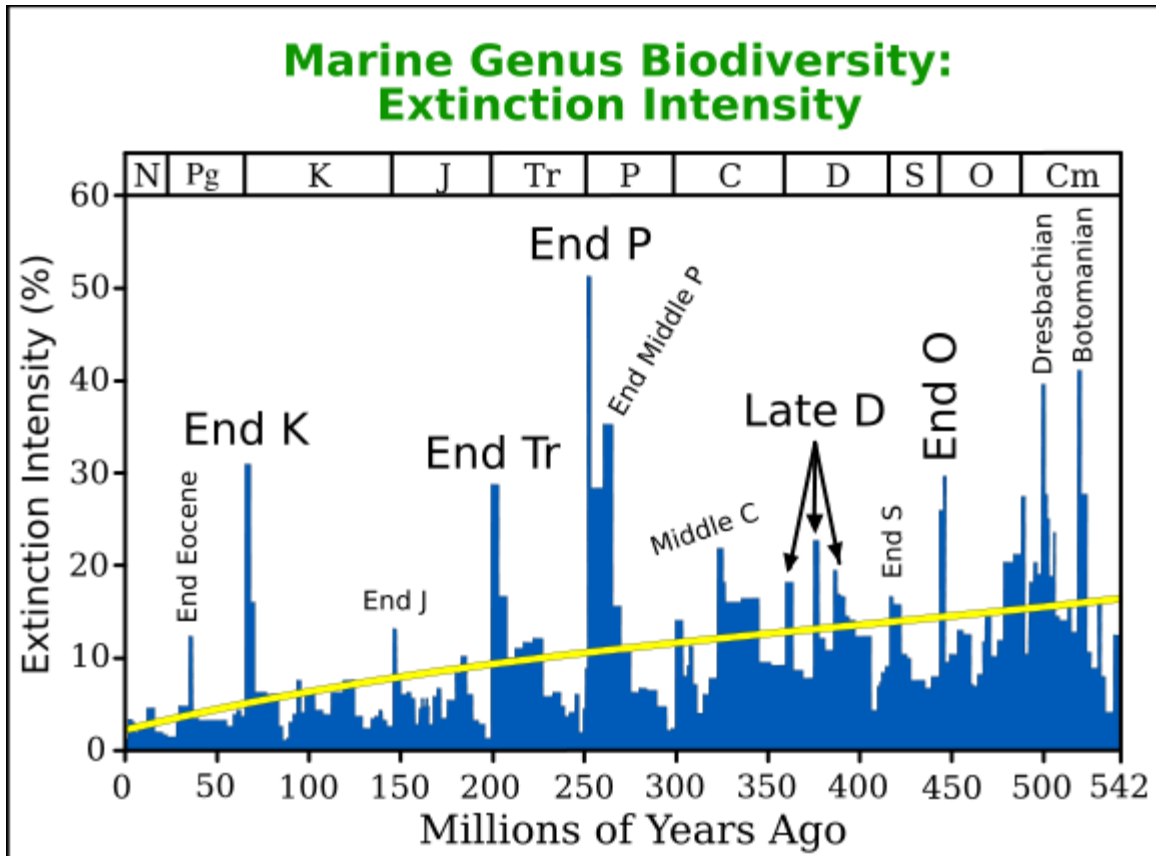
End of Silurian extinction.

The climate and carbon cycle appears to be rather unsettled during the Silurian, which has a higher concentration of isotopic excursions than any other period. The Ireviken event, Mulde event and Lau event each represent isotopic excursions following a minor mass extinction and associated with rapid sea-level change, in addition to the larger extinction at the end of the Silurian. Each home leaves a similar signature in the geological record, both geochemically and biologically; pelagic (free-swimming) organisms were particularly hard hit, as were brachiopods, corals and trilobites, and extinctions rarely occur in a rapid series of fast bursts.

Fauna and flora
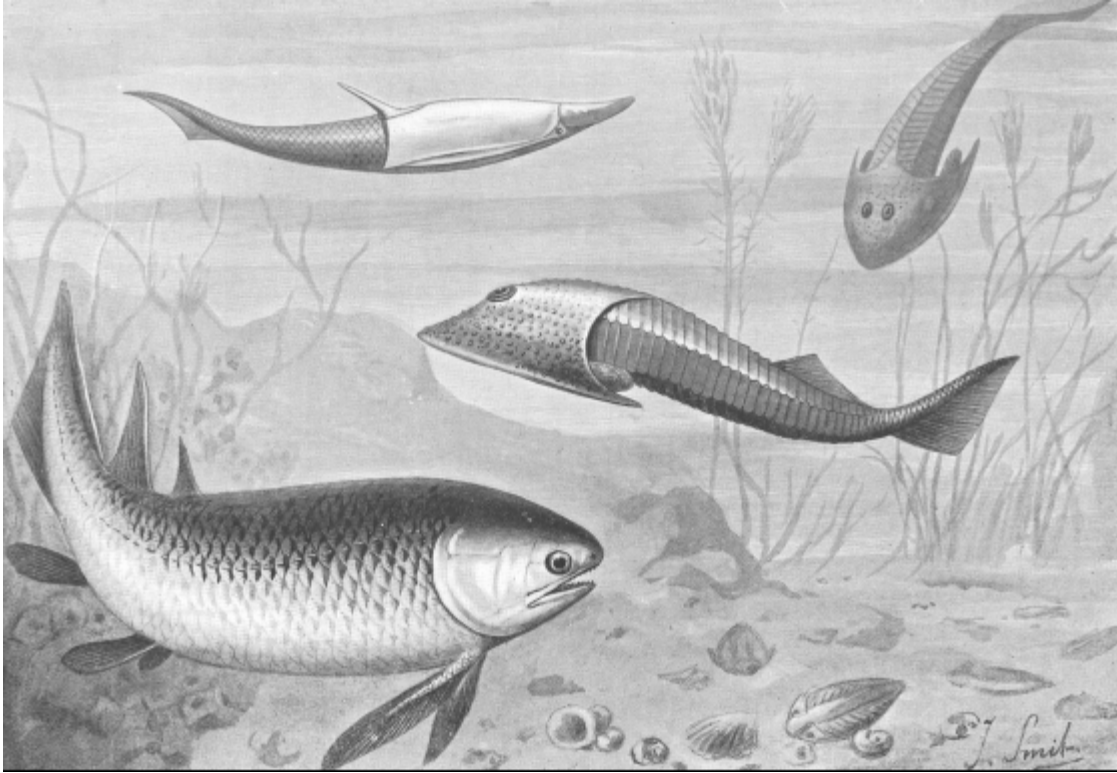
Artist's impression of Silurian fish

The first bony fish, the Osteichthyes, appeared, represented by the Acanthodians covered with bony scales; fish reached considerable diversity and developed movable jaws, adapted from the supports of the front two or three gill arches. A diverse fauna of Eurypterids (Sea Scorpions) -- some of them several meters in length—prowled the shallow Silurian seas of North America; many of their fossils have been found in New York State. Leeches also made their appearance during the Silurian Period. Brachiopods, bryozoa, molluscs, hederelloids and trilobites were abundant and diverse.

Reef abundance was patchy; sometimes they were everywhere, but at other points they are virtually absent from the rock record.
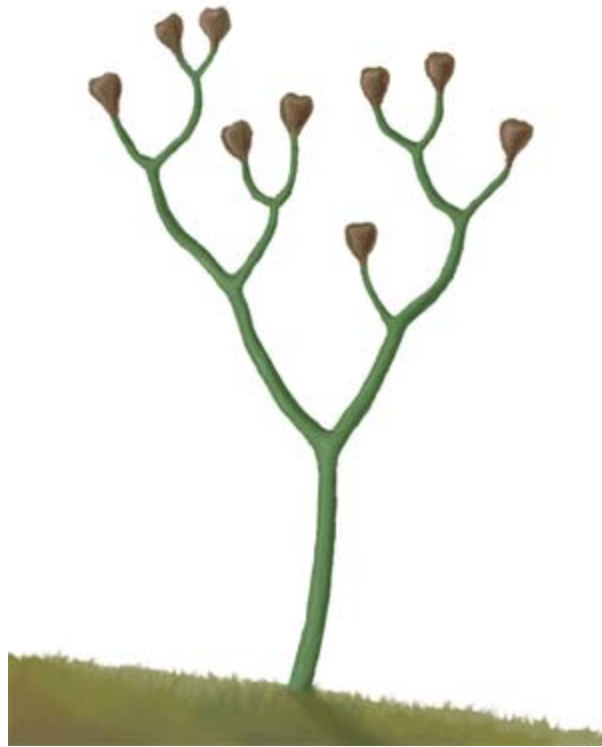
Cooksonia, the earliest vascular plant, middle Silurian

The Silurian was the first period to see macrofossils of extensive terrestrial biota, in the form of moss forests along lakes and streams. However, the land fauna did not have a major impact on the Earth until it diversified in the Devonian.

The first fossil records of vascular plants, that is, land plants with tissues that carry food, appeared in the second half of the Silurian period. The earliest known representatives of this group are the *Cooksonia* (mostly from the northern hemisphere) and *Baragwanathia* (from Australia). A primitive Silurian land plant with xylem and phloem but no differentiation in root, stem or leaf, was much-branched *Psilophyton*, reproducing by spores and breathing through stomata on every surface, and probably photosynthesizing in every tissue exposed to light. Rhyniophyta and primitive lycopods were other land plants that first appear during this period. Neither mosses nor the earliest vascular plants had deep roots. Silurian rocks often have a brownish tints, possibly a result of extensive erosion of the early soils.

Some evidence suggests the presence of predatory trigonotarbid arachnoids and myriapods in Late Silurian facies. Predatory invertebrates would indicate that simple food webs were in place that included non-predatory prey animals. Extrapolating back from Early Devonian biota, Andrew Jeram *et al.* in 1990 suggested a food web based on as yet undiscovered detritivores and grazers on microorganisms.

Chapter- 2

Ordovician–Silurian Extinction Event

The **Ordovician–Silurian extinction event** or quite commonly the **Ordovician extinction**, was the third-largest of the five major extinction events in Earth's history in terms of percentage of genera that went extinct and second largest overall in the overall loss of life. Between about 450 Ma to 440 Ma, two bursts of extinction, separated by one million years, appear to have happened. This was the second biggest extinction of marine life, ranking only below the Permian extinction. At the time, all known life was confined to the seas and oceans. More than 60% of marine invertebrates died including two-thirds of all brachiopod and bryozoan families. Brachiopods, bivalves, echinoderms, bryozoans and corals were particularly affected. The immediate cause of extinction appears to have been the movement of Gondwana into the south polar region. This led to global cooling, glaciation and consequent sea level fall. The falling sea level disrupted or eliminated habitats along the continental shelves. Evidence for the glaciation was found through deposits in the Sahara Desert. A combination of lowering of sea level and glacially-driven cooling are likely driving agents for the Ordovician mass extinction.

