



The Biota of Early Terrestrial Ecosystems: The Rhynie Chert

Learning Resource Site

This module is intended to give an overview of all aspects of our present knowledge of the Rhynie chert. It is sub-divided into the following sixteen numbered sections. Many sections are further sub-divided to give detail on particular aspects of the Rhynie chert flora and fauna. Each of the main sections is a self-contained package, however greatest benefit will be gained by going through the material in numerical order.

The images included within this resource provide for the first time an extensive illustration of the content of the Rhynie chert. New discoveries will be added as they are described in the scientific literature.

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Site Navigation

In conjunction with the hyper-linked table of contents below, use the forward and back icons on your web browser to navigate this site!

Contents

[The Rhynie Chert: At a glance basic information](#)

1. [What is the Rhynie Chert?](#)
2. [History of research at Rhynie](#)
3. [How do we study the Rhynie Chert?](#)
4. [Age of the Rhynie Chert](#)
5. [Geology and setting](#)
6. [Mineralisation and hydrothermal alteration](#)
7. [Chert textures](#)
8. [Taphonomy of the plants and animals and their preservation](#)
9. [Silicification and the conversion of sinter to chert](#)
10. [Fossil flora](#)
11. [Fossil fauna](#)
12. [Evidence for plant/animal interactions](#)
13. [The ancient environment and modern analogues](#)
14. [Significance to science?](#)
15. [Glossary](#)
16. [Bibliography](#)

Click here to find other [links](#) on the Rhynie chert and related topics.





Basic Facts

The Rhynie Chert

- The Rhynie chert is a rock containing exceptionally well-preserved fossil plants and animals (arthropods).
- It is found near the village of Rhynie, Aberdeenshire, Scotland [\[map\]](#).
- Discovered in 1912 by Dr William Mackie [\[History\]](#).
- Chert is a hard silica-rich rock.
- The age of the chert is Early Devonian (Pragian): between 400 and 412 Million years old [\[timescale\]](#).
- At this time Scotland was situated around 28° south of the equator as part of a huge continent made up of northern Europe, North America and Greenland, called Laurussia [\[palaeogeographic map\]](#).
- The cherts are altered siliceous sinters deposited by hot springs and geysers similar to those active today in Yellowstone National Park, USA.
- The sinters coated and fossilised plants and animals preserving them in amazing detail.
- The plant and animal fossils are important because they were some of the earliest colonisers of the land.
- The fossils help us reconstruct early land-based ecosystems.
- The oldest 'insect' fossils known, *Rhyniella* (a type of springtail) and *Rhyniognatha* (a primitive

pterygote insect), have been found in the Rhynie chert.

- The flora includes seven named higher land plants, all less than 40 cm tall. [[plants](#)].
- At least fifteen different (valid) named species of early terrestrial and freshwater arthropods have been described from the chert, and still more are currently being described or await publication [[animals](#)].
- Algae, fungi, a lichen and various bacteria are also fossilised in the chert.
- The hot spring waters that deposited the sinter contained gold, arsenic, antimony and other metals.
- The Rhynie chert is the oldest hot spring system known anywhere in the world where surface features such as geyser vents are preserved.

CONTENTS PAGE



What is the Rhynie Chert?

What is it?

Chert is a sedimentary rock comprised primarily of very finely crystalline silica minerals, mainly a number of varieties of [quartz](#). Some cherts are formed from the accumulation of siliceous animal remains such as radiolaria, diatoms or sponge spicules. Most, however, are formed by chemical precipitation from silica rich fluids either within or replacing pre-existing sediments after they have been buried, or more rarely as a primary surface deposit. The 'Rhynie chert' falls into this last category and was originally deposited as sinter from ancient hot springs. It is a rather unusual variety of bedded chert of predominantly dark blue-grey colours that is of [Early Devonian \(Pragian\)](#) age, between 400 and 412 million years old (see inset right). The most remarkable feature of this particular rock is that it contains exceptionally well preserved fossils of some of the earliest plants and animals to colonise the land.

Right: A polished slab of the Rhynie chert. This shows a vertical section through a chert bed displaying horizontal wavy laminae with occasional beds containing fossilised upright plant stems (centre).



Where is it?

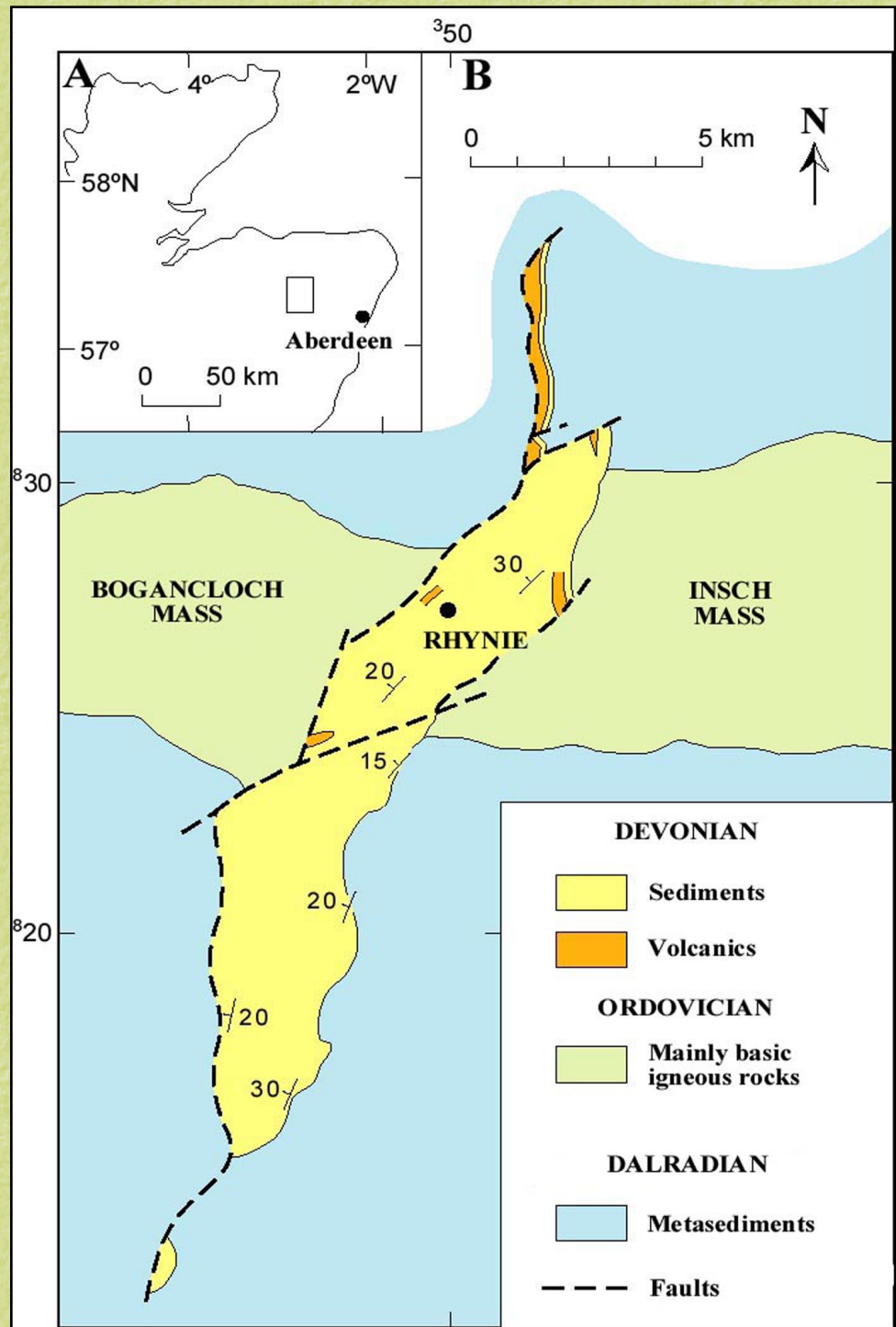


The 'Rhynie chert' is located near the village of Rhynie in north east Scotland, a village approximately 50km north west of Aberdeen (see insets below). The rock itself does not naturally outcrop at the surface. Most fossiliferous chert has been found as loose blocks within the soil. The chert has been located *in situ* by trenching at various times, and more recently by drilling and coring during 1988 and 1997.



Above: Rhynie village looking southeast across the Rhynie chert SSSI (field in foreground).

Right: Locality map for Rhynie, N.E. Scotland. The Rhynie chert occurs towards the top of a sequence of Devonian sediments in a narrow basin which sits on older igneous and metamorphic rocks (for a close up map of the geology of the Rhynie area see the section on [Geology and setting](#)).



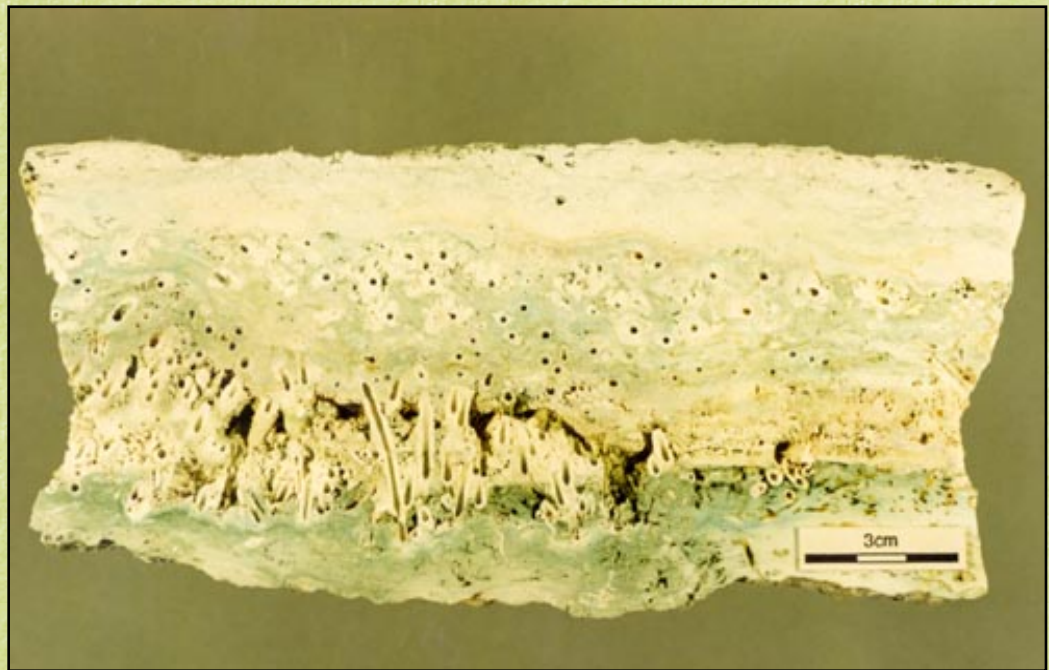
Why is it important to science?

There are a number of factors that give this rock its celebrated status!

- The most important is probably the preservation, in remarkable detail, of an Early Devonian terrestrial and freshwater **community of plants and animals**, together with bacteria and fungi.
- The plants are sometimes preserved in such exquisite detail that their internal anatomy can be described. They are the **best preserved land plants** known from 400 million or more years ago and as such form a cornerstone of palaeobotanical studies.
- The animals represent one of the earliest and certainly the best preserved terrestrial fauna known from the Devonian. Recent finds make this **the most diverse associated fossil arthropod fauna of terrestrial and freshwater origin from rocks of comparable age anywhere in the world**.
- The Rhynie cherts are part of the surface expression of an Early Devonian precious metal-bearing (contains minor gold) hot-spring system. This is **the oldest hot spring system known where surface features such as geyser vents are preserved anywhere in the world**.

How was it formed?

For a short period in the Early Devonian there were hot springs and geysers at Rhynie. The waters contained dissolved silica, and when the erupted water cooled amorphous silica was deposited in the form of **sinter**. Some of the silica coated and trapped plants and animals on the land surface or within shallow ponds, and the organic structures were mineralised (see inset right). Burial of the sinters over millions of years resulted in deposition of more silica and the eventual conversion of sinter to crystalline chert.



Above: A polished slab of recent sinter from New Zealand showing upright moulds of plant stems coated by amorphous opaline silica.

At the present day hot springs depositing siliceous sinters occur in many areas, notably Yellowstone National Park in the USA, and near Rotorua in New Zealand (see insets right and below right).

Right: Geysers in eruption at Yellowstone National Park. Precipitation of amorphous silica from successive eruptions and outflows of hot water create 'cones' and sheets of sinter around the vent.



Right: Poned run-off from Daisy geyser (middle distance) in Yellowstone National Park, creating a localised wetland habitat on a degraded sinter surface colonised by plants.

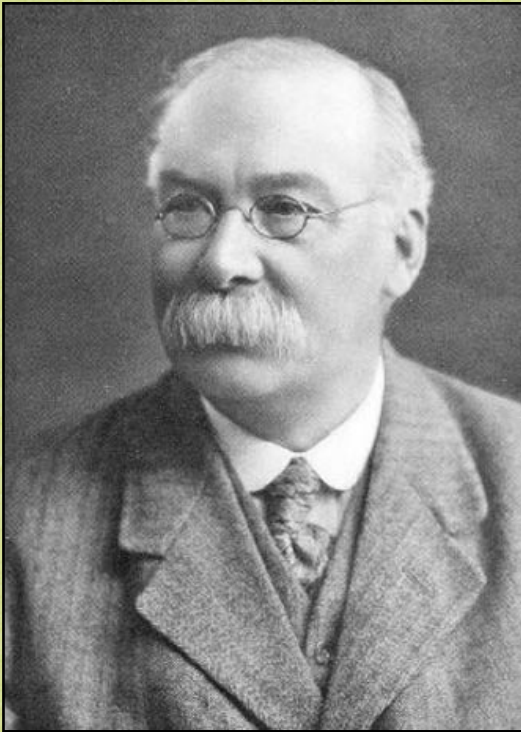


CONTENTS PAGE



History of Research at Rhynie

The Early Days

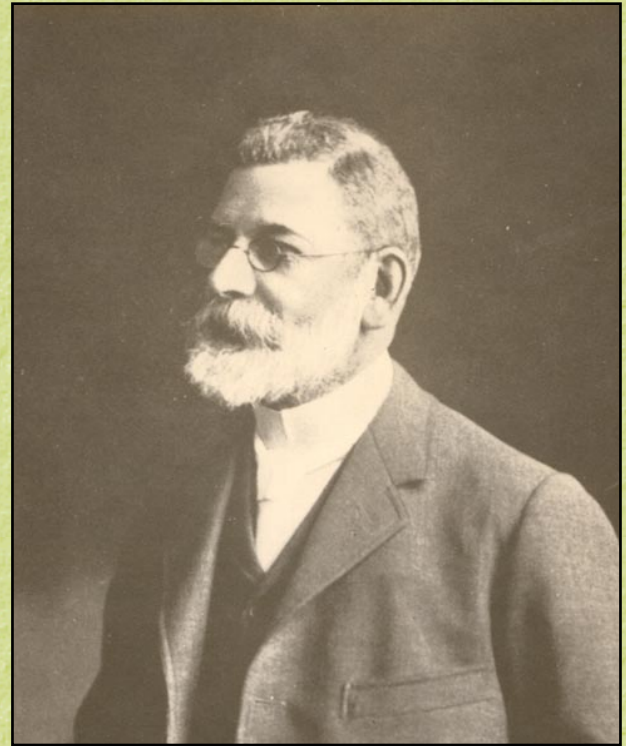


The Rhynie chert was discovered in 1912 by Dr William Mackie (see inset left), a medical practitioner from the town of Elgin to the north of Rhynie, during a study of the geology of Craigbeg and Ord Hill ([Mackie 1913](#)). Whilst geologically mapping the area around Rhynie he found some unusual siliceous rocks incorporated into a dry-stone wall field boundary. Upon making thin sections of the rock, he observed perfectly preserved plant axes (stems) showing detail of individual cellular structure. We are fortunate indeed that he realised the profound significance of this deposit and made his find known to specialist workers in palaeontology.

Above: Dr William Mackie.

In October 1912 a trench was dug in the cherts by Mr. D. Tait (a fossil collector to the Geological Survey). Trenching was coordinated by a committee of the British Association for the Advancement of Science, and the report ([Horne et al. 1917](#)) contains a brief report on the plants by Dr Robert Kidston (see inset right and below), introducing the names *Rhynia gwynne-vaughanii* and *Asteroxylon mackiei*.

In a series of five classic papers Kidston and Professor William Henry Lang described in detail the plants we now know as *Rhynia*, *Aglaophyton*, *Horneophyton* and *Asteroxylon* ([Kidston & Lang 1917](#), [1920a,b](#), [1921a,b](#)). They also described parts of *Nothia* but included it as part of *Asteroxylon*. Kidston died in 1924, and although Lang continued to produce papers on Scottish palaeobotany until 1952, he did not add to his Rhynie work.

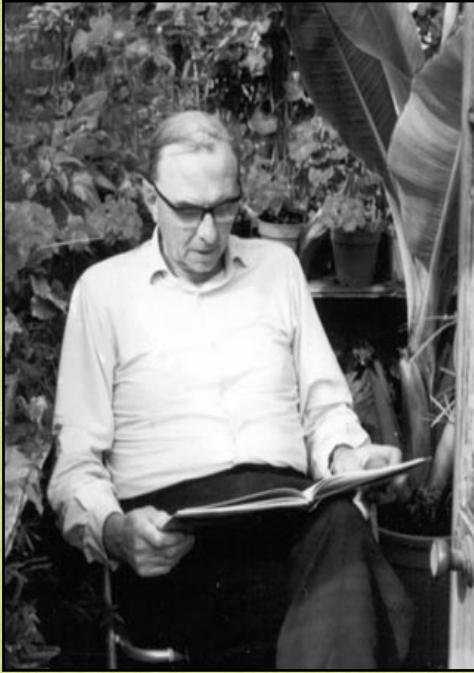


Above: Dr Robert Kidston.



Above: Dr Robert Kidston (right) and the palaeobotanist Professor David Thomas Gwynne-Vaughan (left).

In the 1920's the first arthropods were described from the chert with [Hirst \(1923\)](#) describing the trigonotarbids, [Scourfield \(1926\)](#) the freshwater crustacean *Lepidocaris*, and [Hirst and Maulik \(1926\)](#) the earliest 'insect', a springtail, *Rhyniella*.



Above: The late Dr Geoffrey Lyon, a photograph taken in the greenhouse at his home in Rhynie in 1982.

A period of some thirty years went by without any major contributions, but in the late 1950's interest was rekindled through the work of Dr. A. G. Lyon (see inset left) who described spores fossilised in the process of germination ([Lyon 1957](#)). He and his research students at Cardiff continued to contribute papers on the chert flora using material from trenches dug in the 1960's and 1970's. Dr Lyon owned the Rhynie chert site (a designated SSSI or Site of Special Scientific Interest) for many years, gifting it to Scottish Natural Heritage (SNH) in 1982.

Over the years Geoffrey Lyon gave chert material to many palaeobotanists, but it was the team at the University of Münster, led by the late Professor Remy who had the greatest success (check out the University of Münster Rhynie page [here](#)) finding the small gametophytes of the sexual generation of several of the plants ([Remy & Remy 1980](#); [Remy & Hass 1991a,b,c,d](#)).

Recent Research and Discoveries

By the late 1980's there was increasing production of research papers on the Rhynie flora and fauna. During this time and into the 1990's research by the University of Münster, often in collaboration with various specialists from other institutions, saw the advancement of our knowledge of the Rhynie flora. As well as the discovery of the gametophyte stages of several of the plants, they also discovered a number of new flora, including various types of fungi ([Hass & Remy 1992](#); [Hass et al. 1994](#); [Remy et al. 1994a](#) & [b](#)) and the earliest known fossil lichen. It was also in the early 1990's that the first zosterophyll plant from the chert was discovered, *Trichopherophyton* ([Lyon & Edwards 1991](#)).

However, the basic geology of the Rhynie area had not been revised since Geikie's description in [1878](#). The British Geological Survey remapped the area with the new map published in 1993 (BGS Alford Sheet 76W) but surface outcrop on this poorly exposed area revealed little to augment existing knowledge.

Interest in the area from the University of Aberdeen commenced when [Rice and Trewin \(1988\)](#) demonstrated that the chert and silicified rocks in the area are enriched in gold and arsenic and confirmed the hot spring origin of the cherts. A mineral exploration programme of drilling and trenching ensued, revealing much about the subsurface geology ([Trewin & Rice 1992](#); [Rice *et al.* 1995](#)). The exploration rig used by the mineral exploration company was hired by the university and core was taken through the Rhynie chert sequence. For the first time the unweathered lithologies of sandstone and shale between the chert beds could be examined and the plant sequence and palaeoenvironment interpreted ([Trewin 1994](#); [Trewin 1996](#); [Powell *et al.* 2000b](#)). A second phase of drilling in 1997 (see inset below), followed by more recent trenching programmes and magnetic surveys in the Rhynie area, has produced more surprises, requiring further revision of the geology of the area ([Rice *et al.* 2002](#); [Rice & Ashcroft *in press*](#)).



Above: Drilling rig at Rhynie during the summer of 1997.

The discovery of a fossiliferous chert (the **Windyfield chert**) some 700m from the original chert locality ([Trewin & Rice 1992](#); [Trewin 1994](#)) resulted in recognition of part of a geyser vent rim with typical splash texture (see inset right). This new chert also yielded *Ventarura*, a second zosterophyll plant from the area ([Powell et al. 2000a](#)) to add to *Trichopherophyton* from the Rhynie chert ([Lyon & Edwards 1991](#)). The Windyfield chert is also rich in arthropods, including trigonotarbid arachnids, centipedes, branchiopod crustaceans and euthycarcinoid remains ([Anderson & Trewin 2003](#)). Numerous new arthropods from the Windyfield chert await publication or are currently being described ([Fayers & Trewin in press](#); [Fayers et al. in press](#)).



Above: A block of the 'Windyfield chert' showing splash textures directly comparable to those seen around modern day geyser vents (click on image for a close up!).

Fieldwork during the autumn of 2000 resulted in the discovery of a concentration of numerous chert float blocks near Castlehill (approximately 1500m east of the Rhynie chert locality) ([Rice *et al.* 2002](#)). It remains uncertain as to whether these are sourced locally from weathered *in situ* chert bodies beneath the surface or are glacially derived from the Rhynie area. One block of chert from Castlehill has yielded a completely new branchiopod crustacean, *Castracollis* ([Fayers & Trewin 2003](#)), and the attached fertile elements of the charophyte alga *Palaeonitella* ([Kelman *et al.* in press](#)).

In September 2003 an international meeting entitled "**The Rhynie Hot Spring System: Geology, Biota and Mineralisation**" was held at the University of Aberdeen (click [here](#) for a summary). Numerous papers presented at this conference will form the content of a special volume to be published in the *Transactions of the Royal Society of Edinburgh: Earth Sciences* later in 2004.

A history of research of the Rhynie chert, its palaeontology, and the geology of the Rhynie area is currently awaiting publication ([Trewin in press](#)).

Future Work

Research continues in several universities involving specialists on different groups of plants and animals, and new elements of this ancient biota continue to be found. There is clearly still considerable research potential in the description and interpretation of this remarkable community of plants and animals that lived near the hot springs of Rhynie 400 million years ago.

In September 2003 a new trench was excavated through part of the Rhynie chert succession with permission from Scottish Natural Heritage. During the excavation oriented *in situ* beds of chert were sampled from numerous plant-bearing horizons, each covering an area of at least 1m². Using this material it is hoped further research will enable the **3-dimensional palaeoecology** of the chert to be determined, a study that hitherto has not been attempted. Prof. Dr Nigel Trewin and Dr Stephen Fayers are currently seeking funds to proceed with this research.

CONTENTS PAGE



How do we study the Rhynie Chert?

Introduction

We have already seen in the previous two sections that the Rhynie chert does not crop out anywhere naturally at the surface and thus there are only three main ways of collecting material and/or seeing the chert *in situ*:

- Collecting loose blocks of chert brought to the surface by ploughing.
- Taking cores of the bed rock by [drilling](#).
- Excavating [trenches](#) into the bed rock.

Once the chert is collected, a number of analytical techniques can be used depending upon the information that the researcher is looking for. The following describes four of the main methods that have been employed to study, among other things, the fauna, flora, sedimentology and palaeoenvironments of the cherts.

Cut blocks



Above: A cut and polished slab of chert (in this case from the Windyfield site) showing nodular and brecciated textures (centre) and wavy laminae (top).

One of the first steps, once raw material has been collected, is to cut the blocks of chert with a rock-cutting saw. Before this is done, the chert is cleaned and the surfaces examined to identify, if possible, the top and bottom of the original 'chert bed'. Sometimes examining the surfaces of blocks alone can reveal important diagnostic structures or 'textures' such as the splash textures described above (see [History of Research at Rhynie](#)). Usually a series of sequential slices of the chert are cut perpendicular to the bed and the cut surfaces then polished. This produces clean surfaces where the internal structures and textures through the entire bed can be examined in hand specimen (see inset left), such as internal bedding, plants and **geopetal** or 'way-up' structures (see also the section on [Chert textures](#)).

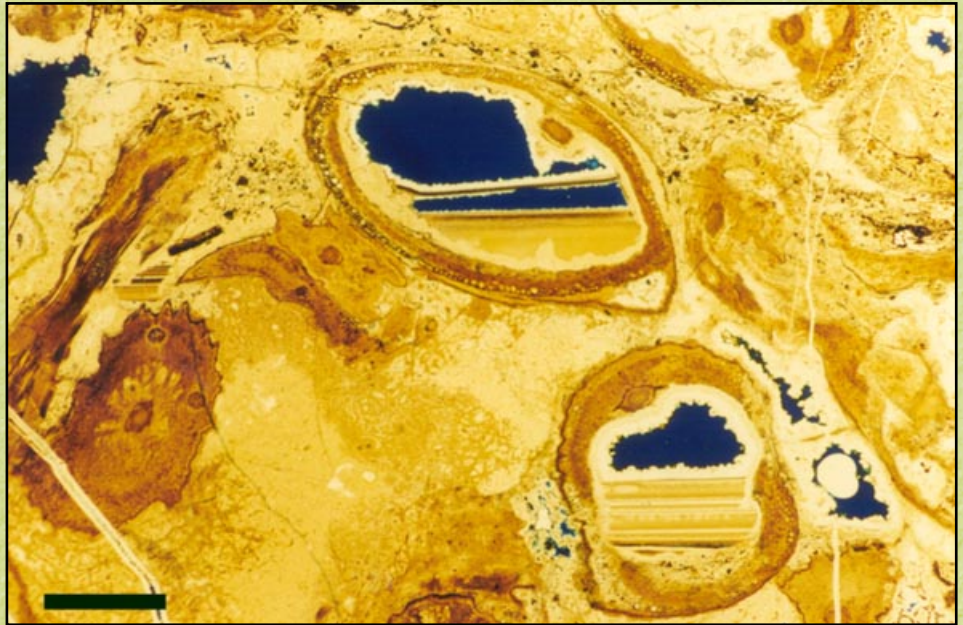
The cut slices of chert can be examined in more detail under reflected light using a binocular microscope after applying a thin veneer of microscopy oil to the cut/polished surface. This enables the identification of, for example, fauna, flora and textures within the chert for more detailed analysis. Further analysis of such features may involve using thin sections, acetate peels and SEM (Scanning Electron Microscope) techniques which are briefly outlined below.

Thin Sections

Thin sections of the rock allow material to be examined under a microscope using transmitted light (i.e.: light that can pass through the rock) as well as reflected light. They are prepared by mounting a small cut and polished sample of chert, using a strong adhesive onto a plate of glass (usually 50x75cm or 25x75cm in size) and then the exposed surface of chert is gradually ground or 'lapped' down to a certain thickness, usually somewhere between 100 and 30 μ m, depending upon the features being examined. This slice of rock is then usually thin enough to transmit light, enabling a lot more details of fossils and textures to be seen. Thin sections may have a glass cover-slip added for protection of the slide, though

alternatively the 'lapped' surface may be polished for examination in back-scattered mode on the SEM (see below).

This technique is particularly useful for examining microscopic details of the plants, animals as well as the sedimentary textures and mineralogy of the cherts (see inset right). By cutting and mounting sequential thin sections through a particular chert block, a whole chert bed can thus be examined in detail (see the section on [Chert textures](#)). Because the thin section of rock on the glass slide has a smooth, flat surface it is easy to photograph.



Above: Detail of a thin section of Rhynie chert showing sections through straws of the plant *Aglaophyton major*. Geopetal layers of very fine sediment within the straws indicate the 'way up'. The blue colour in this thin section is stained epoxy resin infilling pore space (scale bar = 3mm).

Acetate Peels

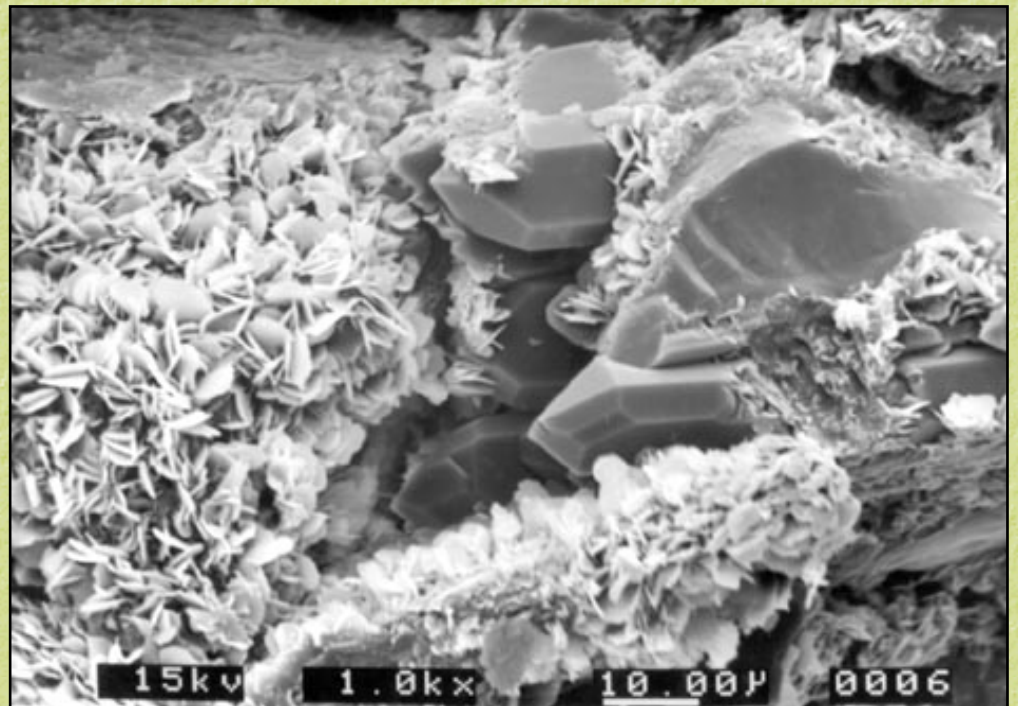
Acetate peels are taken by first etching the cut/polished surface of a chert block with HF (Hydrofluoric acid) for a few seconds. This technique is done under strict safety conditions in a fume cupboard as HF is very dangerous. The acid dissolves away a thin layer of silica leaving a slight positive relief of organic material or any other material that is otherwise insoluble in HF. The etched surface of chert is then flooded with acetone and a sheet of acetate film is then carefully placed over the top and allowed to dry for about 10 minutes. When dry the 'peel' can be pulled from the rock surface and it bears a faithful reproduction of the 'organic' and textural features left in relief after the etching. The peel is then mounted onto a glass slide with a cover-slip for study.

This analytical method has been used extensively in the study of the Rhynie plants and their internal anatomy. Successive peels taken through a plant-bearing block of chert can be helpful in reconstructing the 3D morphology of some of the plants and their growth habit. However, because the features on the peels are often very faint and the peels are not always flat, they are not always so conducive to photography as rock thin sections.

SEM

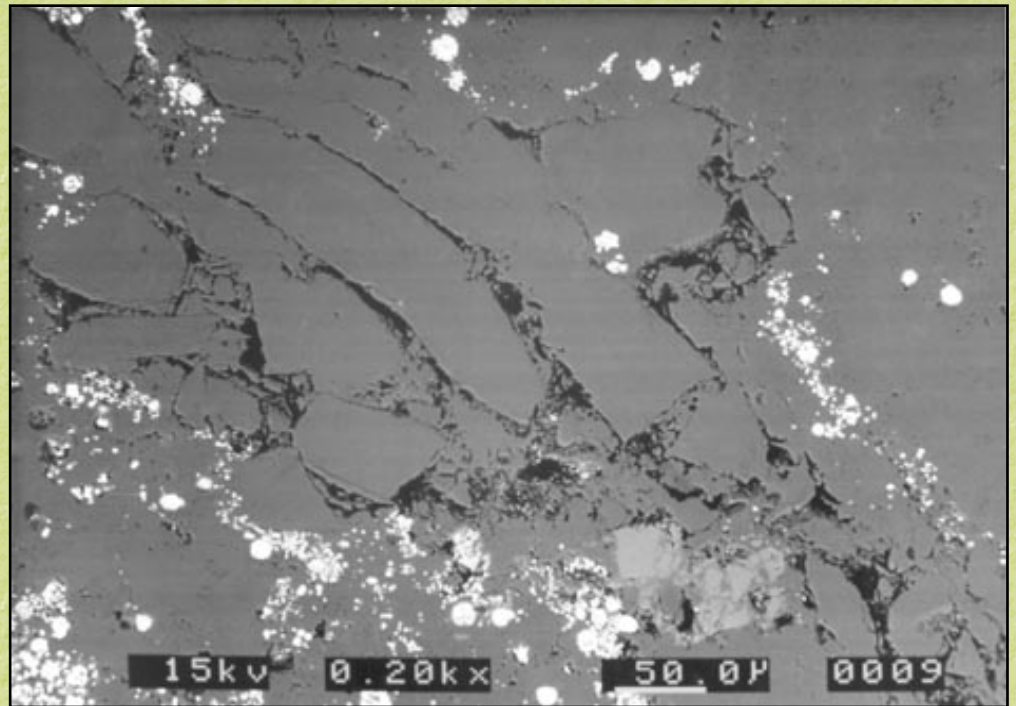
The SEM or Scanning Electron Microscope allows examination of rocks at very high magnifications, showing surface textures and details down to the micron level. This has been a useful technique in looking at many things from clay minerals and **diagenetic** features in the cherts and associated sediments (see inset above right) to the cuticle surfaces of plants where they have been successfully isolated from the host block of chert.

The back-scattered mode on the SEM is particularly useful for



Above: SEM image of diagenetic cements in a sandstone from the Rhynie chert sequence. This shows platy grain-coating chlorite-smectite clays (left and below) with later diagenetic quartz crystals (center and above) infilling a void or 'pore space' between detrital mineral grains.

looking at textures in polished thin sections of chert and sedimentary rock and highlights differences in mineral chemistries (see inset below right).



Above: Back-scattered SEM image of a polished thin section of chert. The very dark areas are voids in the sample representing the original cell walls of a plant. The dark grey is chert that has filled the plant cells. The very light patches are 'framboids' or clusters of micron-sized crystals of pyrite (FeS₂). The lighter grey fragments below right of center are probably detrital feldspar grains.

Other Analytical Techniques

We have seen four of the techniques employed to study certain aspects of the Rhynie chert, but many other analytical methods are also available to study, for example, the mineralogy and geochemistry of the chert and its associated rocks. Such techniques may include XRD (X-Ray Diffraction), XRF (X-Ray Fluorescence), CL (Cathodo Luminescence) and isotope analysis to name but four. A more detailed review of these and other analytical techniques used to study sedimentary rocks may be found in [Tucker \(1988\)](#).

CONTENTS PAGE



Age of the Rhynie Chert

The age of the Rhynie chert and its associated sediments has been calculated by combining two analytical methods: absolute dating and biostratigraphy.

Absolute dating:

Absolute dates for rocks are calculated by examining radioactive isotopes of certain elements in a mineral that take millions of years to 'decay' to a more stable isotope. If the length of time it takes for an isotope to decay to another stable form is known, and also the amount of radioactive isotope that remains in the mineral, then the age of that mineral can be calculated. If the particular mineral has grown at the same time as its host rock formed and remains *in situ* (eg. in igneous rocks), then the age of the rock will be the same as that of the mineral.