Context

The extinction occurred 443.7 million years ago, during one of the most significant diversifications in Earth history. It marks the boundary between the Ordovician and following Silurian period. During this extinction event there were several marked changes in biologically responsive carbon and oxygen isotopes. This complexity may indicate several distinct closely spaced events, or particular phases within one event.

At the time, most complex multicellular organisms lived in the sea, and around 100 marine families became extinct, covering about 49% of faunal genera (a more reliable estimate than species). The brachiopods and bryozoans were decimated, along with many of the trilobite, conodont and graptolite families.

Statistical analysis of marine losses at this time suggests that the decrease in diversity was mainly caused by a sharp increase in extinctions, rather than a decrease in speciation.

Possible causes

These extinctions are currently being intensively studied. The pulses appear to correspond to the beginning and end of the most severe ice age of the Phanerozoic, which marked the end of a longer cooling trend in the Hirnantian faunal stage towards the end of the Ordovician, which had more typically experienced greenhouse conditions.

The event was preceded by a fall in atmospheric CO_2, which selectively affected the shallow seas where most organisms lived. As the southern supercontinent Gondwana drifted over the South Pole, ice caps formed on it. The strata have been detected in late Ordovician rock strata of North Africa and then-adjacent northeastern South America, which were south-polar locations at the time. Glaciation locks up water from the world-ocean, and the interglacials free it, causing sea levels repeatedly to drop and rise; the vast shallow intra-continental Ordovician seas withdrew, which eliminated many ecological niches, then returned, carrying diminished founder populations lacking many whole families of organisms. Then they withdrew again with the next pulse of glaciation, eliminating biological diversity at each change (Emiliani 1992 p. 491). In the North African strata, Julien Moreau reported five pulses of glaciation from seismic sections.

This incurred a shift in the location of bottom-water formation, shifting from low latitudes, characteristic of greenhouse conditions, to high latitudes, characteristic of icehouse conditions, which was accompanied by increased deep-ocean currents and oxygenation of the bottom-water. An opportunistic fauna briefly thrived there, before anoxic conditions returned. The breakdown in the oceanic circulation patterns brought up nutrients from the abyssal waters. Surviving species were those that coped with the changed conditions and filled the ecological niches left by the extinctions.

Gamma ray burst hypothesis

A small minority of scientists have suggested that the initial extinctions could have been caused by a gamma ray burst originating from an hypernova within 6,000 light years of Earth (within a nearby arm of the Milky Way Galaxy). A ten-second burst would have stripped the Earth's atmosphere of half of its ozone almost immediately, causing surface-dwelling organisms, including those responsible for planetary photosynthesis, to be exposed to high levels of ultraviolet radiation. However, there is no unambiguous evidence that such a nearby gamma ray burst has ever actually occurred.

Volcanism and Weathering

A major role of CO_2 is implied by recent research. Through the Late Ordovician outgassing from major volcanism was balanced by heavy weathering of the uplifting Appalachian Mountains, which sequestered CO_2. In the Hirnantian Stage the volcanism ceased, and the continued weathering caused a significant and rapid draw down of CO_2. This coincides with the rapid and short ice age.

End of the event

The end of the second event occurred when melting glaciers caused the sea level to rise and stabilize once more. The rebound of life's diversity with the sustained re-flooding of continental shelves at the onset of the Silurian saw increased biodiversity within the surviving orders.

IGCP project

A major current (2004–08) project of UNESCO's International Geoscience Programme (IGCP), following a successful probe of the Ordovician biodiversification, has as its major objective to seek the possible physical and chemical causes, related to changes in climate, sea level, volcanism, plate movements and extraterrestrial influences, of the Ordovician biodiversification, this end-Ordovician extinction, and the ensuing Silurian radiation.

Chapter- 3

Silurian Extinctions

Arionoceras

Arionoceras Fossil range: M-USilurian	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	Nautiloidea
Order:	Orthocerida
Family:	Arionoceratidae (?)
Genus:	*Arionoceras* Barskov (1966)

*Arionoceras*is an extinct orthocerid genus from the Middle and Upper Silurian, of Europe that is estimated to have lived from 422.9—418.1 mya, existing for approximately 4.8 million years.

Taxonomy

*Arionoceras*was named by Barskov (1966) and originally assigned to the Michelinoceratidae, but attributed by Serpagli and Gnoli (1977) -*ibid* to the Geisonoceratidae Zhuravleva (1959) "on the basis of the (admittedly irregular) occurrence of a lining-like endosiphucular deposit." Dzik (1984) assigned *Arionoceras* to the newly proposed Arionoceratidae as the type genus. Sepkoski (2002) follows previous authors in putting *Arionoceras* in the Orthoceratida.

Morphology

Arionoceras has a straight or slightly curved shell with a circular or depressed cross section, smooth or transversely sculptured surface, and large apically pointed protoconch . The siphuncle is central with very short suborthochoanitc septal necks and cylindrical connecting rings. Apical chambers in adults have cameral deposits.

Nothing is known of the animal which may have been squid-like, probably with 10 subequal arms, and was probably sexually dimorphic.

Choanoceratidae

Choanoceratidae	
Fossil range: M Silurian	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	Nautiloidea
Superorder:	Orthoceratoidea
Order:	Orthocerida
Family:	**Choanoceratidae** Miller (1932)
Genus:	***Choanoceras*** Miller (1932)

The **Choanoceratidae** is a small, mono-generic, family of extinct nautiloid cephalopods in the order Orthocerida that lived in what would be Europe during the middle Silurian from 428.2—426.2 mya, existing for approximately 2 million years.

Taxonomy

Chaonoceratidae was named as the family for its sole member *Choanoceras* by Miller (1932) who, along with Flower (1941) regarded it is belonging to the Ascocerida. It became impossible to trace *Choanoceras* to the ascocerid lineage however and based on closer affinities was assigned to the Michelinoceratida (Orthocerida equivalent) by Flower (1962).

Morphology

Choanoceras had a slender, very gently curved shell with a natural truncation where it discarded the apical portion sometime during its life, somewhat resembling earlier ascocerids, and siphuncle segments that became gradually more expanded during growth. Nothing is known of the animal itself.

Clinoceratidae

Clinoceratidae is an extinct family of actively mobile carnivorous cephalapod of the order Orthocerida that lived in what would be North America and Europe during the middle Ordovician through early Silurian from 466—443.7 mya, existing for approximately 22.3 million years.

Taxonomy

Clinoceratidae was named by Flower (1946). Its type is *Clinoceras*. It was assigned to Michelinoceratida by Flower (1962).

Morphology

The shell is usually long, and may be straight ("orthoconic") or gently curved. In life, these animals may have been similar to the modern squid, except for the long shell.

Cryptocycloceras

Genus: *Cryptocycloceras*

Bogoslovskya is an extinct genus of actively mobile carnivorous cephalapod that lived in what would be Europe during the Silurian from 422.9—418.7 mya, existing for approximately 4.2 million years.

Leurocycloceras

Leurocycloceras **Fossil range: Silurian**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	Orthoceratoidea
Order:	Orthocerida
Genus:	Leurocycloceras

Leurocycloceras is an extinct genus of actively mobile carnivorous cephalapod, essentially a *Nautiloid*, that lived in what would be North America, Europe, and Asia during the Silurian from 443.7—418.7 mya, existing for approximately 25 million years.

Taxonomy

Leurocycloceras was assigned to *Orthocerida* by Sepkoski (2002).

Morphology

The shell is usually long, and may be straight ("orthoconic") or gently curved. In life, these animals may have been similar to the modern squid, except for the long shell.

Fossil distribution

Fossil distribution is exclusive to Great Britain, Wisconsin USA, and northern Ontario, Canada.

Mongoceras

Mongoceras

Mongoceras is an extinct genus of actively mobile carnivorous cephalapod, essentially a *Nautiloid*, that lived in what would be Asia during the Silurian from 443.7—428.2 mya, existing for approximately 15.5 million years.

Taxonomy

Mongoceras was assigned to *Orthocerida* by Sepkoski (2002).

Morphology

The shell is usually long, and may be straight ("orthoconic") or gently curved. In life, these animals may have been similar to the modern squid, except for the long shell.

Fossil distribution

Fossil distribution is exclusive to Sardinia, Wisconsin USA, and northern Ontario, Canada.

Murchisoniceras

Sepkoski (2002)

Genus: Murchisoniceras

Murchisoniceras is an extinct genus of actively mobile carnivorous cephalapod, essentially a *Nautiloid*, that lived in what would be Europe during the Silurian from 418.7—412.3 mya, existing for approximately 6.4 million years.

Taxonomy

Murchisoniceras was assigned to *Orthocerida* by Sepkoski (2002).

Morphology

The shell is usually long, and may be straight ("orthoconic") or gently curved. In life, these animals may have been similar to the modern squid, except for the long shell.

Fossil distribution

Fossil distribution is exclusive to Sardinia.

Neosichuanoceras

Neosichuanoceras Fossil range: Silurian	
Conservation status	
Fossil	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	Orthoceratoidea
Order:	Orthocerida
Genus:	Neosichuanoceras

Neosichuanoceras is an extinct genus of actively mobile carnivorous cephalapod, essentially a *Nautiloid*, that lived in what would be Asia during the Silurian from 436.0—428.2 mya, existing for approximately 7.8 million years.

Taxonomy

Neosichuanoceras was named by Flower (1958). It was assigned to *Endocerida* by Teichert et al. (1964); and to *Orthocerida* by Frey (1981).

Morphology

The shell is usually long, and may be straight ("orthoconic") or gently curved. In life, these animals may have been similar to the modern squid, except for the long shell.

Fossil distribution

Fossil distribution is exclusive to Central China.

Ophidioceras

Ophidioceras **Fossil range: Ordovician**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	Orthoceratoidea
Order:	Orthocerida
Genus:	Ophidioceras

Ophidioceras is an extinct genus of actively mobile carnivorous cephalapod, essentially a *Nautiloid*, that lived in what would be North America, Europe, and Asia during the Silurian from 428.2—418.7 mya, existing for approximately 9.5 million years.

Taxonomy

Ophidioceras was assigned to *Orthocerida* Sepkoski (2002).

Morphology

The shell is usually long, and may be straight ("orthoconic") or gently curved. In life, these animals may have been similar to the modern squid, except for the long shell.

Fossil distribution

Fossil distribution is exclusive to Gotland.