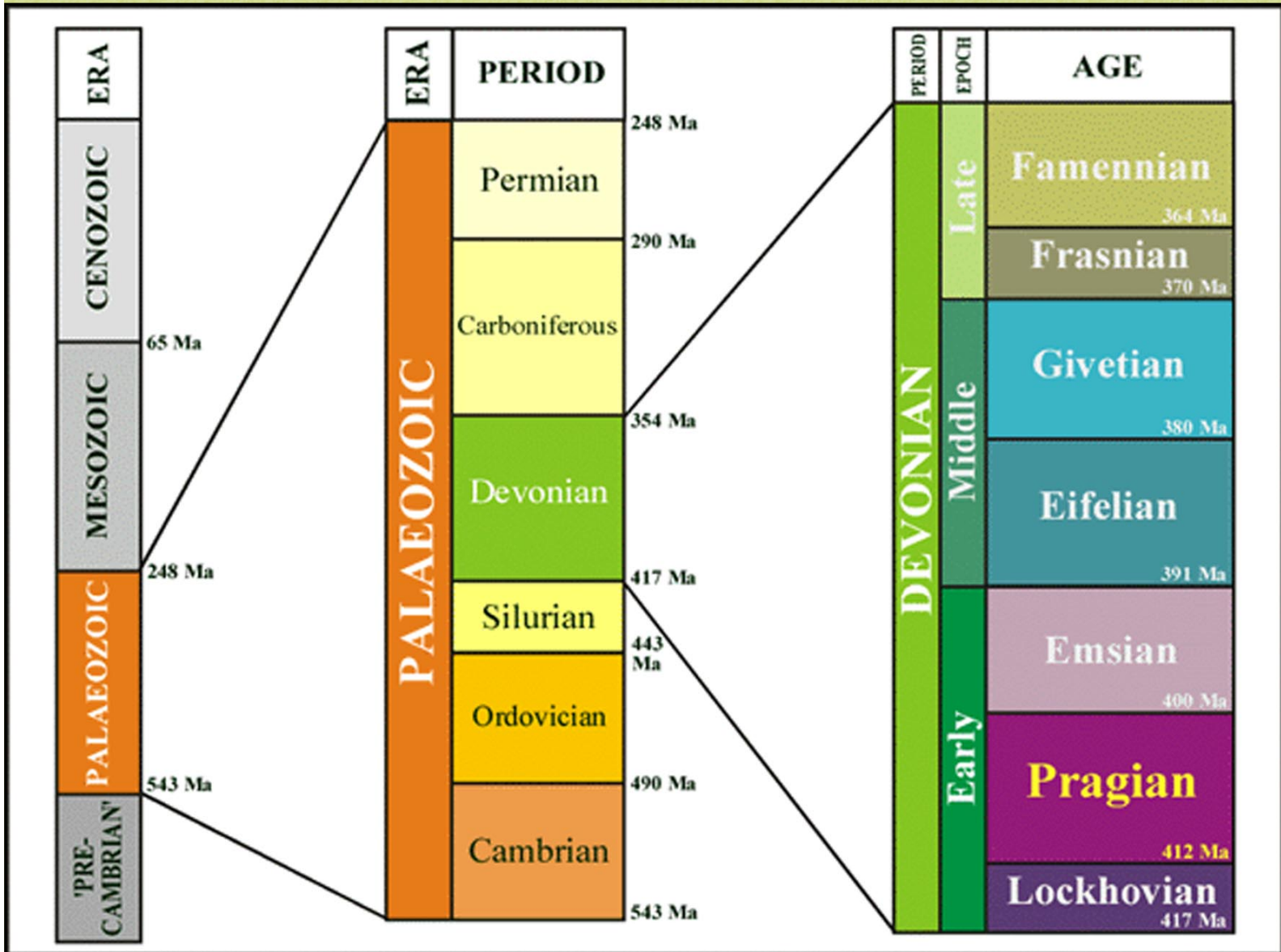
Analysis of the isotopes ^{40}Ar and ^{39}Ar from the cherts have given an age of **396 ± 8 million years** ([Rice *et al.* 1995](#)). Recently the radiometric dating of **zircon** and **titanite** minerals within contemporaneous andesitic lavas at Rhynie have further constrained this date. The results of the zircon and titanite dating are currently being compiled by Stephen Parry and other authors, and will be added here after their publication in the scientific literature.

Biostratigraphy:

With the Rhynie sediments, the other main criterion for dating (or 'relative dating') has been the use of [biostratigraphy](#), primarily using [palynology](#), which includes the study of fossil spores and pollen. In many sedimentary rocks, particularly those of a continental or freshwater origin, fossil spores can be quite widespread, abundant and may be highly diverse and evolved over time. This makes them ideal [zone fossils](#) for biostratigraphy and dating of sedimentary rocks (for some examples of spores, see the section on the [Rhynie flora](#)).

The Rhynie cherts and particularly its associated muddy sediments have yielded many well preserved fossilised spores. Comparing these spores with spore or palynomorph zone fossils collected from other sedimentary rocks of known age at other localities indicates the Rhynie spores fall in a spore [biozone](#) which equates to a time period between approximately 400 and 412 million years (for details of the Rhynie chert palynology see [Wellman 2004](#)).

Combining these dates firmly place the Rhynie cherts and sediments as Early Devonian (see the geological timescale below) and more specifically Pragian in age, although at present an earliest Emsian age cannot be entirely ruled out.



Above: Simplified geological timescale with dates (Ma: Millions of years before present) highlighting the subdivision of the Devonian period. The Rhynie chert and its associated sediments have been assigned to the Pragian age of the Early Devonian.

CONTENTS PAGE



Geology and Setting

[Introduction](#)

[The Boundary Fault](#)

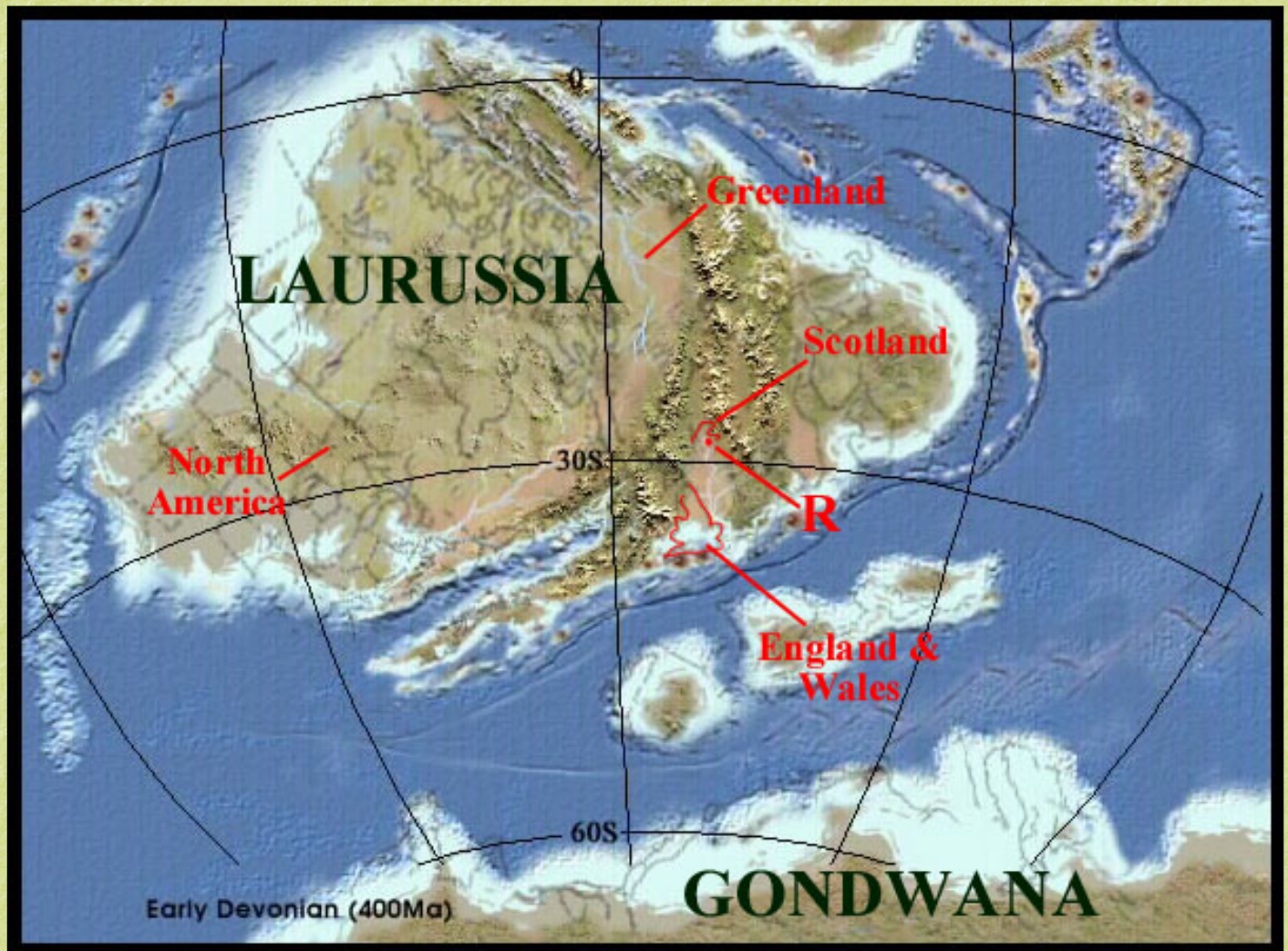
[The Basin Fill](#)

[Basin Evolution](#)

Introduction

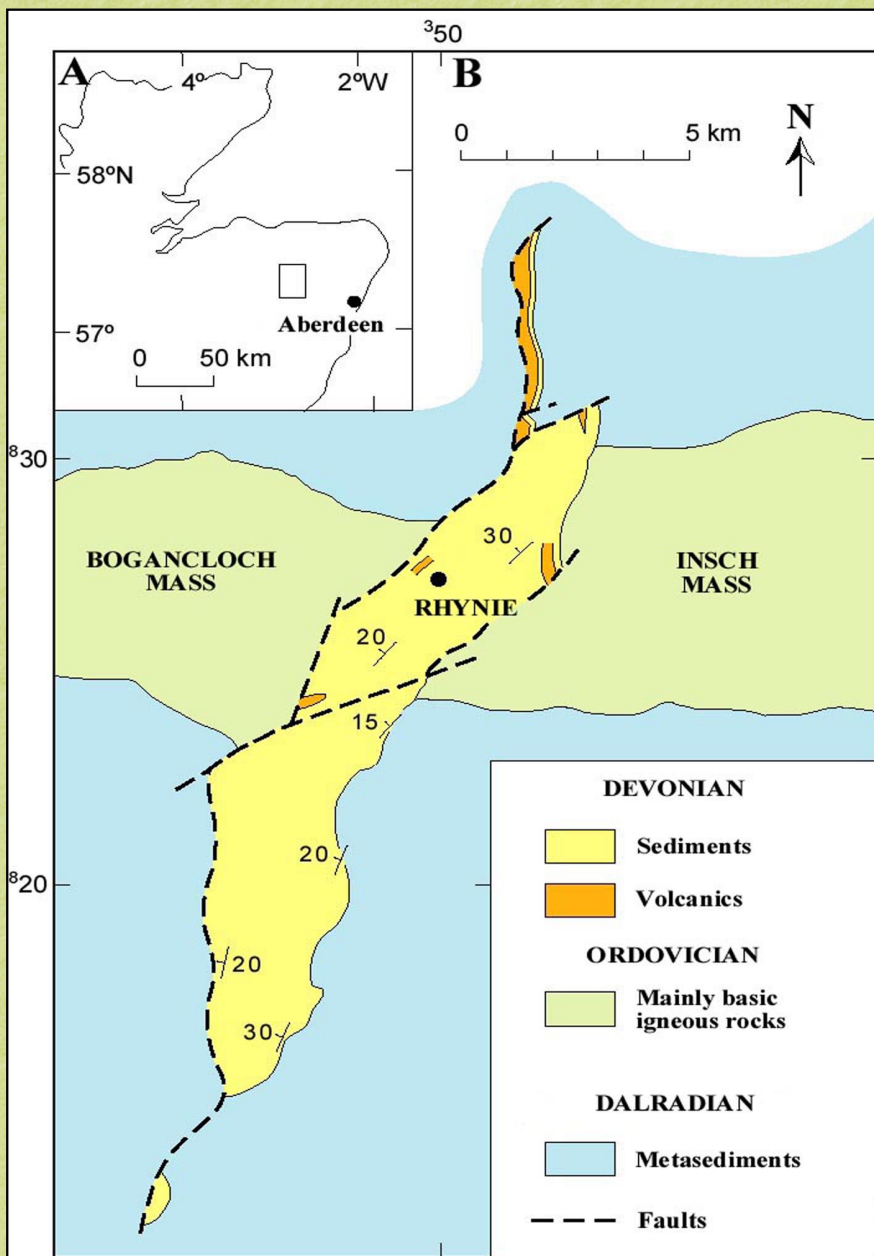
The geology of the Rhynie area was originally mapped and described by [Geikie in 1878](#) with further work by [Wilson and Hinxman \(1890\)](#) and [Read \(1923\)](#). The most recently revised map was published in 1993: BGS Sheet 76W. However, it has only been in recent years following the drilling programmes undertaken by the University of Aberdeen that the geology and particularly the sedimentary succession or [lithostratigraphy](#) is better constrained ([Rice et al. 2002](#)).

The sediments which host the Rhynie chert, as mentioned in previous pages, are Early Devonian (Pragian) in age and form a small part of what is commonly known as the **Old Red Sandstone** or ORS. The ORS comprises a sequence of continental sediments deposited by streams, rivers and lakes throughout the Devonian Period when Scotland, much of northern Europe, Greenland and North America formed a large continent called **Laurussia** or the '**Old Red Continent**', located between 0° and 30° south of the equator. During the Early Devonian (Pragian) the Rhynie area was situated in the subtropics around 28° south of the equator (see inset below).



Above: Palaeogeographical map of Laurussia or the 'Old Red Continent' during the Early Devonian around 400Ma. At this time the Rhynie area (**R**) was situated approximately 28° south of the equator (Copyright owned by Dr Ronald Blakey, Northern Arizona University).

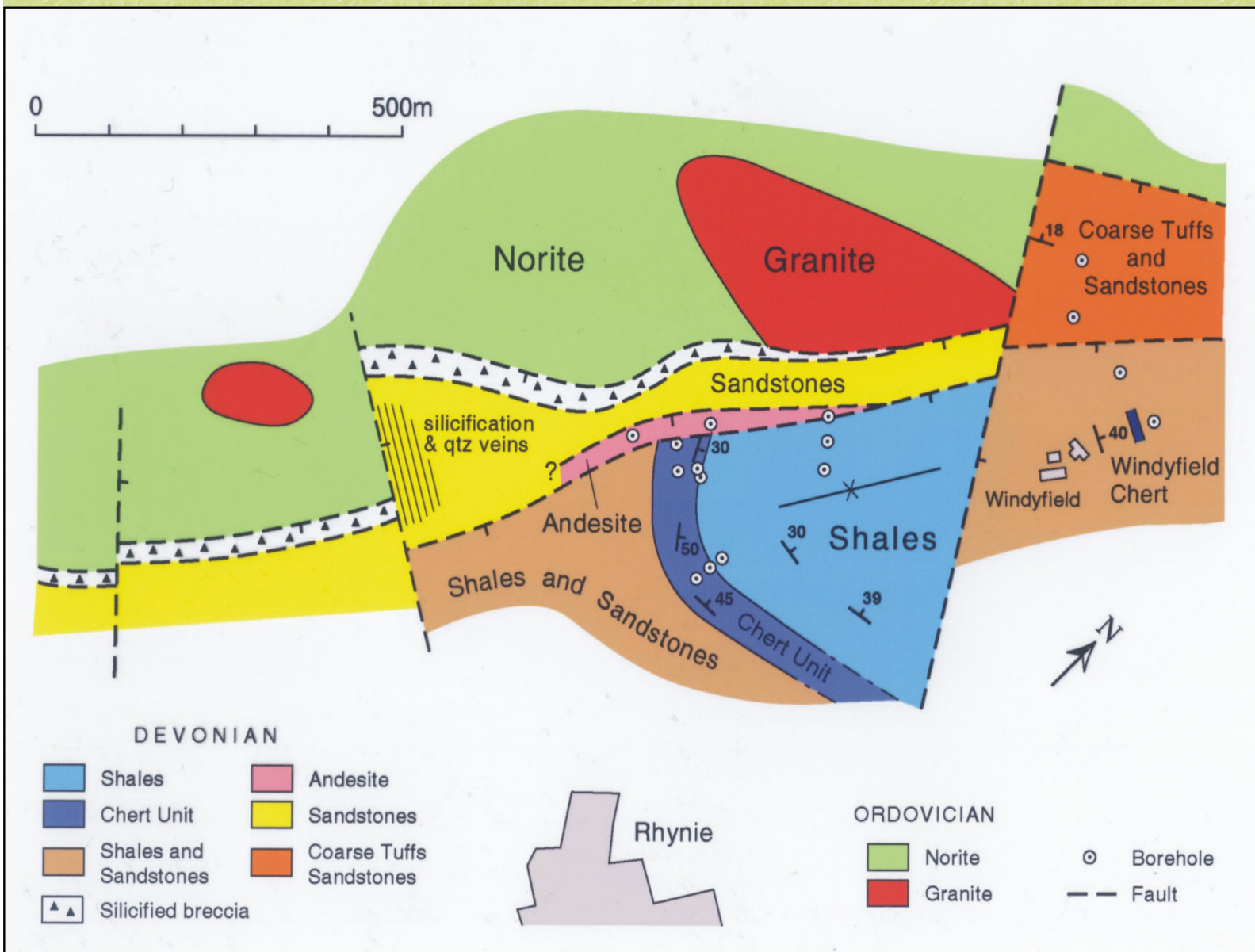
At Rhynie, the sediments which host the chert form an **outlier** surrounded by a basement of Dalradian metamorphic and Ordovician plutonic igneous rocks (see inset left). The Rhynie sediments were deposited in a relatively narrow, northeast - southwest trending basin set within these older rocks.



The basin in the south and the northern most region is a **half graben**, the western edge marked by a low angle (at the current level of erosion) extensional fault system which was active at the time of deposition during the Early Devonian (see below), whereas at the eastern edge of the basin the sediments lay directly on the basement rocks, the contact representing an unconformity. The central to northern area, containing the Rhynie chert locality is now believed to represent a completely fault-bounded strike-slip basin caused by regional trans-tensional forces ([Rice and Ashcroft in press](#)). Within the basin the sedimentary rocks are tilted, generally dipping towards the northwest, though the chert-bearing rocks in the area to the northwest of Rhynie village are folded into a syncline, the axis apparently plunging to the northeast.

Left: Simplified geological map of the Rhynie outlier .

The cherts are associated with shales and sandstones towards the top of the sedimentary succession and are only known to occur *in situ* in the vicinity of the village of Rhynie itself, quite close to the faulted western margin of the basin (see inset below). Results from the drilling programmes suggest much of the sedimentary succession here is heavily disrupted by faulting, with the area being divided into a number of small faulted blocks along the main fault zone. The main features including the sedimentology and lithostratigraphy are described below.

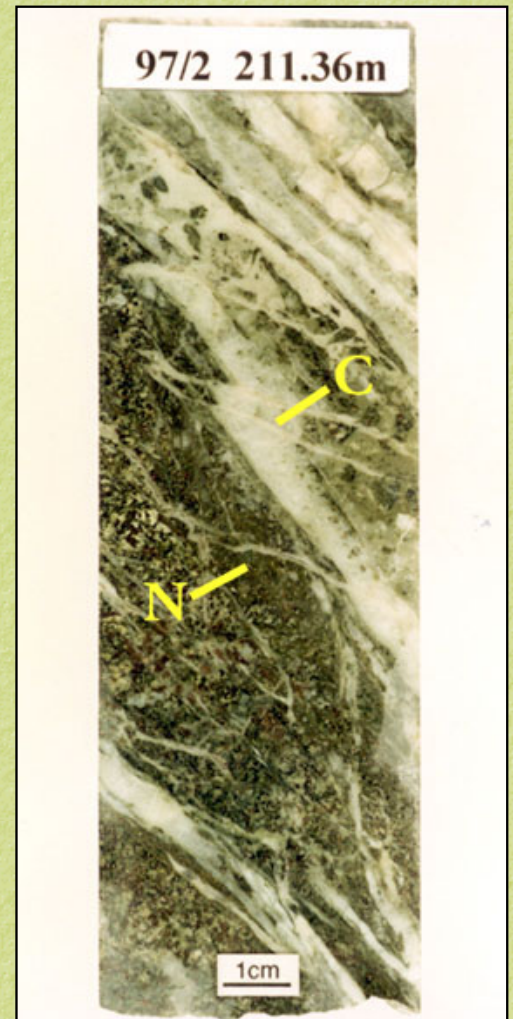


Above: Simplified geological map of the area north and west of Rhynie village (inset above left).

The Boundary Fault

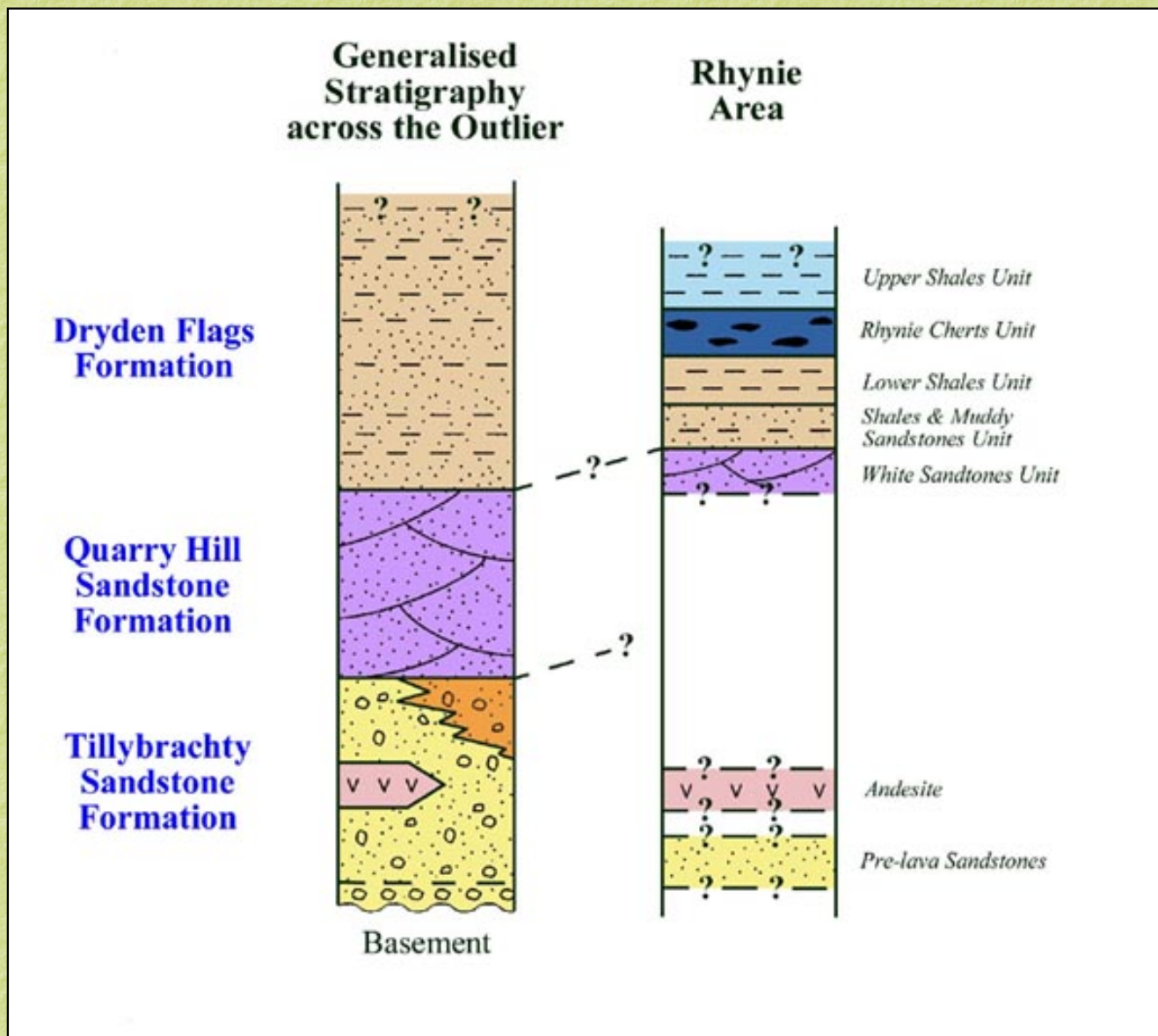
The fault zone forming the western boundary of the basin was cored during the 1997 drilling programme. At the base of the borehole 97/2 and lying between the Devonian sediments and the Ordovician basic igneous rocks ([norite](#)) which make up the basement in the area around Rhynie village, the fault zone is heavily mineralised. This fault which surfaces to the west of Rhynie probably acted as one of the main conduits for the flow of hydrothermal fluids from deep reservoirs to the hot spring surface expressions. The fault zone comprises a multi-phase [breccia](#) of basic igneous rocks set in a matrix of chert and cut by [calcite](#) and quartz veins. The igneous rocks immediately below this fault are also intensely hydrothermally altered, fractured and mineralised (see inset right).

Right: A sample of core from below the fault zone at Rhynie showing green-coloured heavily fractured and hydrothermally altered basic igneous rock, norite (N) with fractures mineralised and sealed by chert (C).



The Basin Fill

There is a variety of rock types that comprise the fill of the Rhynie basin including primarily sedimentary rocks (mainly sandstones and shales) and volcanic rocks. Traditionally the sequence of rocks has been divided into three main lithostratigraphic units: the **Tillybrachty Sandstone**, **Quarry Hill Sandstone** and **Dryden Flags formations**; the latter unit in the Rhynie area hosting the cherts (see inset below). See [Rice *et al.* \(2002\)](#) for details of the stratigraphy. Click on the formation names in the inset below for an outline of the lithologies encountered in each and their inferred environments of deposition:

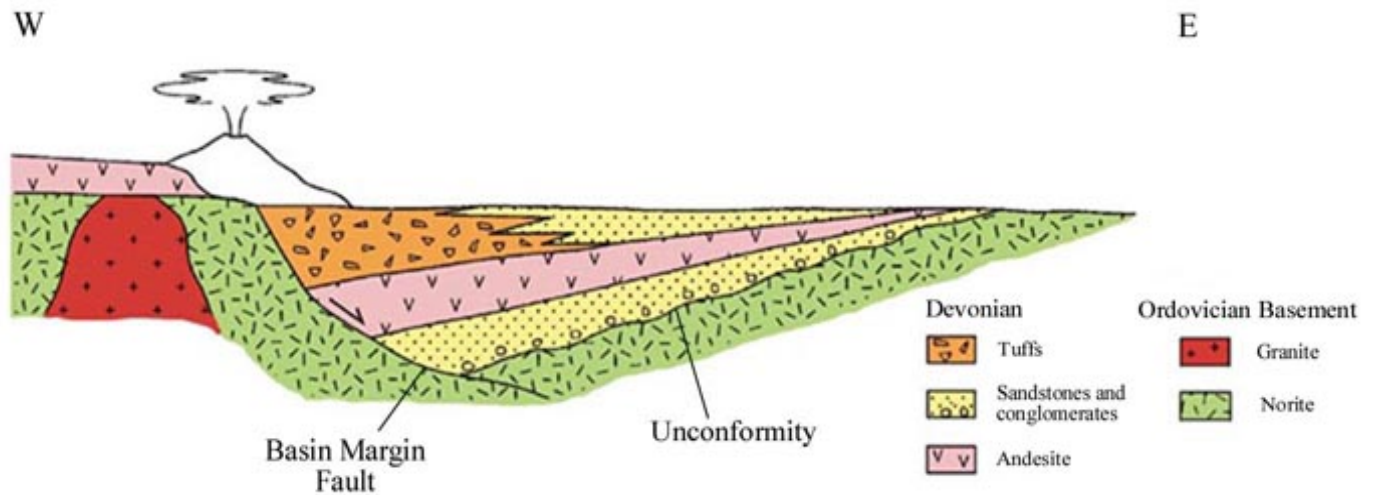


Above: Generalised stratigraphy of the Rhynie outlier (left) and the succession in the area northwest of Rhynie village (right) (after [Rice et al. 2002](#)). Click on formation names on the left for a review of the lithologies and depositional environments.

Basin Evolution

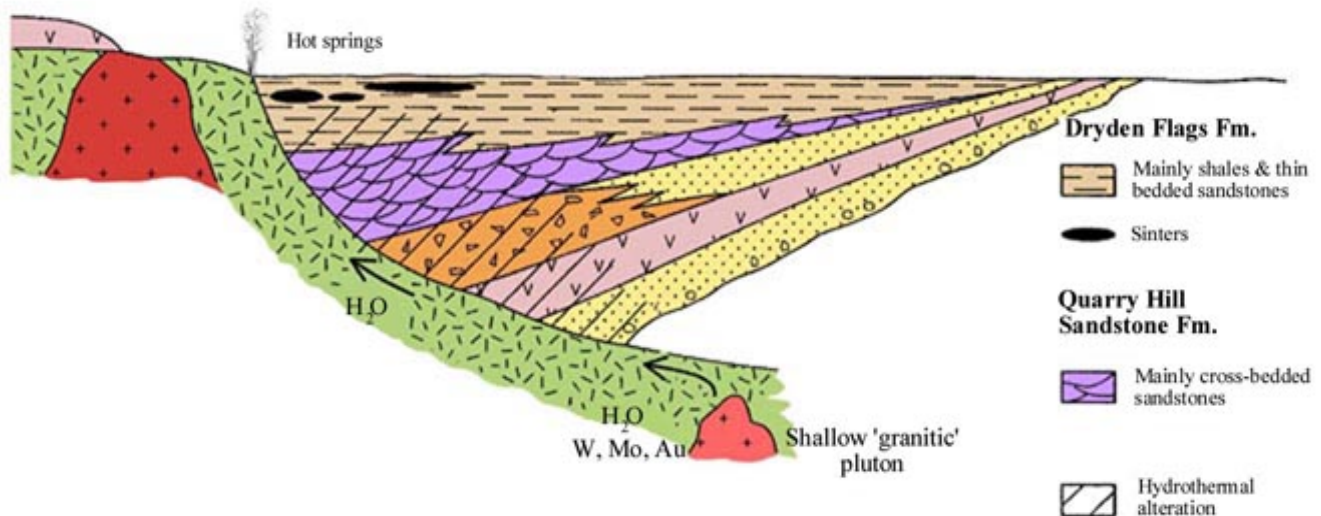
The Rhynie basin was formed as a result of trans-tensional forces affecting the Dalradian metamorphic and Ordovician igneous rocks in the northeast Grampian area following the closure of the Iapetus ocean. Based on present knowledge ([Rice et al. 2002](#)) the evolution of the Rhynie basin can be described in diagrammatic form:

Stage 1: Tillybrachty Sandstone Formation



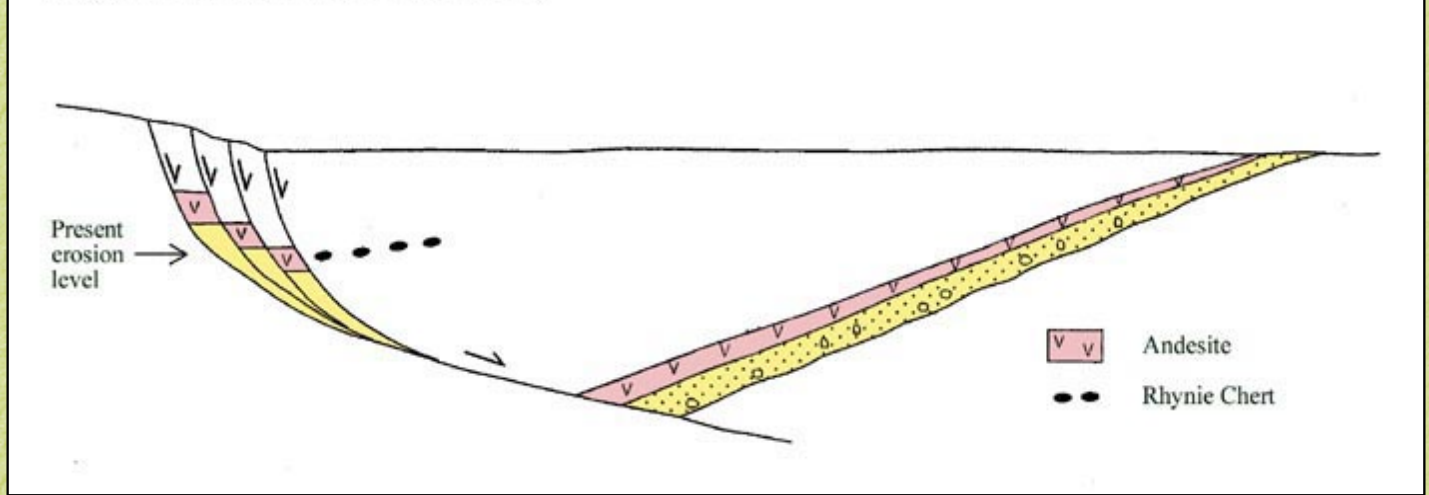
Above: Regional crustal extension and initiation of half-graben basin. Locally derived sands, conglomerates and tuffs with basin-wide andesitic lava flows (after [Rice et al. 2002](#)).

Stage 2: Hydrothermal activity at Rhynie



Above: Continued crustal extension and subsidence. Dominantly a fluvio-lacustrine environment with mature cross-bedded sands deposited in an axial river system and argillaceous sediments deposited on floodplains and in shallow ephemeral lakes. Hydrothermal activity begins, the faulted basement-sediment contact acting as the main conduit. Hydrothermal alteration of subsurface rocks in vicinity of fault zone and deposition of sinters at the surface in the Rhynie area (after [Rice et al. 2002](#)).

Stage 3: Post-hydrothermal activity



Above: Continuing crustal extension and subsidence to present geology. Slices of early basin fill are preserved as slices in the basin margin fault zone (after [Rice et al. 2002](#)).

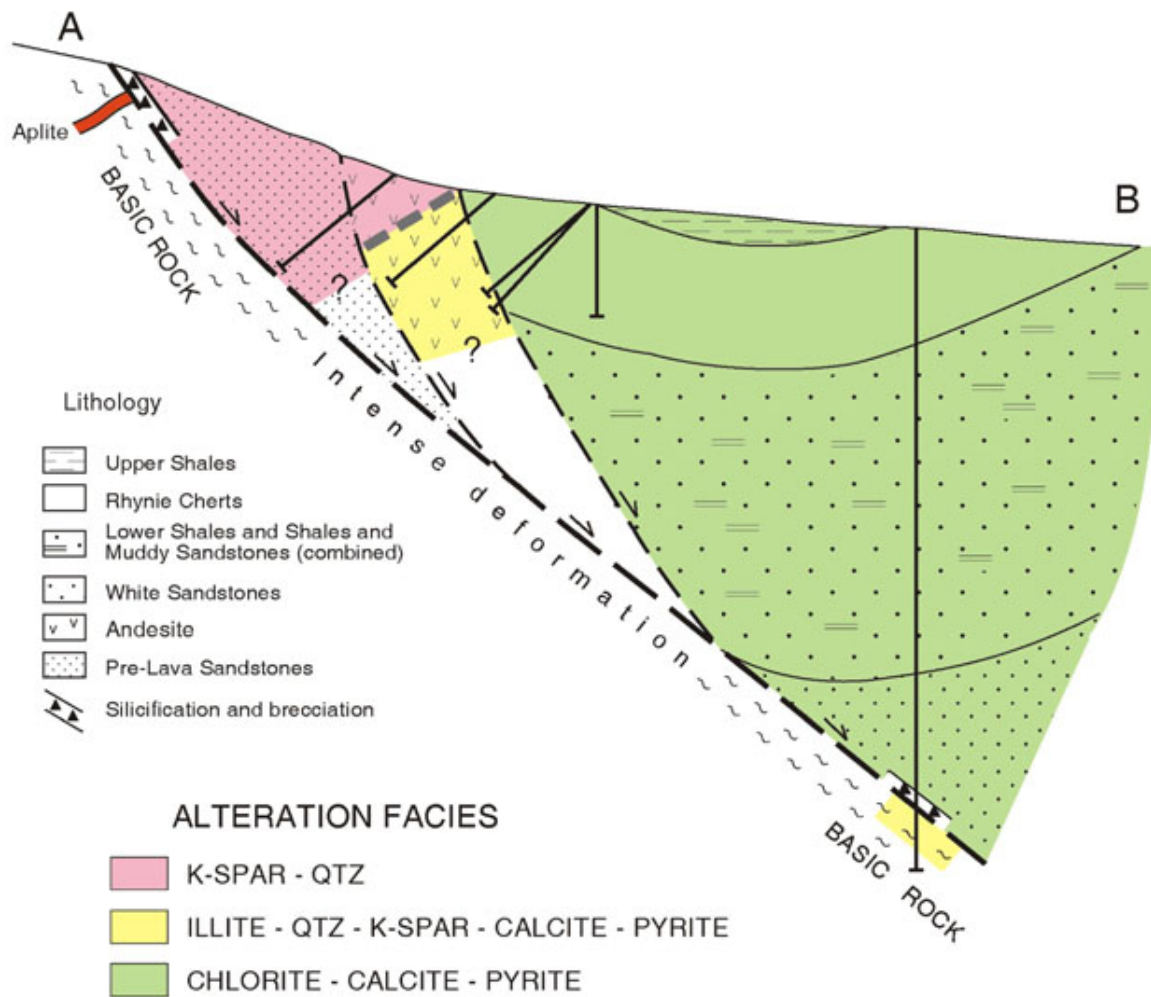
CONTENTS PAGE



Mineralisation and Hydrothermal Alteration

HYDROTHERMAL ALTERATION FACIES CROSS-SECTION ACROSS THE CENTRE OF THE HYDROTHERMAL SYSTEM

(preliminary data - S. Hillier MLURI, K. Czapnik AU)



Above: Diagrammatic cross-section of the basin margin fault zone and the area containing the Rhynie cherts, North of Rhynie village, showing the variation in hydrothermal alteration facies. The K-feldspar-quartz assemblage represents the zone of highest alteration, with the highest gold and arsenic contents, and mainly affects the slices of sandstone and andesite within the basin margin fault zone.

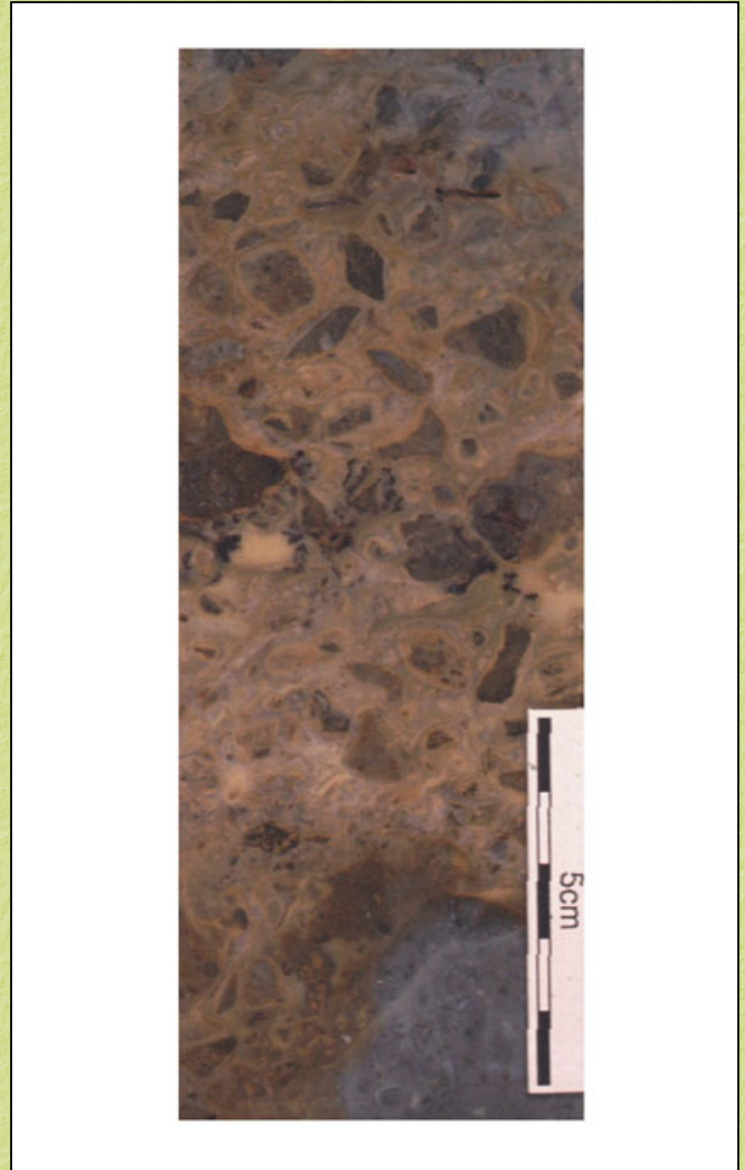
The Early Devonian hydrothermal complex at Rhynie is now dismembered, principally by vertical faulting, and so

different levels are now exposed within and adjacent to the basin margin fault zone. Coring and trenching at various locations in the different fault blocks along the basin margin fault zone has enabled us to sample the rocks and examine the different assemblages of minerals associated with the hydrothermal mineralisation and alteration.