Orthocycloceras

Orthocycloceras
Fossil range: Silurian-Divonian
Scientific classification

Kingdom: Animalia

Phylum: Mollusca

Class: Cephalopoda

Subclass: Orthoceratoidea

Order: Orthocerida

Genus: Orthocycloceras

Orthocycloceras is an extinct genus of actively mobile carnivorous cephalapod, essentially a *Nautiloid*, that lived in what would be Europe during the Silurian to Devonian from 428.2—412.3 mya, existing for approximately 15.9 million years.

Taxonomy

Orthocycloceras was assigned to *Orthocerida* Sepkoski (2002).

Morphology

The shell is usually long, and may be straight ("orthoconic") or gently curved. In life, these animals may have been similar to the modern squid, except for the long shell.

Fossil distribution

Fossil distribution is exclusive to Sardinia and Austria.

Paradnatoceras

Paradnatoceras
Fossil range: Ordovician
Scientific classification

Kingdom: Animalia

Phylum: Mollusca

Class: Cephalopoda

Subclass: Orthoceratoidea
Order: Orthocerida
Genus: Paradnatoceras

Paradnatoceras is an extinct genus of actively mobile carnivorous cephalapod, essentially a *Nautiloid*, that lived in what would be Asia during the Ordovician from 479—460.5 mya, existing for approximately 18.5 million years.

Taxonomy

Palaeocycloceras was assigned to *Orthocerida* by Sepkoski (2002).

Morphology

The shell is usually long, and may be straight ("orthoconic") or gently curved. In life, these animals may have been similar to the modern squid, except for the long shell.

Fossil distribution

Fossil distribution is exclusive to central and soutern China.

Paraphragmitidae
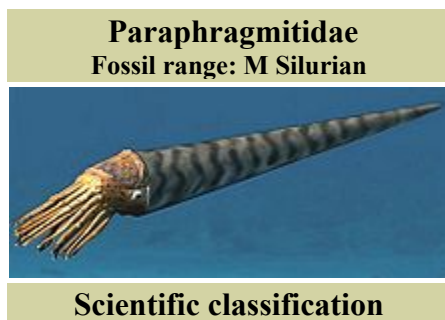
Paraphragmitidae
Fossil range: M Silurian
Scientific classification

Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	Orthoceratoidea
Order:	Orthocerida
Family:	Paraphragmitidae Flower (1950)

Paraphragmitidae is an extinct family of actively mobile aquatic carnivorous cephalapods belonging to the subclass Orthoceratoidea endemic to what would be Asia and Europe during the Silurian living from 436—418.7 mya, existing for approximately 17.3 million years.

In life, these animals may have been similar to the modern squid, except for the long shell. The internal structure of the shell consists of concavo-convex chambers linked by a centrally-placed tube called a siphuncle.

Taxonomy

The Paraphragmitidae was named and defined by Flower (1950) as containing annulated orthocones and cyrtocones included in the Michelinoceratida. Walter Sweet, (in Teichert *et al* 1964), included them in the Orthocerataceae, one of two superfamilies then of the Orthocerida (=Michelinocerida) . With the recognition of the Pseudorthocerida as a separate order the two superfamilies became obsolete leaving the Paraphragmitidae simply an orthocerid family.

Parasphaerorthoceras

Parasphaerorthoceras Fossil range: Silurian	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	Nautiloidea
Infraclass:	Orthoceratoidea
Order:	Orthocerida
Family:	Sphaerorthoceratidae
Genus:	*Parasphaerorthoceras* Ristedt 1968

Parasphaerorthoceras is an extinct orthocerid cephalapod genus, a nautiloid, that lived in what would be Europe and north Africa during the Silurian from 422.9—418.1 mya, having existed for approximately 4.8 million years.

Taxonomy

Parasphaerorthoceras was named by Ristedt 1968 and is the type genus of Sphaerorthoceratidae. Jack Sepkoski (2002) listed it in the Orthocerida where the family had been assigned.

Morphology

The shell of *Parasphaerorthoceras* is generally straight, ("orthoconic") with a circular cross section. The initial chamber is spheroidal, followed by a distinct constriction. The apical part of the shell is wavy but becomes striated, then smooth in later growth stages. The siphuncle is central or subcentral. Septal necks suborthochoanitic. Sutures are straight.

In life, these animals may have been similar to the modern squid, except for the long shell.

Fossil distribution

Parasphaerothoceras species have been found in Austria, Italy, Sardinia, and Morocco.

Protobactrites

Protobactrites Fossil range: M Ordovician-M Silurian	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	Nautiloidea
Infraclass:	Orthoceratoidea
Order:	Orthocerida
Genus:	*Protobactrites* Hyatt in Zittel, 1900

Protobactrites is an extinct nautiloid cephalapod belonging to the Orthoceratoidea that lived in what would be Europe and Asia during the Ordovician and Silurian from 466–421.3 mya, existing for approximately 44.7 million years.

Taxonomy

Protobactrites, named by Hyatt in Zittel (1900), is an orthocerid of unknown familial affiliation where it was retained by Sepkoski (2002). In spite of the name, *Protobactrites* has no known relationship to the Bactritida

Morphology

Protobactrites is characterized by a long slender orthoconic or faintly curved longiconic shell with a circular or subcircular cross section, transverse sutures, long body chamber and oblique aperture. The siphuncle is eccentric; exact structure unknown. The surface has transverse and in some species longitudinal striae. Adult shells may be naturally truncated.

Nothing is known of the living animal which may have had eight or ten arms, and tentacles, like modern coleoids such as modern squid and octopus.

Fossil distribution

Fossil distribution is exclusive to Europe and eastern Asia.

Richmondoceras

Richmondoceras **Fossil range: Ordovician-Silurian**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	Orthoceratoidea
Order:	Orthocerida
Genus:	Richmondoceras Frey (1995)

Richmondoceras is an extinct genus of actively mobile carnivorous cephalapod, essentially a Nautiloid, that lived in what would be North America during the Ordovician and Silurian from 449.5—443.7 mya, existing for approximately 5.8 million years.

Taxonomy

Richmondoceras was named by Frey (1995). Its type is Richmondoceras brevicameratum. It was assigned to Orthocerida by Frey (1995).

Morphology

The shell is usually long, and may be straight ("orthoconic") or gently curved. In life, these animals may have been similar to the modern squid, except for the long shell.

Fossil distribution

Fossil distribution is exclusive to Indiana, USA.

Sactoceras

Sactoceras **Fossil range: Ordovician-Silurian**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	Orthoceratoidea
Order:	Orthocerida
Genus:	Sactoceras Hyatt (1884)

Sactoceras is an extinct genus of actively mobile carnivorous cephalapod, essentially a *Nautiloid*, that lived in what would be North America, Europe, and Asia during the Ordovician and Silurian from 479—418.7 mya, existing for approximately 60.3 million years.

Taxonomy

Sactoceras was named by Hyatt (1884). It was assigned to *Orthocerida* by Sepkoski (2002).

Morphology

The shell is usually long, and may be straight ("orthoconic") or gently curved. In life, these animals may have been similar to the modern squid, except for the long shell.

Fossil distribution

Fossil distribution is found from North America to Europe and Asia.

Tretoceras

Tretoceras	
Fossil range: Ordovician-Silurian	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	Orthoceratoidea
Order:	Orthocerida
Genus:	Tretoceras Salter (1958)

Tretoceras is an extinct genus of actively mobile carnivorous cephalapod, essentially a *Nautiloid*, that lived in what would be Europe during the Ordovician and Silurian from 466—460.5 mya, existing for approximately 60.3 million years.

Taxonomy

Tretoceras was named by Salter (1958). It was assigned to *Orthocerida* by Teichert et al. (1964) and Sepkoski (2002).

Morphology

The shell is usually long, and may be straight ("orthoconic") or gently curved. In life, these animals may have been similar to the modern squid, except for the long shell.

Fossil distribution

Fossil distribution is exclusive to Austria.

Vericeras

Vericeras is an extinct genus of actively mobile carnivorous cephalapod, essentially a Nautiloid, that lived in what would be Europe during the Silurian from 421—418.7 mya, existing for approximately 2.3 million years.

Taxonomy

Vericeras was assigned to Orthocerida by Sepkoski (2002).

Morphology

The shell is usually long, and may be straight ("orthoconic") or gently curved. In life, these animals may have been similar to the modern squid, except for the long shell.

Fossil distribution

Fossil distribution is exclusive to Sardinia.

Chapter- 4

Caledonian Orogeny

Location of the different branches of the Caledonian/Acadian belts at the end of the Caledonian orogeny (Early Devonian). Present day coastlines are indicated in gray for reference. Later in geological history, the Atlantic Ocean opened and the different parts of the orogenic belt moved apart.

The **Caledonian orogeny** is a mountain building era (orogeny) recorded in the northern parts of the British Isles, western Scandinavia, Svalbard, eastern Greenland and parts of north-central Europe. The Caledonian orogeny encompasses events that occurred from the Ordovician to Early Devonian, roughly 490-390 million years ago (Ma). It was

caused by the closure of the Iapetus Ocean when the continents and terranes of Laurentia, Baltica and Avalonia collided.

The Caledonian orogeny has been named for Caledonia, the Latin name for Scotland. The name was first used in 1885 by Austrian geologist Eduard Suess for an episode of mountain building in northern Europe that predated the Devonian period. Geologists like Émile Haug and Hans Stille saw the Caledonian orogeny as one of several episodic phases of mountain building that had occurred during the Earth's history. Current understanding has it that the Caledonian orogeny encompasses a number of tectonic phases that can laterally be diachronous. The name "Caledonian" can therefore not be used for an absolute period of geological time, it applies only to a series of tectonically related events.