The highest level of the hydrothermal complex is found in the Dryden Flags Formation on the south-eastern side of the fault zone and contains sinters, the Rhynie and Windyfield cherts, which are the classic surface expression of hydrothermal activity (see inset above). This sequence is weakly mineralised and contains thin calcite and quartz veins, sparse pyrite and patchy gold, arsenic, tungsten and molybdenum anomalies. The alteration assemblage of the sediments is **chlorite** and **calcite** plus **silica alteration in the sinter-rich intervals**.

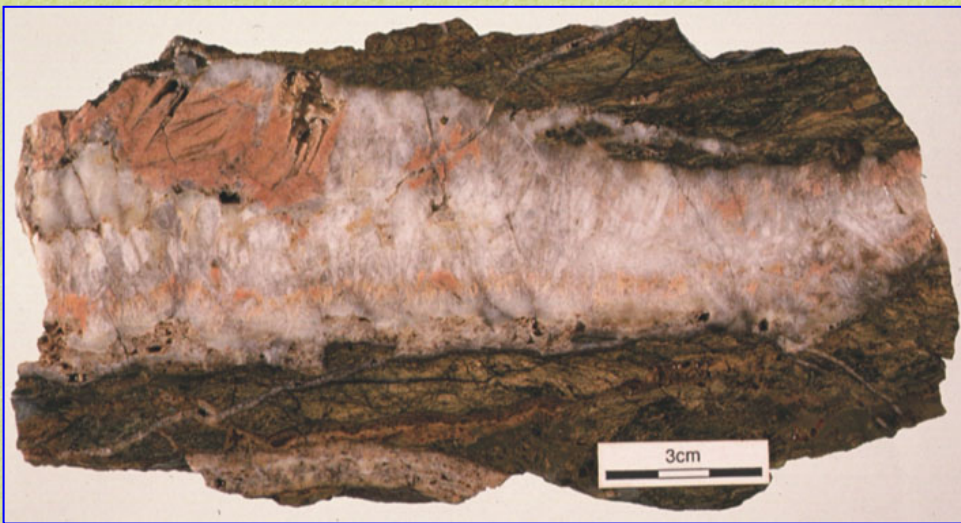
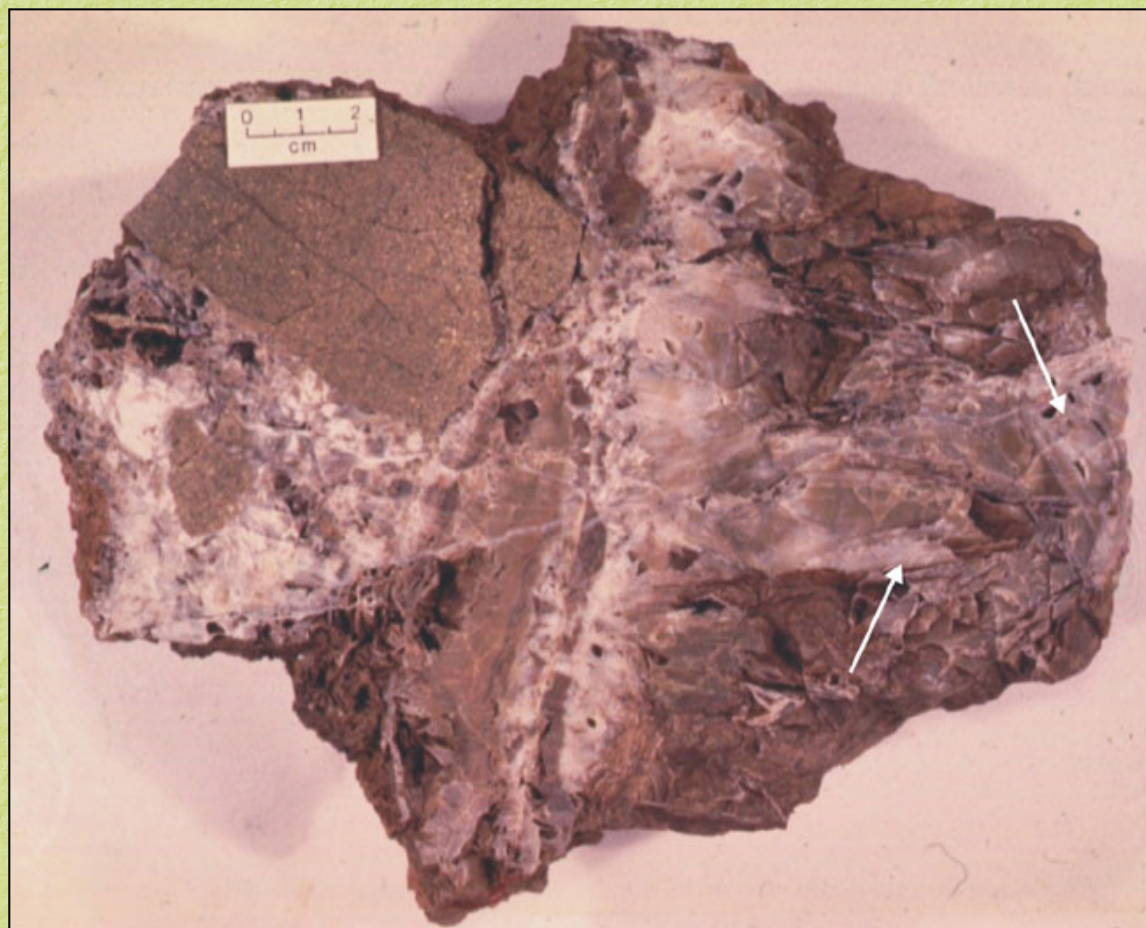
Deeper levels are exposed within the basin margin fault zone. Here intense silicification, brecciation and veining can be traced continuously along strike for 2km and follow the basement-Devonian contact (inset right) (see also the section on [Geology and Setting](#)). This is presumed to be the main conduit for rising hydrothermal fluids at the current erosion level.

Right: Cored section through intense brecciation and silicification in the basin margin fault zone. Many of the brecciated fragments are coated by numerous overlays of chert.

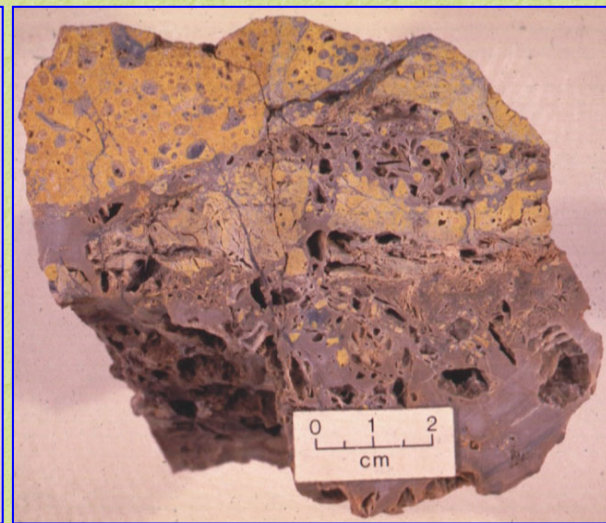


Between this contact and the sinter-bearing sequence lay fault slices of sandstone and andesite that are intensely altered and veined (see insets above, right and below). These slices are interpreted to represent the faulted lateral equivalents of the Quarry Hill and Tillybrachty Sandstone Formations in the Rhynie area. Evidence from textures such as **bladed quartz** (see inset right) and the mineralogy, **K-feldspar** in veins (inset below left) and altered rock (inset below right), indicate this was a zone of boiling.

Right: Bladed quartz crystals (arrowed) in brecciated andesite from one of the many fault slices in the basin margin fault zone at Rhynie.

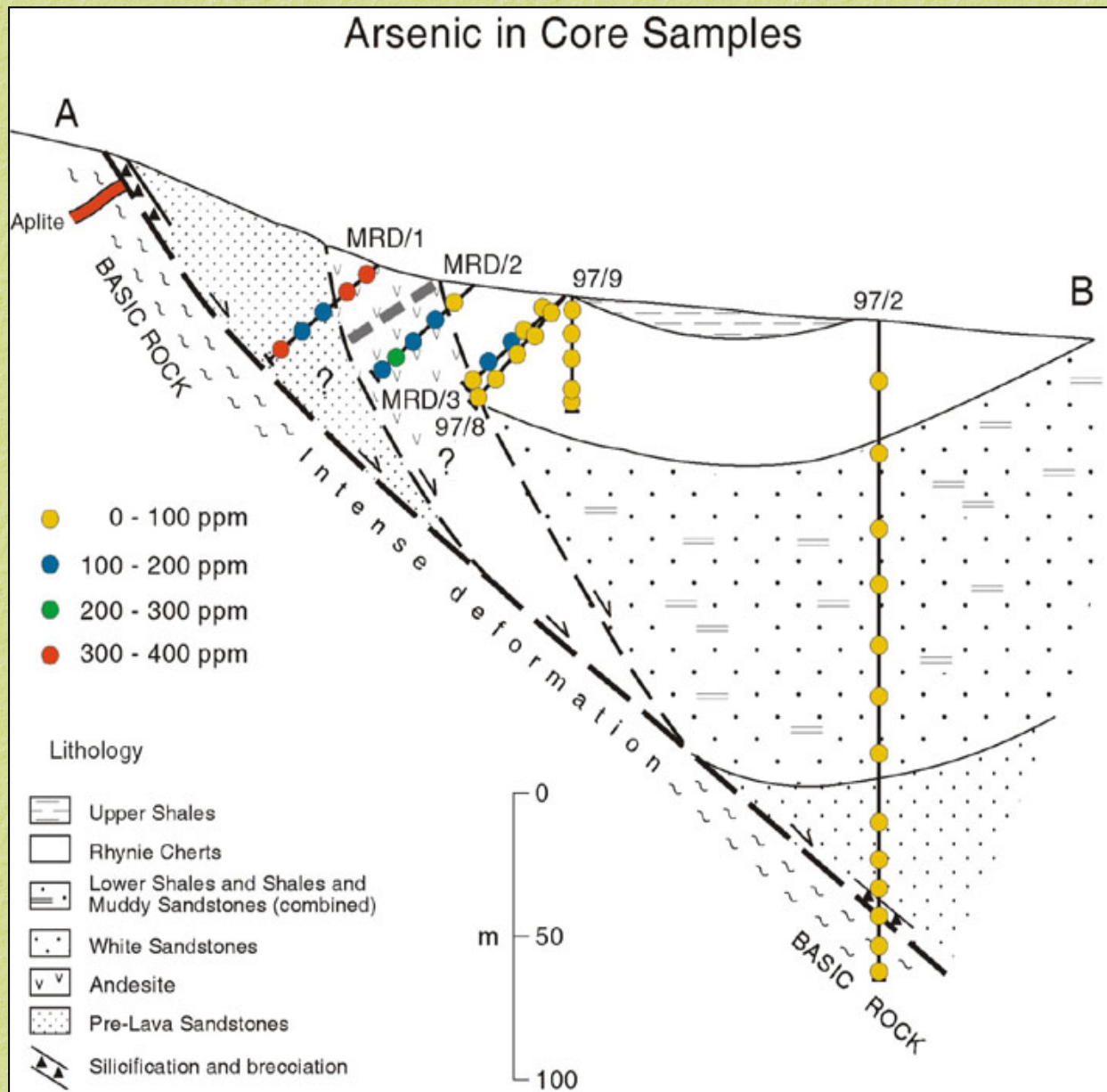


Above: Quartz and K-feldspar vein. The K-feldspar is flesh pink in colour (for a close-up click on the image).

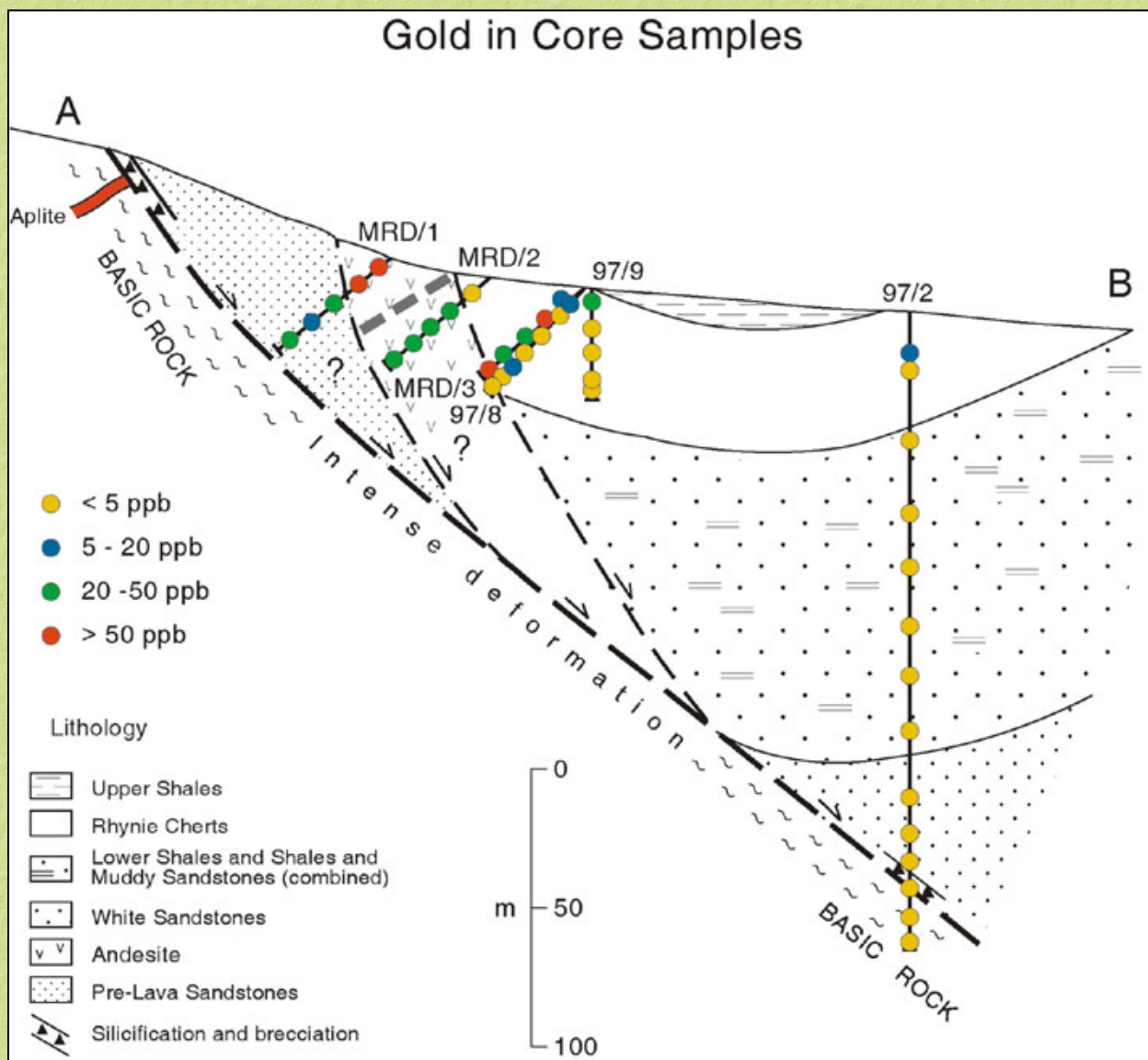


Above: Highly altered brecciated andesite from the basin margin fault zone. The andesite has been altered to quartz and K-feldspar (**adularia**) (for a close-up click on the image).

The veins and altered rocks in the fault slices, especially within the andesites, contain the highest levels of gold, arsenic, and tungsten yet found at Rhynie (see cross-sections below).



Above: Diagrammatic cross-section of the basin margin fault zone and the area containing the Rhynie cherts, North of Rhynie village, showing the variations in arsenic content of rocks recovered from selected cored boreholes (MRD/1, MRD/2, MRD/3, 97/2, 97/8 and 97/9).



Above: Diagrammatic cross-section of the basin margin fault zone and the area containing the Rhynie cherts, showing the variations in gold content of rocks recovered from selected cored boreholes (MRD/1, MRD/2, MRD/3, 97/2, 97/8 and 97/9).

Geochemical analysis of the rocks at Rhynie suggest there is a correlation between the abundance of pyrite and gold. Ion probe analysis of pyrite crystals in altered andesites from the basin margin fault zone indicates most of the gold is probably located in zones of **arsenian pyrite** (see inset right).

Right: Polished thin section of altered andesite showing a cluster of pyrite crystals viewed as a back-scattered image on the SEM. The bright zones relate to arsenic-rich areas (arsenian pyrite) in which gold has been detected by ion probe analysis ([Rice *et al.* 1995](#)).



The hydrothermal fluids were dominated by meteoric water ([Rice *et al.* 1995](#)). The features described above are typical of a low- sulphidation epithermal system.

The information and images on this page have kindly been supplied by Dr. Clive Rice, Dept. of Geology & Petroleum Geology, University of Aberdeen.

CONTENTS PAGE



Chert Textures

[Introduction](#)

[Macro-Textures](#)

[Micro-Textures](#)

Introduction

The Rhynie chert, examined from float blocks, trench and cored material exhibits a wide range of **macro-textures** (those large enough to be visible in hand specimen) and **micro-textures** (those clearly visible using optical microscope techniques). Studying both, together with the biota the individual beds contain, can help elucidate the different palaeoenvironments that were present in this hot spring complex at Rhynie 400 million years ago, useful comparisons can be made with modern hydrothermal deposits and settings (see also the section on [The ancient environment and modern analogues](#)). The following gives a brief summary of the textures observed within the chert beds together with some example images.