Geodynamic history
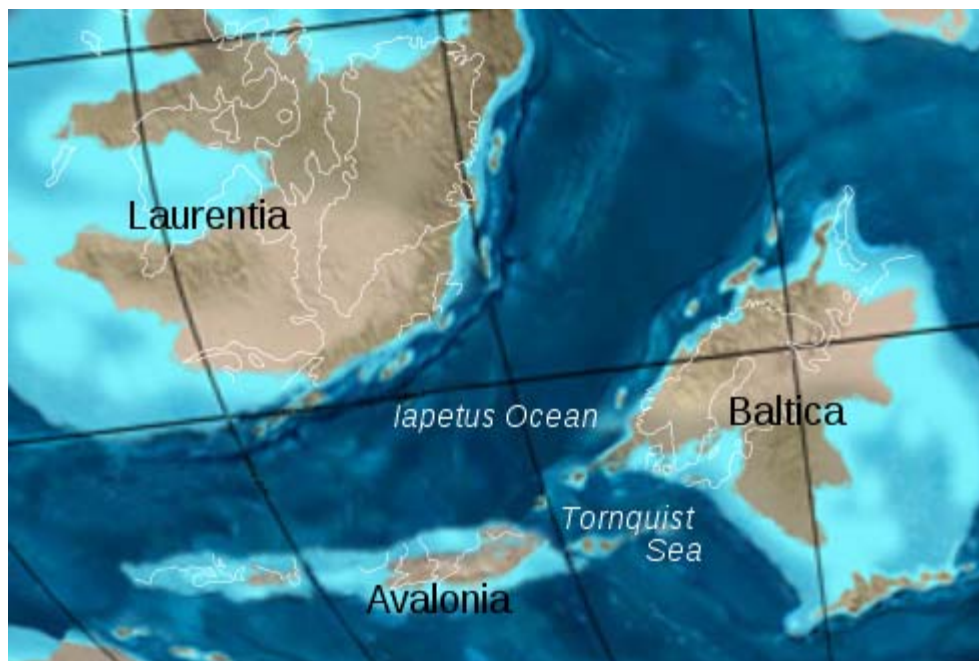
Position of the continents Baltica, Laurentia and Avalonia around 460 million years ago. The Tornquist Sea between Baltica and Avalonia would close first, the main branch of the Iapetus Ocean between Baltica-Avalonia and Laurentia would follow. White lines are present day coast lines.
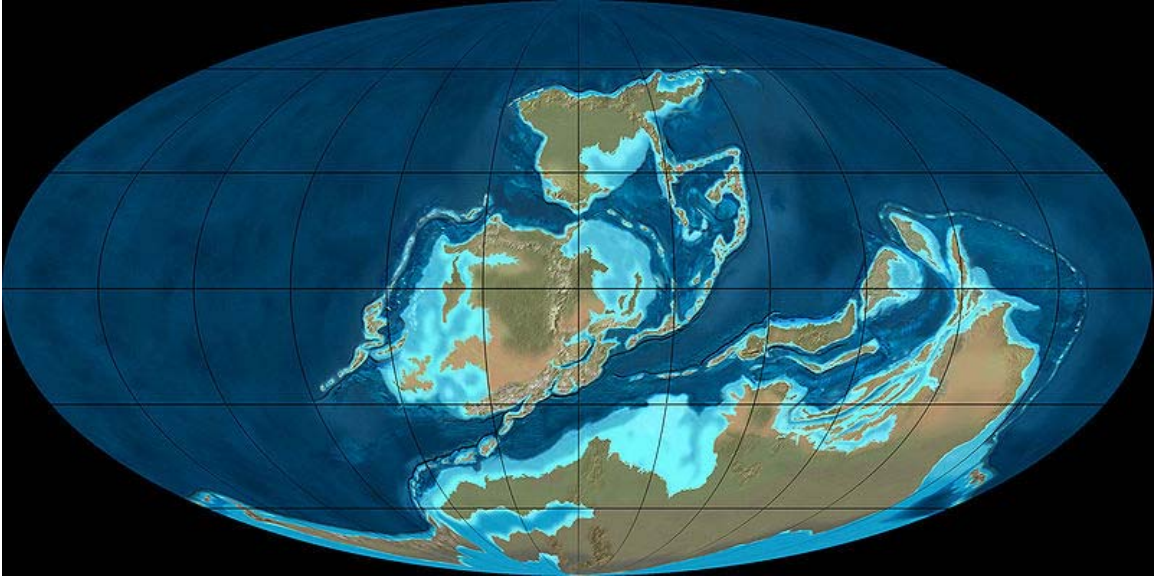
Position of the continents in the Late-Devonian epoch (about 380 million years ago). Laurentia, Baltica and Avalonia have joined during the Caledonian orogeny to form Euramerica.

The Caledonian orogeny was one of several orogenies that would eventually form the supercontinent Pangaea in the Late Paleozoic era. In the Early Paleozoic the majority of all continental landmass was united in the paleocontinent of Gondwana (containing the crust of future Africa, South America, southern Eurasia, Australia and Antarctica), which lay centered around the South Pole. Between 650 and 550 million years ago (in the Ediacaran period) the smaller continents of Laurentia (containing the future northeast section of North America), Baltica and Siberia had separated from Gondwana to move northward towards the equator. In the process, the Iapetus Ocean between Gondwana, Baltica and Laurentia opened.

In the Early Ordovician epoch (about 480 million years ago) the microcontinent (a small fragment of continental lithosphere) Avalonia (at present lithosphere that is scattered over the east of New England, the south of Newfoundland, parts of New Brunswick and Nova Scotia, southern Ireland, most of England and Wales, the low countries and northern Germany) began to separate from the northern margin of Gondwana.

Early phases

Some early phases of deformation and/or metamorphism are recognized in the Scandinavian Caledonides. The first phase that is often included in the Caledonian orogeny is the Finnmarkian phase at 505 million years ago (late Cambrian). Another phase was the Jämmtlandian phase at 455 million years ago. These phases are explained by the assumption that the western edge of Baltica collided with an island arc or microcontinent. In a similar way, the eastern edge of Laurentia collided with an island arc during the Taconic orogeny (between 480 to 435 million years ago).

During the Ordovician, the small continent of Avalonia moved independently in a northeastern direction towards Baltica. This motion was accommodated by the subduction of the southeastern Iapetus Ocean (the so called Tornquist Sea) beneath eastern Avalonia. In the Late Ordovician (about 450 million years ago) continental collision started between Avalonia and Baltica. The Tornquist Sea disappeared in the process, the remaining suture is the Tornquist line, which runs under the North Sea, southern Denmark and northern Germany and Poland.

Scandian/Grampian phase

The main phase of the Caledonian orogeny (from about 425 to 395 million years ago) is called the Scandian phase in Scandinavia and the *Grampian phase* in the British Isles. It was caused by the collision between Laurentia and Baltica. The Iapetus Ocean first closed in the north, then in the south. Therefore the collision between Baltica and Laurentia took place a little earlier than that between Avalonia and Laurentia. Continental collision started in the Mid Silurian and mountain building took place in the Early Devonian (from 407 million years onward). In North America, the collision between Avalonia and Laurentia is called the Acadian orogeny.

According to some authors, the Caledonian continental collisions involved another microcontinent, Armorica (southern Portugal, most of the north of France and parts of southern Germany and Czechia), even smaller than Avalonia. This microcontinent probably did not form one consistent unit, but was instead a series of fragments, of which the current Armorican and Bohemian Massifs are the most important. The ocean between the combined continental mass of Laurentia, Baltica and Avalonia (called Euramerica, Laurussia or Old Red Continent) and Armorica is called the Rheic Ocean.

The paleogeographic position of the Armorica crustal fragments between the Ordovician and Carboniferous is highly disputed though. There are indications that the Bohemian Massif started moving northward from the Ordovician onward, but many authors place the accretion of the Armorican terranes with the southern margin of Laurussia in the Carboniferous Hercynian orogeny (about 340 million years ago). The Rhenohercynian basin, a back-arc basin, formed at the southern margin of Euramerica just after the Caledonian orogeny. According to these authors, a small rim from Euramerica rifted off when this basin formed. The basin closed when these Caledonian deformed terranes were accreted again to Laurussia during the Hercynian orogeny.

Chapter- 5

Old Red Sandstone Formation

Old Red Sandstone
Stratigraphic range: Late Silurian to earliest Carboniferous
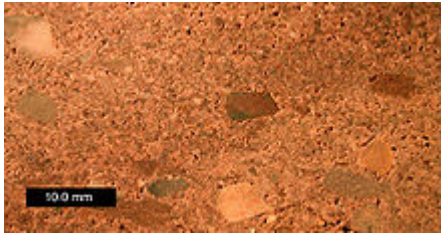
Cross-section showing quartz and chert pebbles in a sample from central England (scale bar is 10 mm).

Type	Geological formation
Lithology	
Primary	sandstone
Other	conglomerate, shale, mudstone, siltstone, limestone
Location	
Country	United Kingdom
Extent	700 km

The **Old Red Sandstone** is a British rock formation of considerable importance to early paleontology. For convenience the short version of the term, 'ORS' is often used in literature on the subject.

Hutton's angular unconformity at Siccar Point where 345 million year old Devonian Old Red Sandstone overlies 425 million year old Silurian greywacke.

Sedimentology

Bedding plane of Old Red Sandstone with quartz and chert pebbles; central England; (scale bar is 10 mm.)

The Old Red Sandstone describes a suite of sedimentary rocks deposited in a variety of environments during the Devonian but extending back into the late Silurian and on into the earliest part of the Carboniferous. The body of rock, or facies, is dominated by alluvial sediments and conglomerates at its base, and progresses to a combination of dunes, lakes and river sediments.

The familiar red colour of these rocks arises from the presence of iron oxide but not all the Old Red Sandstone is red or sandstone — the sequence also includes conglomerates, mudstones, siltstones and thin limestones and colours can range from grey and green through red to purple. These deposits are closely associated with the erosion of the Caledonian Mountain chain which was thrown up by the collision of the former continents of Avalonia, Baltica and Laurentia to form the Old Red Sandstone Continent- an event known as the Caledonian Orogeny.

Many fossils are found within the rocks, including early fishes, arthropods and plants. The rocks may appear paleontologically barren to amateur geologists but careful study, particularly with an accomplished fossil hunter, can uncover pockets of fossils. Rocks of

this age were also laid down in south-west England (hence the name 'Devonian') though these are of true marine origin and are not included within the Old Red Sandstone.

Stratigraphy

Since the Old Red Sandstone consists predominantly of rocks of terrestrial origin, it does not generally contain marine fossils which would otherwise prove useful in correlating one occurrence of the rock with another, both between and within individual sedimentary basins. Accordingly local stage names were devised and these remain in use to some extent today though there is an increasing use of international stage names. Thus in the Anglo-Welsh Basin, there are frequent references to the **Downtonian**, **Dittonian**, **Breconian** and **Farlovian** stages in the literature. The existence of a number of distinct sedimentary basins throughout Britain has been established.

The Orcadian Basin

Lower Old Red Sandstone at Yesnaby, Orkney, cross-bedded aeolian sandstone

The Orcadian Basin extends over a wide area of North East Scotland and the neighbouring seas. It encompasses the Moray Firth and adjoining land areas, Caithness, Orkney and parts of Shetland. South of the Moray Firth, two distinct sub-basins are recognised at Turriff and at Rhynie. The sequence is more than 4 km thick in parts of Shetland. The main basin is considered to be an intramontane basin resulting from crustal rifting associated with post-Caledonian extension, possibly accompanied by strike-slip faulting along the Great Glen Fault system.

The Midland Valley of Scotland

The Midland Valley graben defined by the Highland Boundary Fault in the north and the Southern Uplands Fault in the south harbours not only a considerable amount of Old Red Sandstone sedimentary rocks but also igneous rocks of this age assciated with extensive volcanism. There is a continuous outcrop along the Highland Boundary Fault from Stonehaven on the North Sea coast to Helensburgh and beyond to Arran. A more disconnected series of outcrops occur along the line of the Southern Uplands Fault from Edinburgh to Girvan. Old Red Sandstone often occurs in conjunction with conglomerate formations, one such noteworthy cliffside exposure being the Fowlsheugh Nature Reserve, Kincardineshire.

The Scottish Borders

A series of outcrops occur from East Lothian southwards through Berwickshire. Hutton's famous unconformity at Siccar Point occurs within this basin.

The Anglo-Welsh Basin

This relatively large basin extends across much of South Wales from southern Pembrokeshire in the west through Carmarthenshire into Powys and Monmouthshire and through the southern Welsh Marches, notably into Herefordshire, Worcestershire and Gloucestershire. Outliers in Somerset and north Devon complete the extent of this basin.

With the exception of south Pembrokeshire, all parts of the basin are represented by a range of lithologies assigned to the Lower Devonian and to the Upper Devonian, the contact between the two being unconformable and representing the complete omission of any Middle Devonian sequence. The lowermost formations are of upper Silurian age, these being the **Downton Castle Sandstone Formation** and the overlying **Raglan Mudstone Formation** except in Pembrokeshire where a more complex series of formations is recognised. In the east of the basin, the top of the Raglan Mudstone is marked by a well-developed calcrete, the Bishop's Frome Limestone. The lowermost Devonian formation is the **St Maughans Formation**, itself overlain by the **Brownstones Formation** though with an intervening **Senni Formation** over much of the area. The Upper Devonian sequence is rather thinner and comprises a series of formations which are more laterally restricted. In the Brecon Beacons, the **Plateau Beds Formation** is unconformably overlain by the **Grey Grits Formation** though further east these divisions are replaced by the **Quartz Conglomerate Group** which is itself subdivided into a variety of different formations.

Anglesey

A small and separate basin where both alluvial and lacustrine deposits are recorded. Calcretes are also recorded representing carbonate-rich soils developed between periods of sediment deposition. The present day outcrop occupies a narrow zone from Dulas Bay on Anglesey's northeast coast, southwards to the town of Llangefni.

History of study

In 1787 James Hutton noted what is now known as Hutton's Unconformity at Inchbonny, Jedburgh, and in the Spring of 1788 he set off with John Playfair to the Berwickshire coast and found more examples of this sequence in the valleys of the Tour and Pease Burns near Cockburnspath. They then took a boat trip from Dunglass Burn east along the coast with the geologist Sir James Hall of Dunglass and at Siccar Point found what Hutton called "a beautiful picture of this junction washed bare by the sea", where 345 million year old Devonian Old Red Sandstone overlies 425 million year old Silurian greywacke.

In the early 19th century, the paleontology of the formation was studied intensively by Hugh Miller, Henry Thomas De la Beche, Roderick Murchison, and Adam Sedgwick -- Sedgwick's interpretation was the one that placed it in the Devonian: in fact it was he who coined the name of that period. The term 'Old Red Sandstone' was originally used in 1821 by Scottish naturalist and mineralogist Robert Jameson to refer to the red rocks which underlay the 'Mountain Limestone' i.e. the Carboniferous Limestone. They were thought at that time to be the British version of Germany's Rotliegendes, which is in fact of Permian age. Many of the science of stratigraphy's early debates were about the Old Red Sandstone.

Note that in older geological works predating theories of plate tectonics, the United States' Catskill Delta formation is sometimes referred to as part of the Old Red Sandstone. In the modern day, however, it is recognized that the two are not stratigraphically continuous but are very similar due to being formed at approximately the same time by the same processes.

Use as a Building Stone

St. Helen's Chapel at Siccar Point has walls faced in Old Red Sandstone, with greywacke used on the inner face and surrounding drystane dykes.

The Old Red Sandstone has been widely used as a building stone across those regions where it outcrops. Notable examples of its use can be found in the area surrounding Stirling , Stonehaven , Perth , and Tayside. The inhabitants of Caithness at the northeastern tip of Scotland also used the stone to a considerable extent. Old Red Sandstone has also frequently been used in buildings in Herefordshire, Monmouthshire and the former Brecknockshire (now south Powys) of south Wales.

Notable buildings constructed of Old Red Sandstone

Scotland

St. Magnus Cathedral, Kirkwall, Orkney, constructed of locally quarried sandstone.

- Muchalls Castle, Aberdeenshire
- Stonehaven Tolbooth, Aberdeenshire
- St. Magnus Cathedral, Orkney

Wales and Marches

- Tintern Abbey, Monmouthshire   &
- Ross-on-Wye market hall, Herefordshire
- Shrewsbury Castle, Shropshire

- Raglan Castle , Mons.
- Goodrich Castle, Herefordshire.

Elsewhere

- New York Life Insurance Building, Montreal

Tumblagooda Sandstone Formation & Tuscarora Formation

The **Tumblagooda sandstone** is a geological formation deposited during the Silurian or Ordovician periods, around four to five hundred million years ago, and is now exposed on the west coast of Australia, straddling the boundary of the Carnarvon and Perth basins. Visible trackways may prove to be the earliest evidence of terrestrial animals.

Sedimentology

The Tumblagooda is over 1,400 m (4,500 ft) deep: the bottom has never been found, but seismic data suggests it unconformably overlies a Proterozoic basement. The formation is divided into four *facies associations* (FAs), numbered stratigraphically, that is from bottom to top. These lithified sediments portray an environment dominated by high-energy braided streams, flowing into the sea in places; ephemeral pools were also common.

Facies Association 1

The lowest facies association in the unit is dominated by trough cross-stratification, deposited by broad, high-energy braided rivers, which formed the outwash plain of an alluvial system. Trace fossils are virtually absent, because the high depositional energy meant burrowing organisms could not survive. The downslope flow was to the north west.

Facies Association 2

These facies reflect a quieter environment; the unit is occasionally interrupted by lenses of FA1 sediments. Beds are on the whole thin, planar and well sorted. Beds about 5 centimeters (2 in) thick form 2 meters (7 ft) units of "bedded sandsheets" -- layers of sand blown by the wind -- which form the dominant lithology of this facies.

Low angle (<20°), cross-stratified sandstones form units up to 50 centimeters (19.7 in) thick, sometimes reaching thicknesses as much as 2 meters (7 ft). The current's direction here is to the south east - up slope - and reinforces their interpretation as aeolian dunes. A

further suite of layers contain a dense trace fossil assemblage; other layers bear current ripple marks, which likely formed in shallow streams, with flooded hollows probably hosting the creators of the trace fossils. Cyclicity is absent, suggesting that, rather than being seasonal events, the occasional innundation was based on unpredictable events such as storms, a varying water table, and changing stream courses.

Facies Association 3

This facies is much like FA1, with an increased supply of clastic material represented in the sedimentary record by coarse-grained, poorly sorted, upwards-fining (i.e. largest grains at the bottom of the unit, becoming progressively finer towards the top), pebbly trough cross-bedded units up to four metres thick. Trace fossils are rare. Sheet-like braided rivers are inferred as the dominant control on sedimentation in these facies.

Facies Association 4

The uppermost facies association appears to reflect an environment on the fringes of the sea. Fining-up is observed on 0.5 meters (2 ft) to 2 meters (7 ft) scales, with trough cross bedding at the bases of units overlain by current ripples. Fine sandstones and green shales are also present. The upper units are strongly bioturbated, with an abundance of *Skolithos* - a fossil typically found in marine environments.

It has been interpreted as an inter-distributary bay, or alternatively as a sandy coastline featuring wave-generated bars, perhaps with tidal influence; braided fluvial streams often reworked the sediments.

Age

Since the Tumblagooda sandstone comprises a sedimentary succession with no volcanic layers (which could be dated radiometrically) and with virtually no body fossils, its age is very difficult to constrain. It was first thought to have formed around 100 million years ago, during the Cretaceous period, on the basis of stratigraphy; current estimates place it far earlier, in the lower Ordovician, 440 million years ago. It is hoped that a new technique based on the uranium-thorium dating of diagenetic monazite crystals may produce a more precise estimate of the age, but initial attempts have failed to extract sufficient monazite from the unit.

Such a method would be of great value, as previous attempts to date the unit have been rather inconsistent. The initial Cretaceous estimate was soon reviewed with a "mid-Cambrian to early Ordovician" (~500 million years ago) estimate based on trace fossils, and was shortly afterwards replaced by a mid-Silurian age based on spores and acritarchs. This was apparently confirmed by the identification in the overlying beds of a conodont fauna with a recognizably Silurian character, but when the palæomagnetism of the area was studied, an early Ordovician age was deduced. A single conodont element, again drawn from overlying sediments, was taken to support a late Cambrian to early Ordovician age , but this was refuted by the observation that the trace fossil assemblages

bore great similarity to well constrained lower Silurian assemblages from Antarctica. The current early Ordovician age estimation is based on a much more diverse and numerous -- therefore more securely dated -- assemblage of conodonts, again from overlying sediments.

Tectonic history

In common with most of the Australian cratonic rocks, the Tumblagooda has undergone minimal tectonic activity since its formation. Therefore faulting is rare, and units continue laterally for great distances. Jointing is the dominant control of the landscape, with meandering rivers enhancing joint locations. Miocene uplift has resulted in the formation of deep (approximately 60m/200 ft) gorges exposing large cliff sections; with the sparse vegetation characteristic of arid Western Australia, this means the unit is exceptionally exposed, making detailed study easy. Despite this, the unit was not studied until 1948, due to its inaccessibility - the 600 miles (1000 km) from Perth were mainly dirt tracks until the 1970s.

Palæontology

Only one body fossil, *Kalbarria* (an early euthycarcinoidic arthropod) has been found in the Tumblagooda, mainly due to the large clast size and the abundance of predatory and burrowing organisms. (This meant that oxygen could penetrate to good depths in the sediment, permitting decomposing organisms to decay anything that burrowing animals had not eaten too rapidly for fossils to form.) Since *Kalbarria* had 11 pairs of legs, it can be tentatively matched to some *Protoichnites* arthropod trackways of the same size. *Protoichnites* is abundant in subaerial facies in FA2-4. Marks which can only have been made on exposed wet sand are seen: for example "splurges" where the legs of the organism flipped sand out behind them. The marks vary in crispness and character according to the wetability of the underlying sediment; this is particularly marked where the traces cross ripples, with the lee slopes recording a trace markedly different in appearance to those in the troughs, and the stoss slopes recording no trace at all. Behaviour can be inferred from these traces; in places, they parallel features which modern observation notes forming at the edge of a wind-blown pond, just on the landward side of the shore. This behaviour has been interpreted as a feeding trace; presumably the trace-maker dined on organic matter blown out of the pool, or detritus left as the pool had shrunk. Further tracks can be traced across dunes; a slow walk up turns into a skid as the organism slid down the lee slope and into the pool on the other side. Another instance shows the trackways of two organisms converging, then becoming one trackway, before one individual swerves away to the left, leaving the other to walk onwards. These trackways are the earliest evidence of terrestrial animals. Due to the poor dating of the unit, it is currently impossible to speculate whether the plants, which colonised the land in the mid-Ordovician, got there first.