Macro-Textures

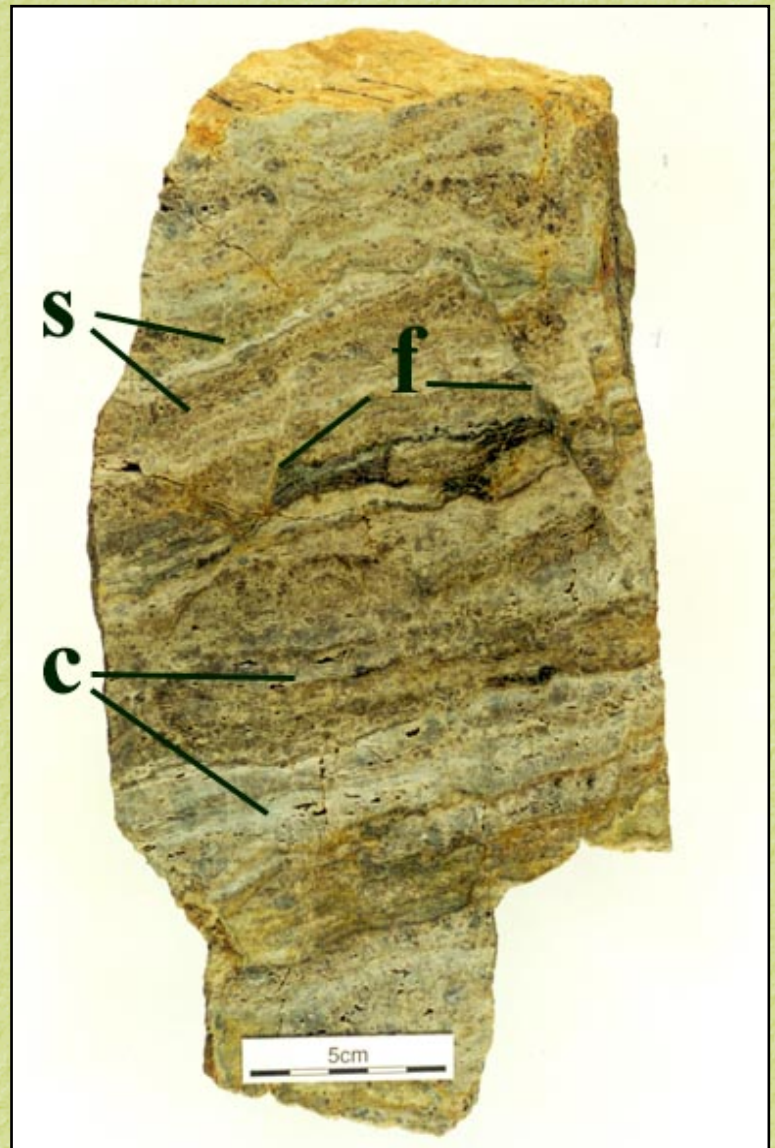
Five basic textures have been described from the chert beds ([Trewin 1994](#)). However, within individual beds, particularly in composite beds of chert, more than one textural type may be present and there are often gradations between the textural types:

Laminated Cherts

Cherts displaying irregular, sub-parallel, wavy to crenulated laminations on a sub-millimetre to centimetre scale, consisting of variable thicknesses of stacked chert laminae with fine sandstone partings (see inset right). Plants, if at all present, are confined to specific chert bands. Locally fine organic detritus including spores may be present. Under the microscope possible fossilised cyanobacteria may be occasionally present in the chert laminae (see section on [Cyanophytes](#)).

This particular texture most probably originated by deposition from successive inundations by silica-rich waters, with periods of silica precipitation occasionally interrupted by the influx of detrital material.

Right: Tabular bed of laminated chert showing wavy and crenulated laminae of chert (c) with fine sandstone partings (s). Notice also the syn-sedimentary fracturing and brecciation in this bed (f).



Vuggy to Massive Cherts

Cherts with commonly well-preserved plants, the latter often **autochthonous** with upright stems (see inset below), prostrate or flattened stems; or **allochthonous**, inverted stems (see inset right). Sediment and silica cement forming geopetal in-fills are often seen within plant straws and vugs or cavities within the chert (see below). Vugs that have not been totally occluded by silica cements are typically lined by euhedral (well formed) quartz crystals.

The mode of formation of these cherts is variable, but examining the micro-textures (see below) for further evidence may indicate silicification in areas of terrestrial plant growth, suddenly flooded by silica-rich waters, or silicification of the contents of small ponds.

Right: Bed of predominantly massive and vuggy chert (in this example a block of the Windyfield chert) showing vugs (v) and well preserved, inverted plant stems of *Ventarura lyonii* (p). In this case these plants have been transported and were then preserved in the chert upside down.





Above: Polished slab of predominantly massive and vuggy chert with exceptionally well preserved stems of the plant *Rhynia gwynne-vaughanii* in growth position. The crude lamination in the centre of the bed most likely represents a silicified microbial mat that in life probably bound the plant stems.

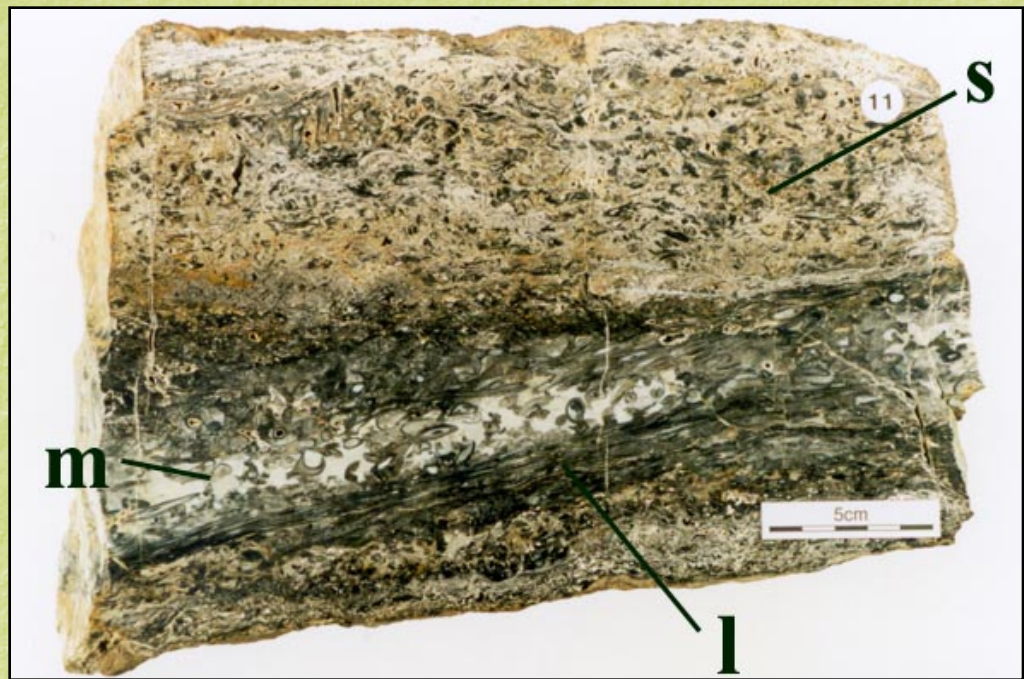
Lenticular Cherts

Cherts comprising irregular, laterally discontinuous, dark, organic, often plant-rich lenses. These lenses display partings of carbonaceous cherty sandstone (see inset right). The cherty sandstones occasionally show **organo-stylolites** formed as a result of the compaction of plant material within the sediment. The centres of the chert lenses often grade into the massive texture

described above (inset right).
Lenticular cherts often occur in thick composite beds.

The patchy silicification of these plant-rich lenses and their gradation into cherty sandstone interbeds tends to suggest patchy and poor silicification just beneath the ground surface.

Right: Bed of lenticular chert, showing dark organic-rich lenses (**l**) with a milky, massive centre (**m**), and bounding cherty sandstone (**s**).



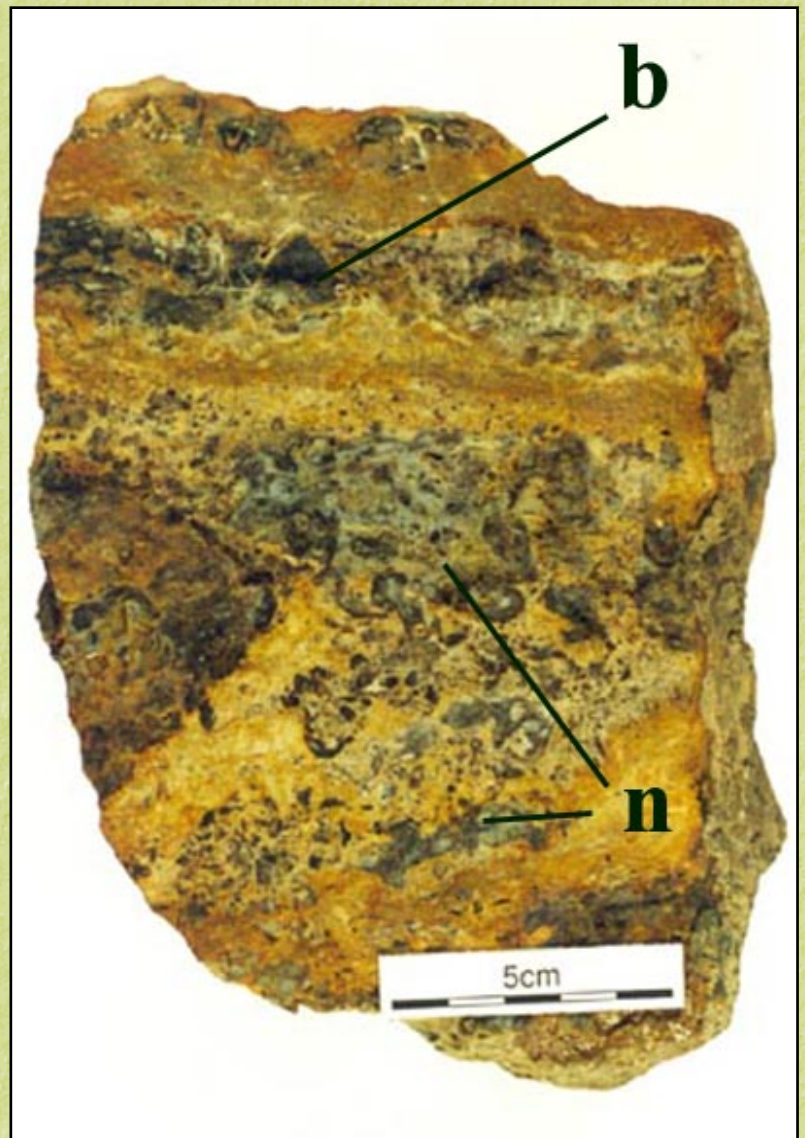
Nodular Cherts

Cherts occurring as nodules usually under 5cm in size, set within a cherty sandstone matrix. The latter typically appears compacted around the nodules (see inset right) and may display organo-stylolites. The chert nodules are often dark and may be plant-bearing, however, cellular preservation is often poor. This textural type also often occurs together with brecciated and lenticular chert textures (inset right).

As with the lenticular cherts, this texture appears to be associated with patchy and rather poor silicification, some of which may have been formed at the surface, but much probably occurring just below the sediment surface.

Right: Block of Windyfield chert showing nodular texture (**n**) with variable plant preservation, enclosed in a cherty sandstone

matrix. Brecciated wavy laminated chert occurs towards the top of this bed (**b**) (see below).



Brecciated Cherts

In this case, cherts of all the textures described above may be extensively fractured and resealed with chert or quartz. In a few instances brecciated chert beds recovered from below the surface weathering zone, fractures are cemented by calcite, baryte and rarely fluorite. Timing of brecciation appears to vary, some is clearly related to fracturing and faulting at depth in the sediment

pile, the fractured chert being cemented by late quartz cements. Other examples occurred at the surface as a result of desiccation and weathering of the sinter, evidenced by the fractures being in-filled with sediment (see inset right) and/or resealed with chert containing later silicified elements of the biota, such as fungi and algae.

Right: Heavily brecciated laminated chert (**b**) and brecciated nodular chert (**n**) in a cherty sandstone matrix.



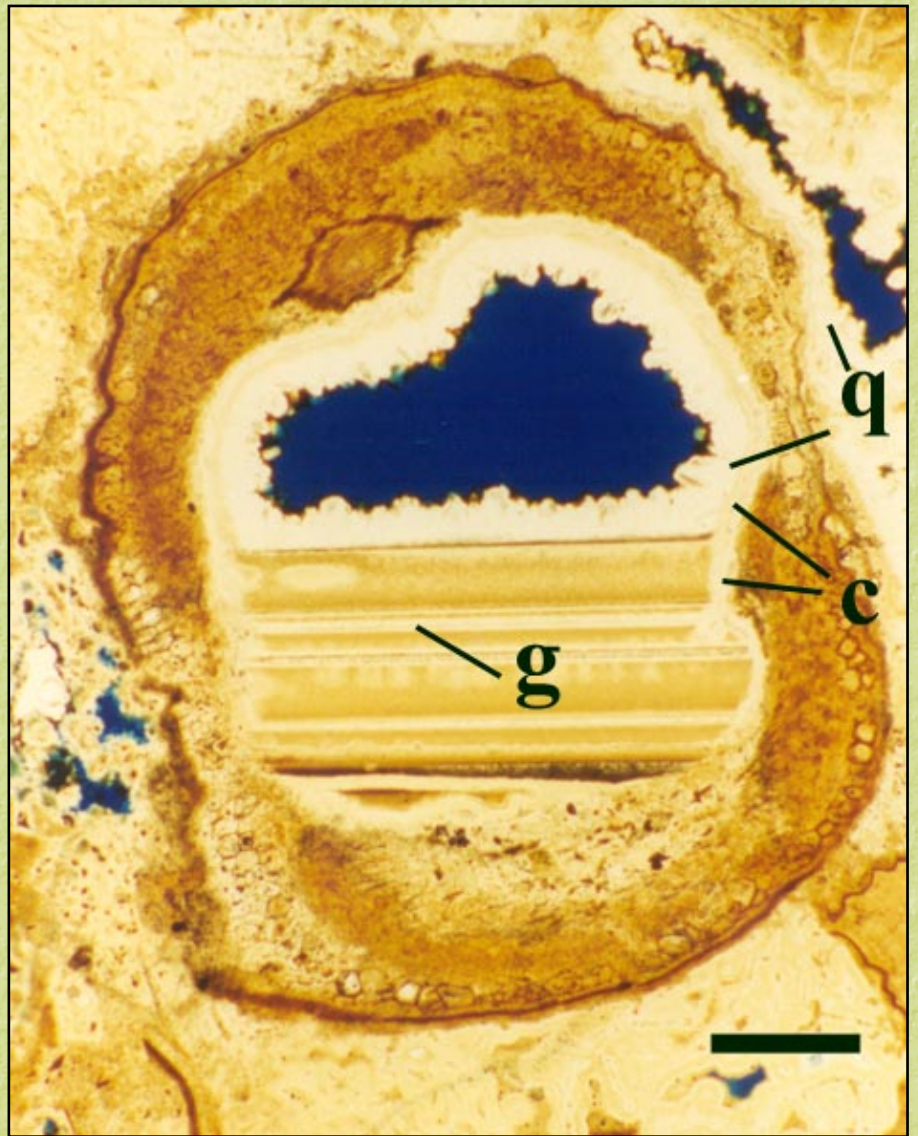
Micro-Textures

Apart from the studied large scale morphological features, optical microscope techniques provide a wealth of further information with which, for example, we can deduce the 'way-up' of the beds; and the burial history of the beds (in other words their **diagenesis**). Textural information can be used to elucidate the palaeoenvironment in which the individual beds were deposited. The following includes examples of micro-textural information that can be used to solve these problems:

Geopetal Textures

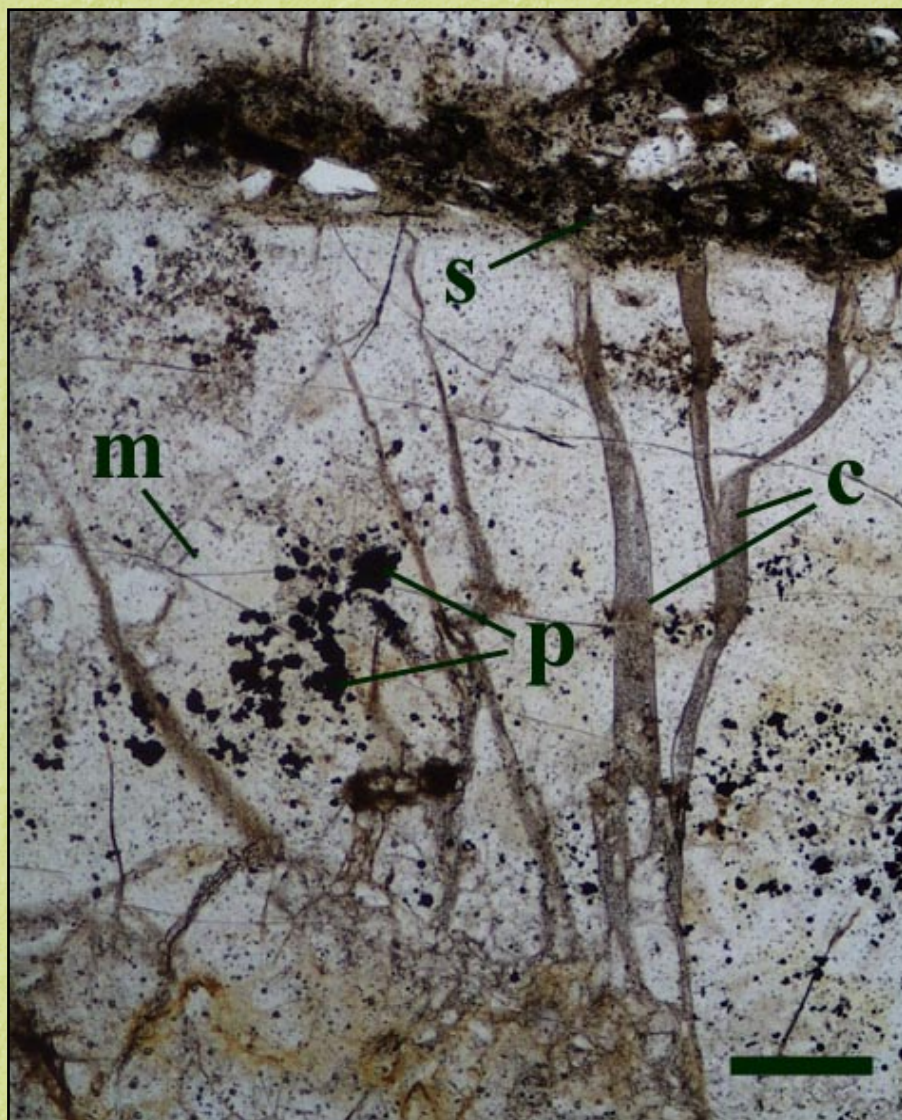
There are a number of methods used to determine the 'way-up' of a layer of sedimentary rock. In the Rhynie chert one of the most common way-up indicators are **geopetal layers**. These are in effect fossil spirit-levels and although recognisable in hand specimen they are more clearly viewed using a microscope (see inset right). They generally tend to form by the accumulation of very fine infiltrated organic and detrital material as a layer within voids in sediment, such as in the hollow straws of plant stems. Similarly, in the chert beds geopetal layers may also form from successive generations of silica cement. They are perhaps most common in the vuggy to massive cherts described above.