Aquatic trace fossils are also abundant. Two major ichnofacies are observed, bearing close resemblance to assemblages found in Antarctica and demonstrating proximity of

western Australia and Antarctica at the time of deposition. One is dominated by *Skolithos*, suggesting marine deposition. The fabric of the other is dominated by *Heimdallia*, a strange planar trace that does not have a circular cross-section; it is interrupted in places by *Beaconella*, a wide trace thought to be constructed by a burrowing arthropod ploughing through the sediment for food, leaving a mound of piled sediment at the end of each trace. This may suggest the *Beaconella* organism feeding on *Heimdallia*. *Daedalus*, a trace fossil resembling a giant garlic, is also present in this assemblage.

Tuscarora Formation

Tuscarora Formation Stratigraphic range: Early Silurian	
Outcrop of Tuscarora Formation in Thickhead Wild Area, Centre County, Pennsylvania	
Type	sedimentary
Sub-units	Castanea Member
Underlies	Clinton Group
Overlies	Juniata Formation
Lithology	
Primary	quartzarenite (sandstone)
Other	conglomerate
Location	
Named for	Tuscarora Mountain
Named by	Darton and Taff
Region	Appalachian Mountains
Extent	Pennsylvania, Maryland, Virginia, West Virginia

The Silurian **Tuscarora Formation** — also known as **Tuscarora Sandstone** or **Tuscarora Quartzite** — is a mapped bedrock unit in Pennsylvania, Maryland, Virginia and West Virginia.

Description

Sample of Silurian Tuscarora Formation collected from Bald Eagle Mountain, Centre County, Pennsylvania, showing *Diplocraterion* trace fossil at left. Specimen is ~22cm high.

The Tuscarora is a thin- to thick-bedded fine-grained to coarse-grained orthoquartzite. It is a white to medium-gray or gray-green subgraywacke, sandstone, siltstone and shale, cross-stratified and conglomeratic conglomerate in parts, containing a few shale interbeds.   There is one named member of this formation: Castanea, occurring at the top, leaving the Lower and Middle Tuscarora Formation at the bottom.

The Tuscarora is a lateral equivalent of the Minsi and Weiders members of the Shawangunk Formation in eastern Pennsylvania, New Jersey, and New York, and of the Massanutten Formation sandstone in Virginia. The Tuscarora and its lateral equivalents are the primary ridge-formers of the Ridge-and-Valley Appalachians in the eastern

United States It is typically 935 feet thick in Pennsylvania, and in Maryland varies from 60 feet to 400 feet thick from east to west.

The Tuscarora formation is also very much in evidence in Pendleton County, West Virginia. The strata were laid down approximetly 440 million years ago, and are 250 feet thick. 250-230 million years ago, enormous forces associated with the formation of the Appalachian and Allegheny mountains forced the Tuscarora formation into huge domes; at the edges of the domes, the Tuscarora formation was turned a full 90 degrees from horizontal to vertical. Over time, erosion wore away the arch, but the vertical sections resisted erosion and remain to this day as the River Knobs. Some of the better known River Knobs include Champe Rocks, Seneca Rocks, Judy Rocks, and Nelson Rocks. The River Knobs are clearly visible along highways 55 and 33.

Depositional environment

The depositional environment of the Tuscarora has always been interpreted as mostly terrestrial or shallow marine deposits resulting in a molasse sequence produced by the Taconic orogeny. It is thought to represent a vast sand shoal along the margin of the Iapetus Ocean.

Fossils

Very few fossils exist in the Tuscarora, and most of them are trace fossils. Ripple marks are seldom found.

At least two Eurypterids have been discovered in the Tuscarora.

Notable Exposures

Two of the most complete exposures are in two quarries at the crest and south end of Canoe Mountain (Frankstown Quadrangle).

The Tuscarora is exposed on the north and south sides of the Narrows in central Bedford County, Pennsylvania, where it is nearly vertical.

Age

Conformable contact of overlying Tuscarora Formation (white rock, left) with underlying Juniata Formation (red rock, right) at the Narrows along rt. 30 in Bedford County, Pennsylvania.

Relative age dating of the Tuscarora places it in the Lower Silurian period, being deposited between 440 to 417 (±10) million years ago. It rests conformably atop the Juniata Formation and conformably below the Clinton Group in Pennsylvania.

Economic uses

The Tuscarora may have been used as a ganister for making furnace liners in 19th century iron smelting blast furnaces of central Pennsylvania.

The Tuscarora has also become very important to the tourism industry of eastern West Virginia. Seneca Rocks has become a world renowned rock climbing location. It is the only true peak on the East Coast of the US; a true peak is a peak inaccessible except by technical rock climbing techniques. Two climbing schools at Seneca, Seneca Rocks Mountain Guides and the Senecea Rocks Climbing School, and many other guide services offer guided climbing trips on the 300+ climbing routes at Seneca. Seneca Rocks is managed by the US Forest Service, and is located on the Monongahela National Forest. Seneca Rocks is part of the Spruce Knob Recreation Area.

Another unique tourism opportunity is at Nelson Rocks, near Circleville West Virginia. Nelson Rocks is located on the Nelson Rocks Preserve, a privately owned and operated nature preserve dedicated to preserving Nelson Rocks and the environment around them as a cultural, educational, and recreational resource. A via ferrata has been built at the Nelson Rocks Preserve. While via ferratas are very popular in Europe, there are only six located in the United States. The Via Ferrata at Nelson Rocks Preserve was the second to be built in the United States.
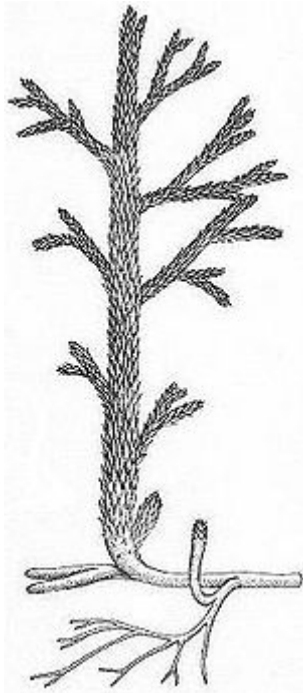
Chapter- 7

Silurian Life

Asteroxylon

Scientific classification

Kingdom: Plantae

Division: Lycopodiophyta

Class: Lycopodiopsida

Order: Drepanophycales

Family: Asteroxylaceae
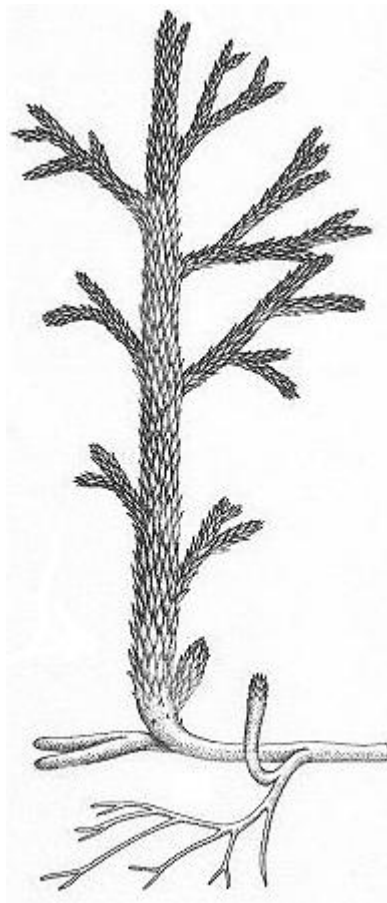
Genus: *Asteroxylon*

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.

Baragwanathia

Baragwanathia Fossil range: Early Ludlow (Gorstian, late Silurian) - Early Devonian	
Scientific classification	
Kingdom:	Plantae
Division:	Lycopodiophyta
Class:	Lycopodiopsida
Order:	Drepanophycales
Family:	Drepanophycaceae
Genus:	*Baragwanathia* † Lang & Cookson, 1935
Species	

- *Baragwanathia longifolia* LANG & COOKSON (Type species)
- *Baragwanathia abitibiensis* HUEBER
- *Baragwanathia* sp. HAO & GENSEL

Baragwanathia is a genus of extinct plants of the division Lycopodiophyta of Late Silurian to Early Devonian age, fossils of which have been found in Australia, Canada and China.

Description

Baragwanathia is a primitive lycopod, differing from such taxa as *Asteroxylon* in the presence of vascular tissue in its leaves - *Asteroxylon* has vascule-free enations. It is set apart from the closely related genus *Drepanophycus*, of the same period, in the position of the sporangia and the arrangement and shape of the leaves. These extinct terrestrial vascular plants had stems varying in diameter and length (up to a few cm for the diameter and a few metres for the length). They were erect or arched, dichotomized occasionally, and were furnished with true roots at the base. Vascular bundle actinostele, tracheids of

primitive annular or helical type (so-called G-type). Leaves were unbranched strap-shaped microphylls 1-2 cm long with a single prominent vascular thread, arranged spirally on the stem. Sporangia axillary (exact position not known), broader than long, dehiscing by a slit on top. Spores were trilete; the gametophyte is currently unknown. The name apparently derives from William Baragwanath, director of the Victorian Geological Survey at the time of discovery.

Chaetocladus

Chaetocladus is a non-calcifying genus of unicellular green alga known from the Upper Silurian.

Morphology

Chaetocladus thalli range from 2–6 cm in height and average 1 cm in diameter. They comprise a parallel-sided, unbranching axis which is surrounded by leaf-like ramifications.

The holotype of Chaetocladus plumula (USNM 41 137, from LoDuca 1997)

Fossil record

Chaetocladus is known from upper Silurian konservat lagerstatte, and found in association with other algae, arthropods, and annelid worms. Similar Dasycladean algae are reported from late-Ordovician lagerstatte.

Classification

Due to its morphological similarity to the extant order Dasycladales, *Chaetocladus* is considered to be an early cousin of this order. Unlike the majority of Dasycladales, *Chaetocladus* does not form deposit calcite - therefore it required much rarer taphonomic conditions to be preserved. Some genera now recognised as *Chaetocladus* were originally described as Graptolites.

Cooksonia

Cooksonia
Fossil range: Mid-Silurian to early Devonian

A cartoon of *Cooksonia*, reconstructed with non-photosynthetic axes, dependent on its gametophyte, as per Boyce (2008)

Scientific classification

Kingdom:	Plantae
Superdivision:	Polysporangiomorpha
Division:	*Incertae sedis*
Genus:	***Cooksonia***

Species

C. pertoni
C. hemisphaerica
C. cambrensis
C. caledonica
C. paranensis
C. banksii
C. bohemica

Cooksonia is an extinct grouping of primitive land plants. The earliest *Cooksonia* date from the middle Silurian, about 425 million years ago; the group continues to be an important component of the flora until the early Devonian. For historical reasons, while *Cooksonia* fossils are distributed globally, most type specimens come from Britain.

Morphology

Only the sporophyte phase of *Cooksonia* is currently known. Individuals were small, a few centimetres tall, and had a simple structure; they lacked leaves, flowers and roots — although it has been speculated that they grew from an unpreserved rhizome. They had a simple stalk, that branched dichotomously a few times. Each branch ended in a sporangium, a rounded, spore-bearing structure. Specimens of one species of *Cooksonia* have a dark stripe in the centre of their stalks, which has been interpreted as the earliest remains of water carrying tissue. Other *Cooksonia* species lacked such conducting tissue.

Cooksonia specimens occur in a range of sizes, and varied in width from ~0.03 to 3 mm. Specimens of different sizes were probably different species, not fragments of larger organisms: fossils occur in consistent size groupings, and sporangia and spore details are different in organisms of different sizes. The organisms probably exhibited determinate growth.

Some *Cooksonia* species can be shown to bear stomata, which had a role in gas exchange; this was probably to assist in transpiration-driven transport of solutes in the xylem, rather than primarily in photosynthesis, as suggested by their concentration at the tips of the axes. These clusterings of stomata are typically associated with a bulging in the axis at the neck of the sporangium, which may have contained photosynthetic tissue, reminiscent of some mosses.

Physiology

While reconstructions traditionally depict *Cooksonia* as a green and red, photosynthesising, self-sufficient stem, it is likely that the fossils instead preserve a sporophyte generation which was dependent on a gametophyte for its nutrition – a relationship that occurs in modern mosses and liverworts.

However, no fossil evidence of a gametophyte of *Cooksonia* has been discovered to date. Study of smaller *Cooksonia* fossils showed that once the tissue required to support the axes, protect them from desiccation, and transport water had been accounted for, no room remained for photosynthetic tissue. Further, the axis thickness is what would be expected if their sole role was to support the sporangium on their ends. It appears that, originally at least, the role of the axes was solely to ensure continued spore dispersal, even if the axis desiccated.

The widths of *Cooksonia* fossils span an order of magnitude; while the smaller ones could not possibly be self-sufficient, the larger axes could; this provides a possible illustration of the evolution of an independent sporophyte generation.

Taxonomy

The relationships between the known species of *Cooksonia* and modern plants remain unclear. They appear to represent plants that are near to the branching between Rhyniophyta and to the club mosses. It is considered likely that *Cooksonia* is not a clade, but rather represents a evolutionary grade or form genus. Indeed, four different forms of spore, probably representing four different species, have been found in sporangia identified as *C. pertoni*.

Specimens

The first *Cooksonia* species were described by William Henry Lang in 1937 and named in honor of Isabel Cookson, with whom he had collaborated, and who collected the type specimens of *Cooksonia pertoni* in Perton Quarry in 1934.

Five species of *Cooksonia* have been clearly identified. *C. pertoni*, *C. hemisphaerica*, *C. cambrensis*, *C. caledonica* and *C. paranensis*. They are distinguished primarily by the shape of the sporangia.

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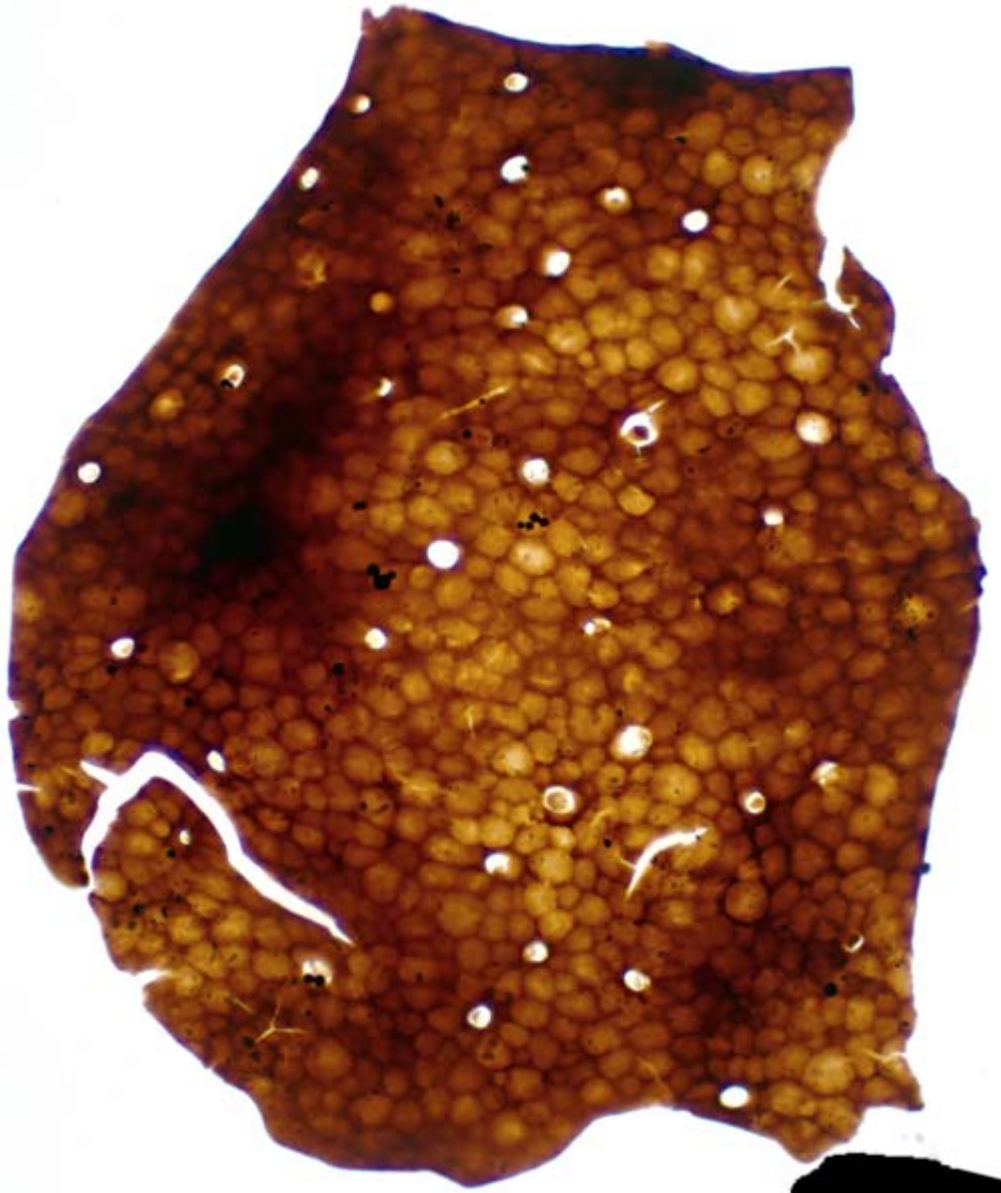
Cuticle of Cosmochlaina, retrieved from the Burgsvik beds by acid maceration. Cells about 12 μm in diameter.

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.

Cryptospores

Cryptospores are fossilised primitive plant spores that first appear in the fossil record during the late Ordovician to early Silurian period.

Evidence that cryptospores derive from land plants

Occurrence

Cryptospores are generally found in non-marine rocks and decrease in abundance with distance offshore. This suggests that any cryptospores found in the marine environment were transported there by the wind from the land, rather than originating from the marine environment.

Wall Ultrastructure

The walls of cryptospores consist of many lamellae (thin sheets). Liverworts, thought to be the most primitive land plants, also have this spore wall morphology.

Other information

Recently, fossils of plant sporangia have been found in Oman with cryptospores showing concentric lamellae in their walls, similar to liverworts.

Drepanophycaceae

Drepanophycaceae is a family of extinct plants of the division Lycopodiophyta of Late Silurian to Late Devonian age, found in North America, China, Russia, Europe, and Australia.

Description

Extinct terrestrial vascular plants of the Silurian to Devonian periods. Stem of the order of several mm to several cm in diameter and several cm to several metres long, erect or arched, dichotomizing occasionally, furnished with true roots at the base . Vascular bundle an exarch actinostele, tracheids of primitive annular or helical type (so-called G-

type). Leaves are unbranched microphylls several mm to 2 cm or more long with a single prominent vascular thread, arranged spirally to randomly on the stem. Homosporous sporangia borne singly on the upper leaf surface or in an axillary position.

List of genera

- *Drepanophycus* Göppert (type genus)
  - microphylls short, tapering rapidly from wide base (thorn-shaped)
  - microphylls arranged spirally or randomly on stem
  - sporangia borne on upper surface of microphylls
- *Baragwanathia* Lang & Cookson
  - microphylls long, not tapering over most of length (strap-shaped)
  - microphylls arranged spirally on stem
  - sporangia borne axially (whether on microphylls or on stem is not known)

Drepanophycales

Drepanophycales
Fossil range: late Silurian–Devonian
Asteroxylon sp.
Scientific classification

Kingdom:	Plantae
Division:	Lycopodiophyta
Class:	Lycopodiopsida
Order:	**Drepanophycales** † Pichi-Sermolli, 1958

Families

Asteroxylaceae
Drepanophycaceae

Drepanophycales is an order of extinct plants of the Division Lycopodiophyta of ?Late Silurian to Late Devonian age, found in North America, China, Russia, Europe, and Australia. Sometimes known as the Asteroxylales or Baragwanathiales.

Description

Extinct terrestrial vascular plants of the Silurian to Devonian periods. Stem of the order of several mm to several cm in diameter and several cm to several metres long, erect or arched, dichotomizing occasionally, furnished with true roots at the base. Vascular bundle an exarch actinostele, tracheids of primitive annular or helical type (so-called G-type). Stem clothed in either microphylls (leaves with a single vascular thread or 'vein'), or with leaf-like enations (unvascularized projections) with a vascular trace into the base of each enation. Homosporous, with sporangia borne singly and dehiscing by a single slit.