Right: Geopetal layers (**g**) in a straw of *Aglaophyton major*, denoting the image is the correct 'way-up'. Notice also earlier 'straw-lining' overlay of chert cement (**c**) and the later generation of quartz cement (**q**) lining the remaining void space after the geopetal fill (scale bar = 1mm).



Cement and Compactional Textures

A number of micro-textures combined with the mineralogy can be used to determine the diagenetic history of the chert beds. The order of different cement generations, any dissolution, compaction and fracturing of the chert during deposition and later burial can be deduced to a greater or lesser degree. In the image above right, for example, the pore-lining quartz cement (**q**) clearly came after the geopetal layers (**g**) which in turn post-date an earlier generation of chert cement (**c**) which lines the straw. The straw does not appear to be fractured and has therefore not undergone any significant burial compaction suggesting early silicification of the plant and surrounding matrix prior to burial.



The image on the left is another example. Here is a thin section of a brecciated nodular chert. The chert matrix (m) has been heavily fractured then resealed by later very fine, cryptocrystalline chert (c). The framboidal **pyrite** (p) is only present within and surrounded by the matrix chert and must therefore predate this or was formed at the same time. Notice how the resealed fractures stop where the nodule meets the sandstone (s), this suggests the sediment was not fully silicified at the time the chert nodules were fractured, being more ductile to compactional deformation than the brittle nodule.

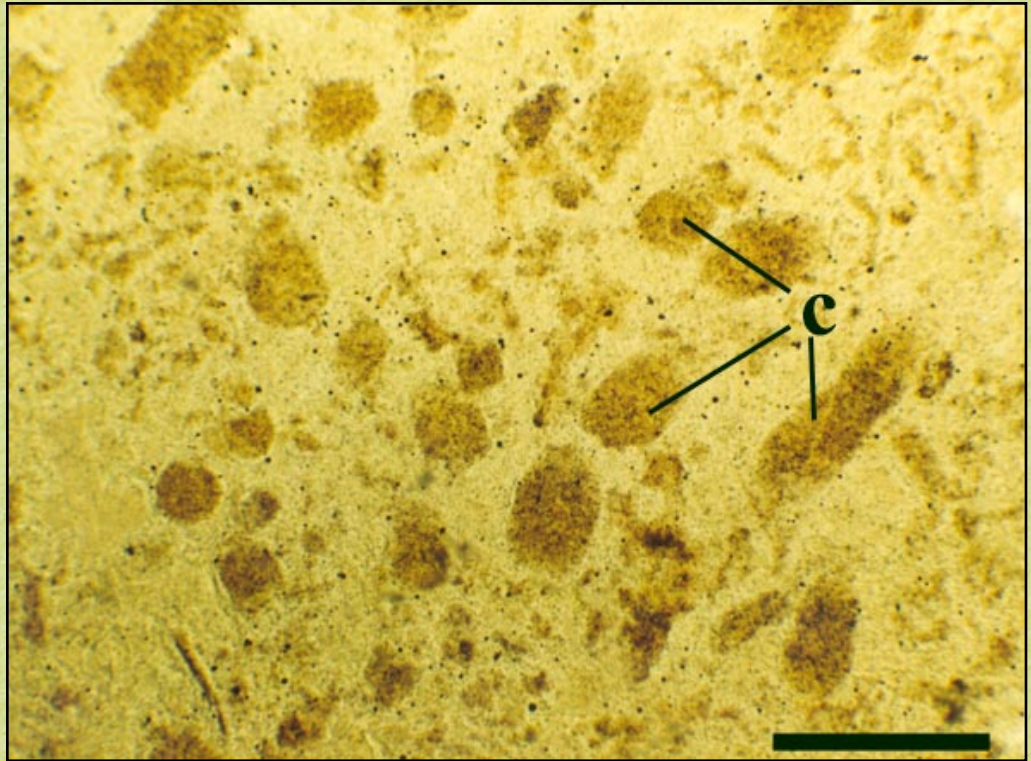
Left: Brecciated nodular chert showing chert matrix (m) with scattered framboids of pyrite (p). Fractures resealed by later cryptocrystalline chert (c) have not affected the intercalated sediment (s) (scale bar = 300µm).

These are just two relatively simple examples of how micro-textures in the cherts can be used to elucidate the diagenetic history.

Micro-Textures for Determining Palaeoenvironment

A number of micro-textures are found in the various chert beds that together with the biota present help to determine the palaeoenvironments in which individual chert beds were deposited. For the purposes of this resource we shall only consider a couple of examples here:

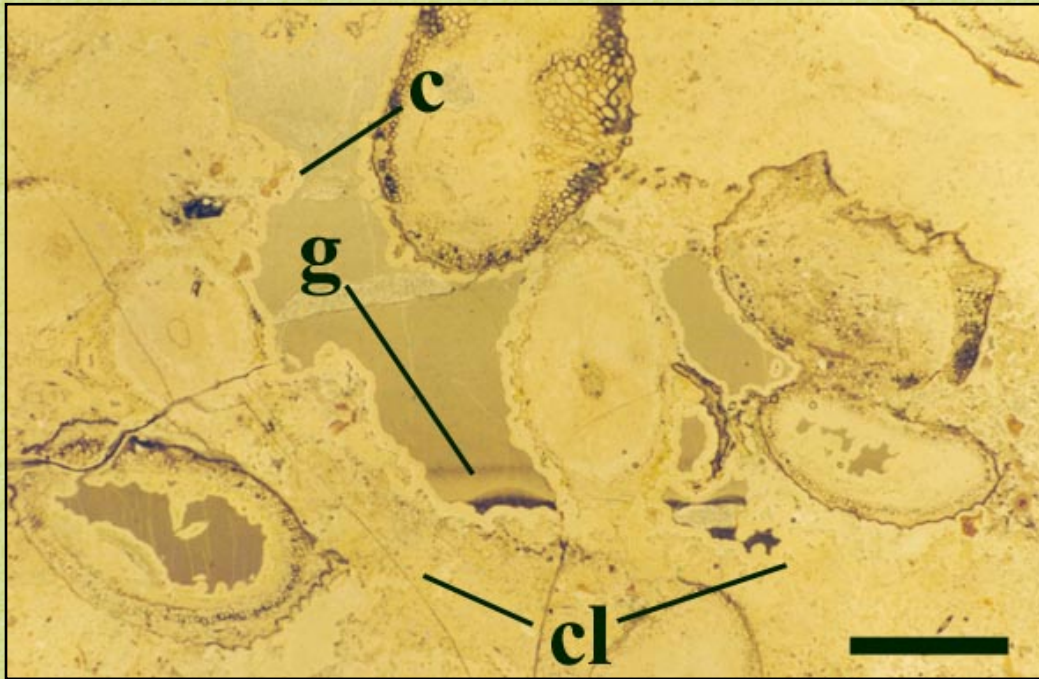
The image on the right is of a thin section taken from a block of Windyfield chert. This texture is quite distinctive and diagnostic. The amorphous, organic-rich, ellipsoidal, elongate and spherical bodies are actually fossilised faecal pellets, termed **coprolites**. It is most likely that the bed this sample came from was deposited in an aquatic setting, perhaps a pond or ephemeral body of water. These features, at least at this scale, are rarely preserved in terrestrial settings. Secondly, it is likely that the silicification of this deposit was very early because the coprolites are not squashed and compacted together, in fact there is a very open 'framework' between the pellets.



By studying coprolites, in terms of their size, geometry and content it may be possible to determine what type of organism produced them. Thus by understanding coprolites a lot of information can be also gained on the interactions between fauna and flora (see [Habgood *et al.* in press](#)).

Above: Chert with loosely packed coprolites (c). The bed this particular thin section came from must have been deposited in an aquatic environment, possibly a pond. These coprolites were probably produced by small crustaceans (scale bar = 500µm).

An interesting point to note is that the coprolitic micro-texture (inset above right) is often a good 'pathfinder' texture when prospecting for well preserved arthropods in the chert.



Above: Thin section of Windyfield chert, from the same massive and vuggy block illustrated above, showing partially decayed stems and sporangia of *Ventarura lyonii* enclosed in a patchy, organic-rich, clotted chert matrix (cl). Open voids in the matrix have been lined with an overlay of chert cement (c) and later in filled by geopetal sediment (g) and cryptocrystalline chert. The preservation of this open framework suggests initial silicification of the matrix and plants occurred whilst still in an aquatic setting before exposure and/or burial (scale bar = 2mm).

The image on the left shows a similar chert sample taken at a lower magnification. The coprolites often occur together with a fine meshwork of filaments (fungal and/or cyanobacterial), unicells and aggregated fine amorphous organic material forming an open, loose, plexus-like matrix that often binds and coats floral and faunal remains, giving the chert a 'clotted' appearance in thin section (cl). Often associated with this texture are fossils of aquatic biota such as [charophyte algae](#) and [branchiopod crustaceans](#), though remains of terrestrial plants and arthropods may also be common.

This distinctive **clotted chert texture** is directly comparable to **mulm**, the amorphous organic material that is often found in modern freshwater ponds ([Anderson & Trewin 2003](#); [Trewin et al. 2003](#); [Fayers & Trewin in press](#)). The presence of this texture in some of the chert beds is useful in a number of respects. As mentioned above, it acts as a useful 'pathfinder' texture for finding well-preserved arthropods. It also indicates that silicification in these particular beds took place in an aquatic setting with no desiccation prior to preservation, since desiccation would have led to the collapse and degradation

of these fine, open organic mesh-works ([Fayers & Trewin 2003](#); [Fayers & Trewin in press](#)).

Very often chert beds displaying these textures and containing some of the most exquisitely preserved plants and arthropods also exhibit finely disseminated **pyrite** in the chert matrix, occasionally occurring in framboidal clusters (see above). The pyrite appears to be contemporaneous with the earliest stages of silicification. Its presence indicates the waters from which it precipitated were at least mildly reducing, suggesting that some of these small ponds were at times stagnant. Such localised reducing conditions would inhibit the rapid decay of organic matter and may in part explain the fantastic preservation of some of the fossils ([Fayers & Trewin 2003](#)).

[CONTENTS PAGE](#)



Taphonomy of the Rhynie Chert

[Introduction](#)

[Preservation of the Biota](#)

Introduction

Taphonomy is the study of the various overlapping, consecutive processes which can affect organic remains prior to burial and their inclusion in the fossil record. These processes include the following:

- **Necrolysis** - decomposition of soft tissues and possible break-up of parts.
- **Biostratinomy** - processes affecting the organic remains during deposition and before final burial (such as dissociation, scavenging, bioerosion, transport, breakage).
- **Diagenesis** - processes affecting organic remains and sediments after burial (such as mechanical compaction, chemical dissolution, mineralogical transformations, cementation).
- **Metamorphism** - the mineralogical and structural alteration of rocks by increased heat and pressure, typically during deep burial and tectonism. This may result in the tectonic distortion of fossils, but most often metamorphism completely obliterates any fossil remains.

As we have seen in earlier sections of this resource the Rhynie chert is a unique deposit because it preserves in remarkable detail an Early Devonian terrestrial and freshwater community of plants and animals. The plants and animals are sometimes preserved in such exquisite detail that their internal anatomy can be described. This 'mother lode' of exceptionally preserved organisms means that the Rhynie chert may be referred to as a **konservat lagerstätte**. This is a term used to describe those few geological sites where, for a combination of chemical and physical environmental conditions at the time of deposition and burial, organisms with delicate non-mineralised tissues not usually seen in the fossil record are well preserved and have undergone very little decay. Other examples of konservat lagerstätte include insects in amber and Siberian mammoths preserved in ice.

In the case of the Rhynie chert the method of mineralisation and its timing with respect to the death and decay of the plants and animals is the key to their remarkable preservation. Within the Rhynie chert the organisms have been preserved relatively early, very often at or soon after death by their inundation by hot spring fluids supersaturated with respect to dissolved silica. The silica coming rapidly out of solution as a result of the gradual temperature drop and evaporation of the flowing water, encrusted and permineralised the organic matter at a cellular level, and continuing silica precipitation both at the surface and during early burial ensured the inclusion of the Rhynie biota in the rock record.

Note: The means of silicification of organic material and soft tissues and the conversion of sinter to chert is complex, but will be summarised in the following section on [silicification and the conversion of sinter to chert](#).

Preservation of the Biota

The preservation of the flora (plants) and fauna (animals) is variable depending mainly on two things; their condition at the time of fossilisation (for example the amount of cellular decay) and secondly on the degree and timing of silica [permineralisation](#) and [petrification](#). Therefore, there is a whole range of preservation types, ranging from the exquisitely preserved 3D internal anatomy of those organisms that were completely silicified at or soon after death, to organisms preserved as compressed, unidentifiable, coalified laminae that were silicified after decay and burial. The diagram below right, gives an idea of the effects of degradation prior to silicification and the effects of silicification itself, specifically with respect to the preservation of the flora ([Trewin 1996](#)).

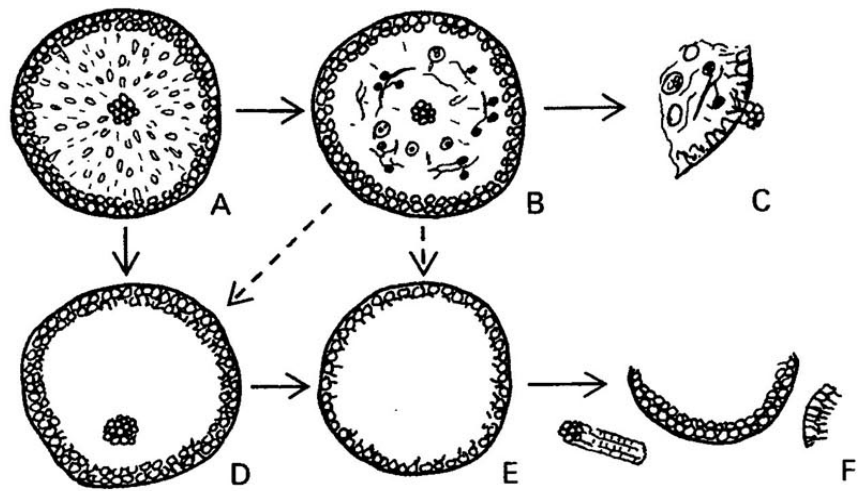
Right: Simplified diagram showing the various effects of (1) Plant degradation prior to silicification, and (2) the silicification process in the cherts.

(1) Plant degradation: (A) Unaltered plant axis. (B) Decay of plant axis by fungal and bacterial pathogens. (C) Fragments of infected plants. (D) Decay of less resistant cells resulting in xylem strand falling to base of hollow 'straw'. (E) Hollow straw. (F) Fragments of xylem strand and outer cuticle.

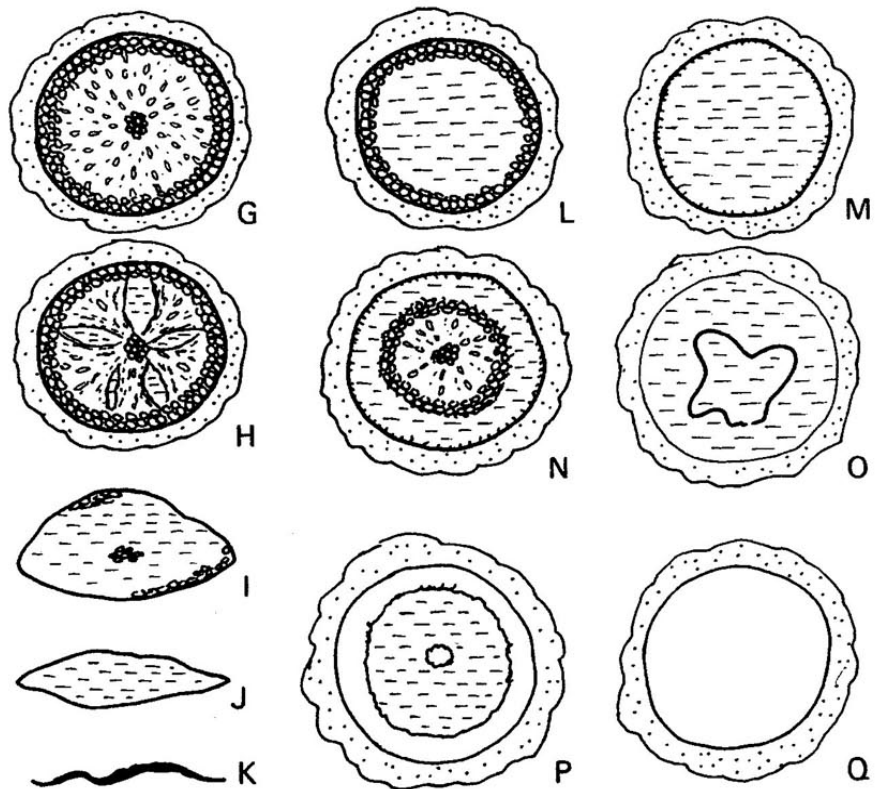
(2) Preservation / silicification effects:

(G-K) Range from perfect 3D cellular preservation (G) to coalified compression (K) with intermediate stages. (H) Shrinkage of plant tissue producing radial chert-filled gashes. (I) Partial compaction with loss of cellular structure. (J) Lens of chert with no internal structure. (L) Permeation and silicification only of outer ring of cells, decay of inner tissue creates void later filled with chert (cf. E). (M) Only the outer cuticle is preserved. (N) Plant tissue shrunk away from cuticle and resulting annulus later filled with chert. (O) Cuticle shrunk away from enclosing chert, void later filled with chert. (P) Chert filling void in straw followed by loss of xylem strand and outer ring of cells resulting in pore space. (Q) Only a single void to show the previous presence of a plant axis (after [Trewin 1996](#)).

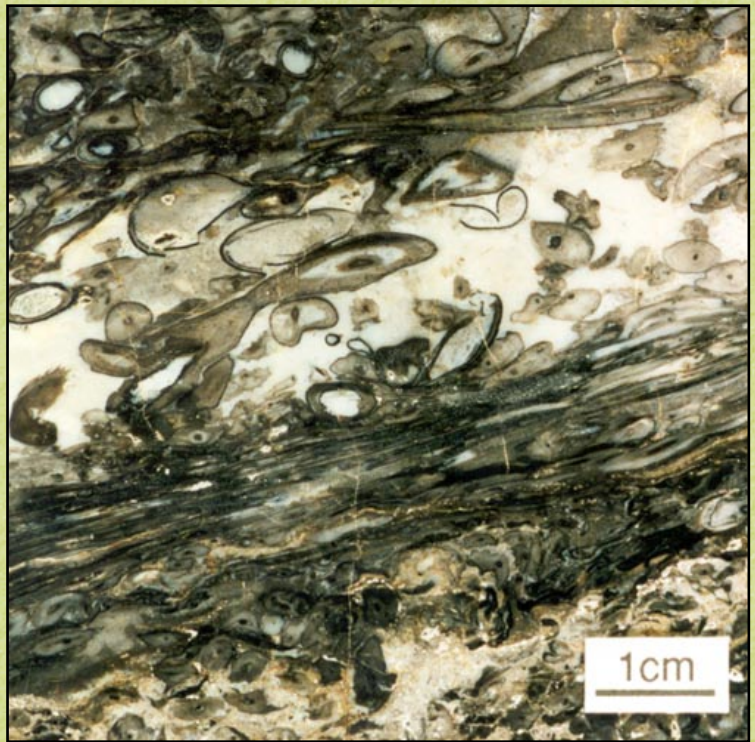
1. PLANT DEGRADATION



2. PRESERVATION EFFECTS IN CHERT



With regards to the preservation of the plants, their orientation is also variable, ranging from [autochthonous](#) upright stems with horizontal attached rhizomes, evidently in growth position; to collapsed and decayed, prostrate stems apparently representing plant litter. [Allochthonous](#) or transported plant material is also often recognisable (see also the section on the [Rhynie Chert Flora](#)).