Asteroxylon
mittleres Devon
(Elberfeld bei Wuppertal,
Nordrhein-Westfalen)

List of families

- Drepanophycaceae Kräusel & Weyland
  - stem with microphylls
- Asteroxylaceae
  - stem with unvascularized enations

Drepanophycus

Scientific classification

Kingdom:	Plantae
Division:	Lycopodiophyta
Class:	Lycopodiopsida
Order:	Drepanophycales
Family:	Drepanophycaceae
Genus:	***Drepanophycus*** Göppert, 1852

Species

- *Drepanophycus spinaeformis* Göppert (Type species)
- *Drepanophycus crepini* (Gilkinet)
- *Drepanophycus qujingensis* Li & Edwards
- *Drepanophycus gaspianus* (Dawson) Kräusel & Weyland
- *Drepanophycus spinosus*

Another species has been described: *Drepanophycus colophyllus* Grierson & Banks - but this has since been removed to the genus *Haskinsia*.

Drepanophycus is a genus of extinct plants of the Division Lycopodiophyta of Early to Late Devonian age, found in Eastern Canada and Northeast USA, China, Russia, and various parts of Northern Europe and Britain.

Description

Extinct terrestrial vascular plants of the Devonian period. Stem of the order of several mm to several cm in diameter and several cm to a metre long, erect or arched, dichotomizing occasionally, furnished with true roots at the base. Vascular bundle actinostele, tracheids of primitive annular or helical type (so-called G-type). Leaves are unbranched thorn-shaped (i.e. with a wide base, tapering to a blunt point) microphylls several mm long with a single prominent vascular thread, arranged spirally to randomly on the stem. Sporangia borne singly on the upper leaf surface.

Drepanophycus differs from a closely related genus of the same period, Baragwanathia, in the position of the sporangia, and the arrangement and shape of the leaves.

It is more derived than the coexisting genus *Asteroxylon*, which has enations lacking vascules, in contrast to the true leaves of *Drepanophycus*.

Nematothallus

Nematothallus **Fossil range: Ludfordian–Downtonian**
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 (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.
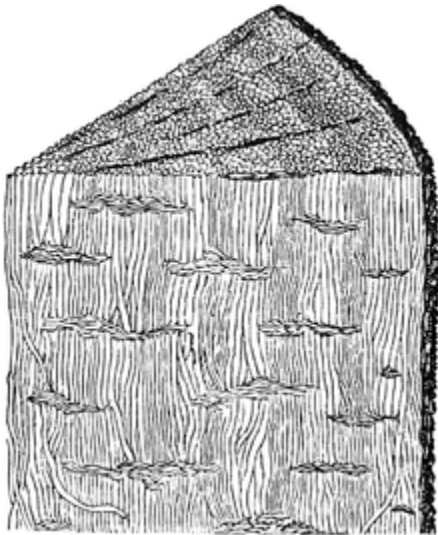
Sherwood-Pike and Gray's "fungus"

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.

Prototaxites

Prototaxites
Fossil range: 420–370 Ma

PreЄ

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| Pg |
| N |

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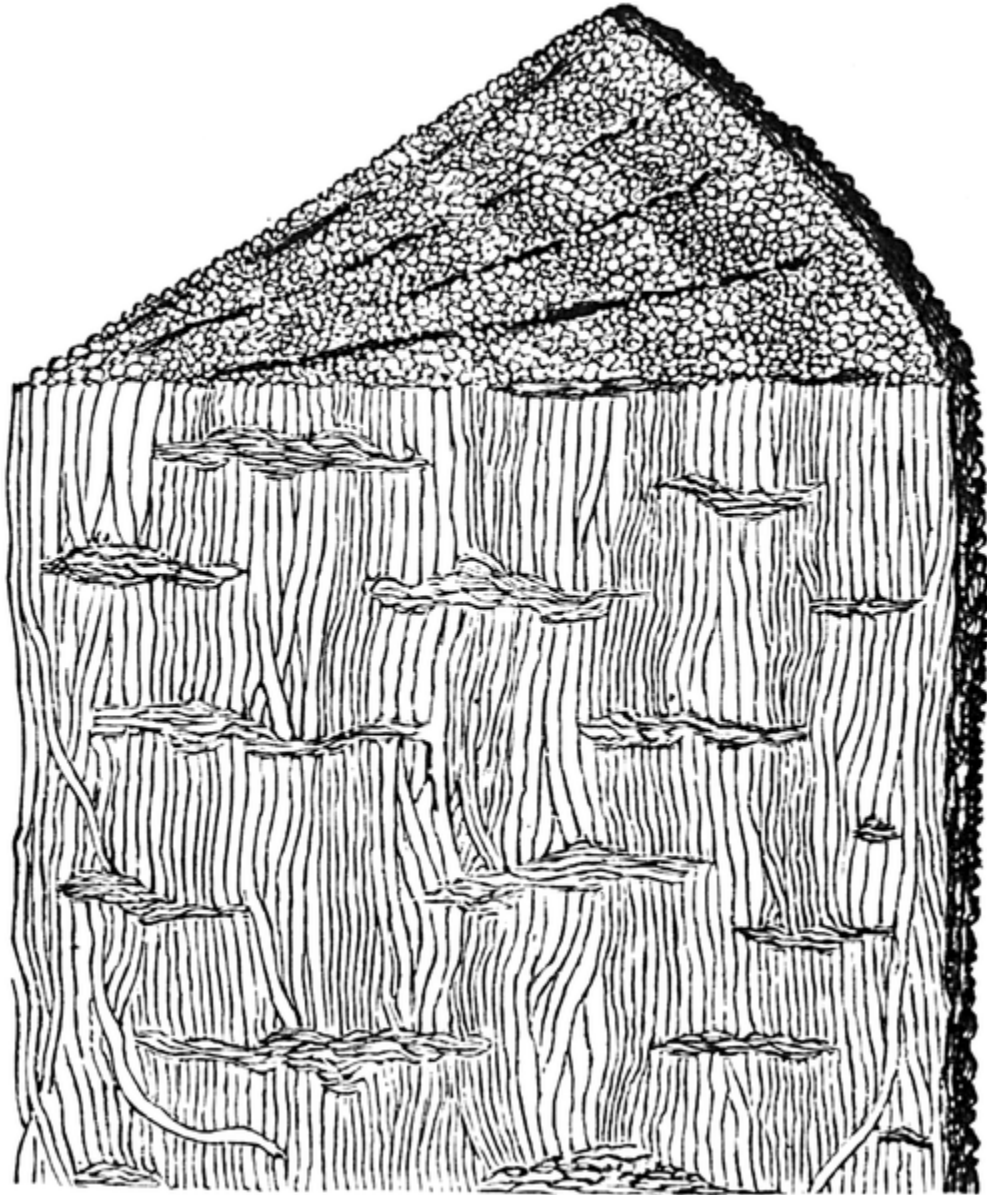
An opposing view has been presented that *Prototaxites* was not a fungus but consisted of enrolled liverwort mats with associated cyanobacteria and fungal tubular elements.

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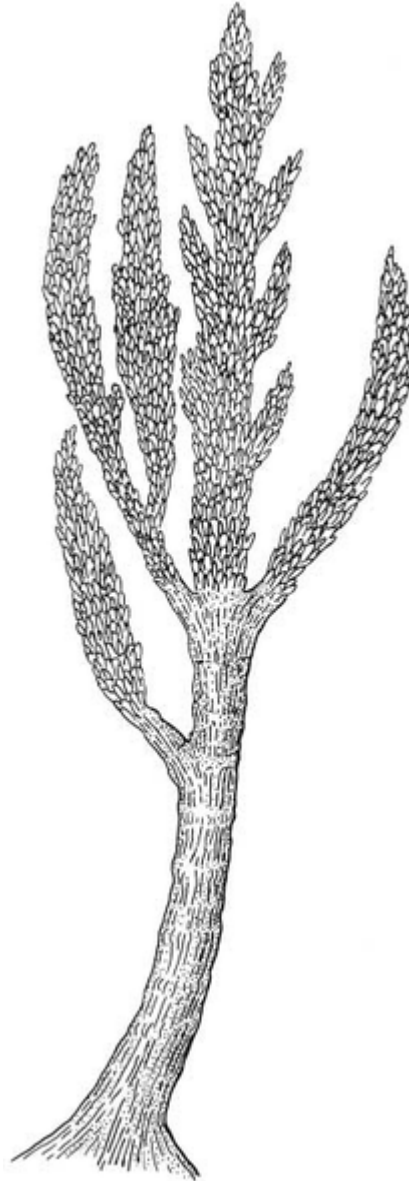
Dawson's 1888 reconstruction of a conifer-like *Prototaxites*

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.

Zosterophyllaceae

Zosterophyllaceae
Fossil range: Late Silurian (late Ludlow, 420Ma) - Devonian
Zosterophyllum species fossils
Scientific classification

Kingdom:	Plantae
Division:	Lycopodiophyta
Class:	†Zosterophyllopsida
Order:	**Zosterophyllales** Cleal & B.A. Thomas, 1994
Family:	**Zosterophyllaceae**

Genera

- *Gumuia*
- *Rebuchia*
- *Zosterophyllum*

The **Zosterophyllaceae** or **Zosterophylls** (class **Zosterophyllopsida**) were probably stem-group lycophytes, forming a sister group to the ancestors of the lycophytes. They were among the first vascular plants in the fossil record, and had a world-wide distribution. By the late Silurian (late Ludlovian, about 420 million years ago) a diverse assemblage of species existed, examples of which have been found fossilised in what is now Bathurst Island in Arctic Canada.

The stems of Zosterophylls were either smooth or covered with small spines known as enations, branched dichotomously, and grew at the ends by unrolling, a process known as circinate vernation. The stems had a central vascular stele in which the protoxylem was exarch, and the metaxylem developed centripetally. The sporangia were kidney-shaped (reniform), with conspicuous lateral dehiscence and were borne laterally in a fertile zone towards the tips of the branches.

The Zosterophylls were named after the aquatic flowering plant *Zostera* from a mistaken belief that the two groups were related. David P. Penhallow's generic description of the type genus *Zosterophyllum* refers to "Aquatic plants with creeping stems, from which arise narrow dichotomous branches and narrow linear leaves of the aspect of *Zostera*." *Zosterophyllum rhenanum* was reconstructed as aquatic, the lack of stomata on the lower axes giving support to this interpretation. However, current opinion is that the Zosterophylls were terrestrial plants, and Penhallow's "linear leaves" are interpreted as the aerial stems of the plant that had become flattened during fossilization.

Stomata were present, particlularly on the upper axes. Their absence on the lower portions of the axes suggests that this part of the plants may have been submerged, and that the plants dwelt in boggy ground or even shallow water. In many fossils these appear to consist of a slit-like opening in the middle of a single elongated guard cell, leading to comparison with the stomata of some mosses. However, this is now thought to result from the loss of the wall separating paired guard cells during fossilisation.