Right: Polished slab of Rhynie chert showing variations in plant preservation: well preserved *Aglaophyton* rhizomes, uncompacted in an open framework of milky chert (centre) and flattened partially decayed stems (bottom).

With regards to the fauna, the preservation is locally so exquisite that entrapment and silicification must have also happened at or very soon after death, since in a few cases where the whole bodies of arthropods have been found (i.e. as opposed to moulted exoskeletons) gut contents have been found preserved, and even delicate features such as lungs and tracheal elements are perfectly silicified (see the section on the [Rhynie Chert Fauna](#)). Many of the animals, particularly the crustaceans and even their **exuviae** (moulted shells) appear to have remained cohesive and articulated during preservation with little or no signs of prior desiccation suggesting silicification occurred whilst they were still in an aquatic environment.

Therefore, not only can information be gleaned about the internal anatomy of the plants and animals, but also about their preservation, distribution, growth habit, association and interaction with other Rhynie flora and fauna.

For a general overview of taphonomy refer to [Goldring \(1991\)](#), and for a more detailed treatment refer to [Allison & Briggs \(1991\)](#).

CONTENTS PAGE



Silicification and the Conversion of Sinter to Chert

[Introduction](#)

[Silicification in Hot Spring Environments](#)

[The Conversion of Sinter to Chert](#)

[Other Useful References](#)

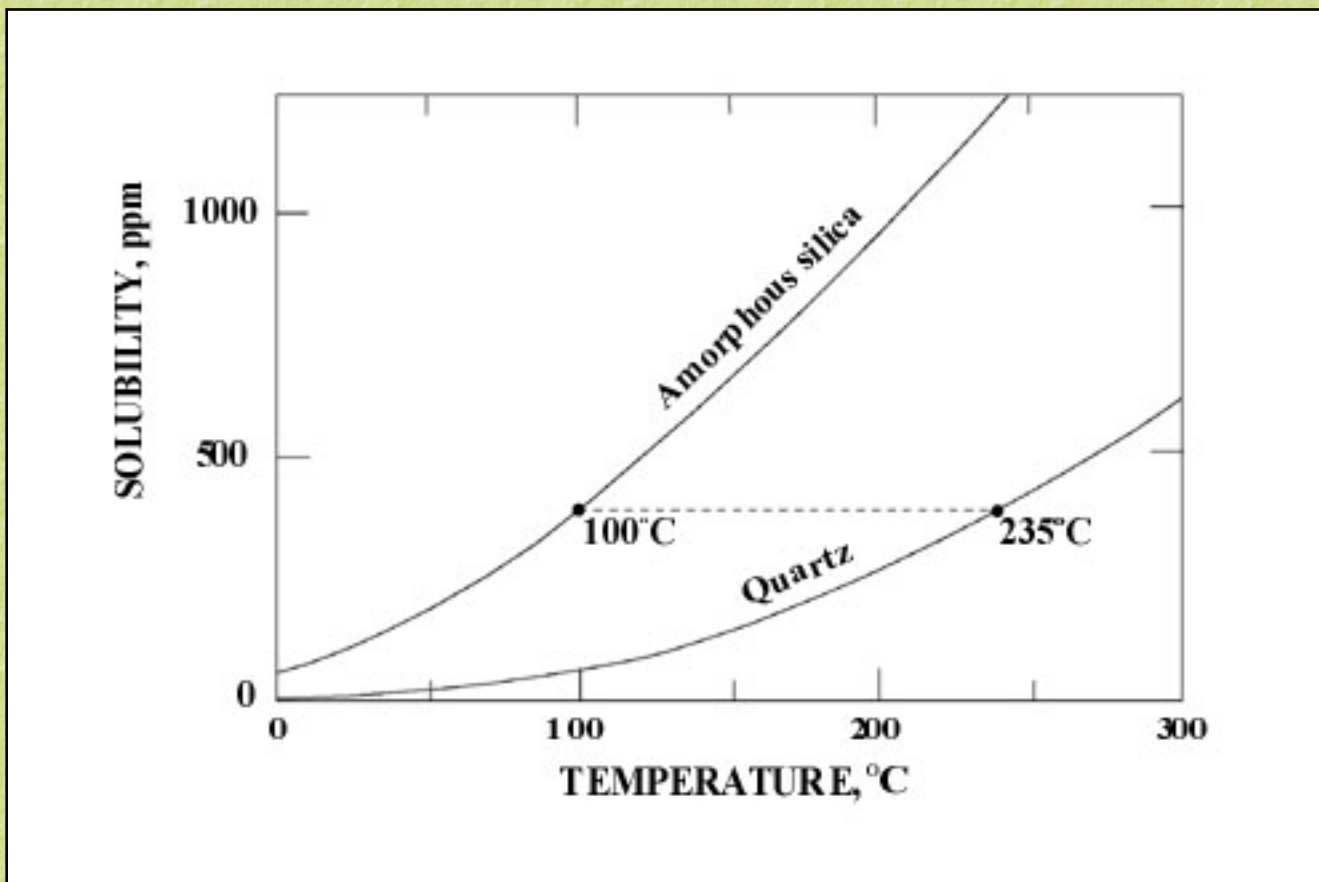
Introduction

Understanding the form of mineralisation as well as its timing is important in understanding the remarkable preservation of the biota in the Rhynie chert. In this section we shall consider the processes of silicification in hot spring environments and its role in the preservation of organic matter, and also how after burial and time siliceous sinter is converted to chert.

Silicification in Hot Spring Environments

In hot spring environments, silica that is precipitated to form sinter is primarily precipitated in the form or **phase** of silica called **Opal-A**. As a primary precipitate this form of opaline silica is characteristically amorphous and hydrated with variable amounts of water. For precipitation the hydrothermal solutions must be supersaturated with respect to Opal-A. In the reservoir at depth, the concentration of dissolved silica is controlled by the solubility of quartz (see [Williams *et al.* 1985](#)). It has been calculated that a

hydrothermal solution that precipitates Opal-A at the surface at 100°C must contain at least 370ppm dissolved silicon. This in equilibrium with quartz would require a subsurface reservoir temperature of at least 235°C ([Hesse 1989](#)). Precipitation of Opal-A at 75°C would require a reservoir temperature of 206°C (see inset below).



Above: The 'quartz-geothermometer' is widely applied for hydrothermal systems (based on [Rimstidt & Cole 1983](#)). Showing the solubility of amorphous silica (Opal-A) and quartz as a function of temperature. In this example, a hydrothermal solution precipitating Opal-A at 100°C contains at least 370ppm dissolved silicon, in equilibrium with quartz requires a reservoir temperature of 235°C.

When the hydrothermal solution, supersaturated with respect to Opal-A, is erupted at the surface from a geyser or out flows from a hot spring it begins to cool and evaporate. The drop in temperature of the fluid and the evaporation of water means the amount of dissolved silica in the fluid can no longer be kept in solution and therefore the Opal-A begins to precipitate. As well as the drop in temperature and evaporation of the hydrothermal fluids, other factors may also affect precipitation such as the pH of the fluids, the presence of other dissolved minerals, the presence of organic matter and even by the mediation of living organisms such as cyanobacteria (e.g. [Konhauser *et al.* 2001](#)).

So how are plants and other organic remains silicified in these environments? A lot is now known about the processes of silicification of organic remains, specifically in the case of silicified wood, following experimental studies by [Drum \(1968\)](#), [Leo and Barghoorn \(1976\)](#) and [Sigleo \(1978\)](#). Experiments have shown that the silicification of wood and plant material is a permeation and void-filling processes (or [permineralisation](#)) rather than the direct replacement of cell walls (or [petrification](#)), where the organic structure acts as a template for silica deposition.

During the experiments conducted by [Leo and Barghoorn \(1976\)](#), they hydrolysed ethyl silicate with water to form monosilicic acid, which is the main soluble form of silica in nature. Their experiments showed that as the concentration of the solution increases with respect to the amorphous silica, the monosilicic acid polymerises with the formation of siloxane bonds and the elimination of water:



As polymerization continues amorphous silica begins to precipitate, and with further loss of water and crystallization of the silica, opaline silica forms. The mechanism for the nucleation of amorphous silica on wood and plant material involves hydrogen-bonding between the hydroxyl groups in the silicic acid and cellulose and lignin within the organic tissue:



Polymerization of the silicic acid that has permeated plant cells and organic tissue leads to dehydration and silica precipitation within the cells and openings between cell walls. The silica deposition thus replicates the histological character of the plant. Leo and Barghoorn's experiments suggest that these initial phases of silicification of organic matter may occur in a matter of days to a number of years. For complete and pervasive silicification a high influx of silica-bearing solutions would be required for continued silica deposition. In hydrothermally active areas regular out flows of solutions from hot springs and geysers would provide a suitable flux. It is this rapid and pervasive silicification prior to significant cellular decay that has led to the exquisite preservation of the plants in many of the beds of Rhynie chert.

The silicification of prokaryotes has also been studied. Work by [Ferris *et al.* \(1988\)](#) has shown that for

the preservation of cellular structure in microbes, the retention of metal cations, in particular iron, in the solutions prior to silicification is significant. This is because metal cations inhibit cellular decomposition by [autolysins](#). Experiments have shown that bacteria cultures aged for 150 days at 70°C in solutions containing just dissolved silica displayed almost complete cellular collapse whereas cultures treated with dissolved silica and iron retained their cell shape. The retention of iron therefore is important for the preservation of microbial cellular structure before silicification.

The Conversion of Sinter to Chert

During burial and over time the amorphous silica phase, Opal-A, that is initially precipitated as sinter becomes unstable and gradually changes in its structure to more stable, ordered, crystalline forms or phases of silica, namely quartz. The diagenetic pathway of silica is controlled by the solubility of the different silica phases. This solubility is primarily a function of crystal structure and size of the different silica phases (see [Williams *et al.* 1985](#)) and usually proceeds from the amorphous, disordered **Opal-A** through **Opal-CT** to more ordered, crystalline **quartz** by dissolution / reprecipitation reactions.

The Opal-A to quartz transformation may occur due to a number of factors. With increasing depth of burial, increasing temperatures and pressures are two of the principal factors. The chemistry of pore waters percolating through the sinter may also affect this mineral transformation, particularly if the pore waters are undersaturated with respect to dissolved Opal-A and supersaturated with respect to quartz. As the sinter is being transformed from Opal-A to quartz, percolating silica-bearing fluids may precipitate yet more crystals as a cement infilling pore space and fractures within the rock, depending on the pore water chemistry and concentrations of dissolved silica phases present. Therefore during the conversion of sinter to chert, not only is there a transformation in the form of silica, but also the abundant pore spaces and voids within the original deposit are filled or occluded by more silica so that in many cases the resulting chert has almost no remaining original porosity.

Other useful references

For a comprehensive review of the processes and mechanisms for the silicification of fossils and their taphonomy see [Carson \(1991\)](#). For silicification and fossilisation processes in hydrothermal areas see [Cady and Farmer \(1996\)](#).

CONTENTS PAGE



The Rhynie Chert Flora



Above: Polished slab of Rhynie chert showing very well preserved vertical axes of *Rhynia gwynne-vaughanii*, set in horizontally bedded chert.

[Introduction](#)

['Higher Land Plants'](#)

['Other Non-Vascular Plants'](#)

Introduction

The early land plants found as fossils in the Rhynie chert are locally preserved in such exquisite detail that cellular details can be examined. This has allowed detailed anatomical studies to be performed on the Rhynie plants. The plants are relatively simple in their level of organisation and include seven identified 'higher land plants', two enigmatic nematophytes and a number of other plants including various types of fungi, algae and the earliest fossil lichen.

We can demonstrate that at least seven of the plants are true subaerial plants by most or all of the following features being preserved:

- **Cuticle** with **cutan** that helps preserve moisture.
- **Stomata** for gaseous exchange with the atmosphere.
- **Intercellular air space network** for gas diffusion.
- A **vascular strand** with **lignin** for water conduction and support.
- **Sporangia** with a well developed dehiscence ('splitting') system to release spores.
- **Spores**

The taxonomy of the Rhynie plants poses difficulties for subdivision into currently accepted taxonomic groups. For the purposes of this resource, we have made a simple subdivision into the 'higher land plants' - those with the features listed above, and 'other non-vascular plants' from the chert.

'Higher Land Plants'

The seven higher land plants of the Rhynie chert 'macroflora' that have been described to date are detailed below. Various life stages have also been described for a number of the plants with both the **sporophyte** and **gametophyte** stages having been identified (e.g.: [Remy & Hass 1986](#), [1991a,b,c,d](#); [Remy & Remy 1980a,b](#); [Remy et al. 1993](#) and [Kerp et al. in press](#)). A number of these plants exhibit other delicate features such as **mycorrhizae**, bacterial infections and various forms of pathological damage. Five of the plants are true vascular plants or **tracheophytes**, showing **tracheids** in the water-conducting cells. Two plants, *Aglaophyton* and *Nothia* do not show tracheids and can therefore not be considered as tracheophytes.

Click on the hyperlinks below for a basic overview of the plants and the following individual plant names for a more detailed description of their morphologies.

The Plants:

- [Basic information on the higher plants in the Rhynie chert](#)

Click on the following names for more detailed descriptions of the individual genera and their palaeoecology:

- [Aglaophyton](#)
- [Asteroxylon](#)
- [Horneophyton](#)
- [Nothia](#)
- [Rhynia](#)
- [Trichopherophyton](#)
- [Ventarura](#)

Spores:

Apart from the fossil plants in their own right, fossilised spores are also found, not only in the chert but also in the associated sediments, particularly the shales and mudstones. Many species have been identified and described and have been useful for biostratigraphic purposes in dating the sediments (see section on [Age of the Rhynie Chert](#)). There remains, however, a degree of uncertainty as to which of the vascular plants each belongs, and there may well be spores present from other plants that have not yet been found preserved in the cherts. Click [here](#) to learn more.

'Other Non-Vascular Plants'

The described flora of the Rhynie chert also includes non-vascular plants such as nematophytes, algae, fungi and a lichen.

Click on the hyperlink below for a basic overview of the microflora:

- [Basic information on the remaining plant groups in the Rhynie chert](#)

Click on the following hyperlinks for a more detailed description of the other forms of plant fossils in the Rhynie chert:.

- [Nematophytes](#)
- [Cyanophytes](#)
- [Chlorophytes](#)
- [Charophytes](#)
- [Fungi](#)
- [Lichens](#)

CONTENTS PAGE



The Rhynie Chert Fauna

[Introduction](#)

[The Animals](#)

Introduction

The fauna of the Rhynie chert is far less abundant than the flora, and many of the animals are known from only a few specimens that were fortuitously trapped in the hot-spring sinter. However, when a block of chert containing animals is found, they can be quite common. Thus the distribution of animal fossils is very patchy in the chert deposits.

Recently, by careful examination of the Windyfield chert, several new animals have been discovered at Rhynie. Some are described by [Anderson and Trewin \(2003\)](#), [Dunlop *et al.* \(2003\)](#), [Fayers and Trewin \(2003\)](#), and others are currently being described. The fauna includes [arthropods](#) that lived in both terrestrial and freshwater environments. With recent additions to the faunal list, the Rhynie fauna is now the most diverse associated freshwater and terrestrial fauna known from the Devonian and earlier periods of geological time.

The Animals

To date, seven distinct groups of arthropods have been identified from the Rhynie chert, and are described below.

Note: There are a number of fossil arthropods described and named from the Rhynie chert of which only a few fragmentary remains have been found and which lack sufficient diagnostic features to assign the animals to a higher group. For the purpose of this resource, these will be only be mentioned in the general list given below.

Click on the hyperlink below for a basic overview of the animals:

- [A general list of the fauna together with illustrations](#)

Click on the group name for detailed descriptions of the animals and their palaeoecology:

Arthropods:

- [Trigonotarbid arachnids](#)
- [Harvestmen](#)
- [Mites](#)
- [Myriapods](#)
- [Collembolans](#)
- [Crustaceans](#)
- [Euthycarcinoids](#)

CONTENTS PAGE



Evidence for Plant/Animal Interactions

[Introduction](#)

[Evidence for Coaction](#)

[Evidence for Reaction](#)

[Evidence for Action](#)

Introduction

By studying the associated *in situ* biota in the individual chert beds, much information can be gathered on the interactions between fauna, flora and the inorganic environment at Rhynie during the Early Devonian some 400 million years ago, thus helping to build a picture of this early terrestrial and freshwater ecosystem.

Of course, to understand how an ancient palaeoecosystem worked, such as the food chain, trophic resources, habitat space, etc. is extremely difficult for three main reasons. Fossils cannot be observed as living organisms; many environmental parameters, including modes of life, are not necessarily directly comparable with modern examples; and the fossil record is strongly influenced by taphonomy, biostratigraphy and diagenesis and thus only organisms capable of being fossilised are generally preserved.

However, the remarkable preservation of the biota in the Rhynie chert means that although by no means complete, the palaeoecology of this deposit can be better understood than that of many other fossil

assemblages. There are three types of 'interaction' in an ecosystem:

- **Coaction:** where an organism affects another organism.
- **Reaction:** where an organism affects the inorganic environment.
- **Action:** where the inorganic environment affects an organism.

Evidence, to a greater or lesser degree, has been found of all three interaction types in the different beds of chert.

Evidence for Coaction

Most living organisms survive by directly or indirectly exploiting others, such organisms are incapable of producing food from inorganic substances, with the exception of green plants and algae which produce carbohydrate from photosynthesis. Few organisms, even green plants, live entirely independently, nearly all survive as parts of a living community. For example, certain organisms live by **predation**, others by **parasitism**, other organisms may be **herbivorous**, and others **saprophytic**, living off dead organic matter. Perhaps the greatest degree of interdependence occurs when two different organisms live attached to one another in an association which is mutually beneficial to both organisms, known as **symbiosis**.

In the Rhynie chert, one of the most common pieces of evidence for coaction is the symbiotic relationship between fungal endotrophic mycorrhizae and the Rhynie plants, where the fungus supplied water and nutrients to the plant whilst the plant supplied the fungus with carbohydrate from photosynthesis ([Taylor *et al.* 1995b](#)) (see inset right).

Right: Endotrophic mycorrhizae (**f**) occupying intercellular spaces within the cortex of *Aglaophyton major* (scale bar = 30µm) (Copyright owned by University Münster).



The cyanolichen *Winfrenatia reticulata* is another example of symbiosis in the Rhynie chert, the lichen thallus comprises layers of fungal hyphae with pockets of hyphal meshes on the upper surface, enclosing cells of a cyanobacterium (Taylor *et al.* 1995, 1997) (see inset right). The fungus would have provided the cyanobacterium water and nutrients from the soil, whereas the cyanobacterium would have provided the fungus carbohydrates from photosynthesis.



Right: *Winfrenatia reticulata*; a net of fungal hyphae (**h**) enclosing cells of the cyanobacterium (**c**) (Copyright owned by University Münster).

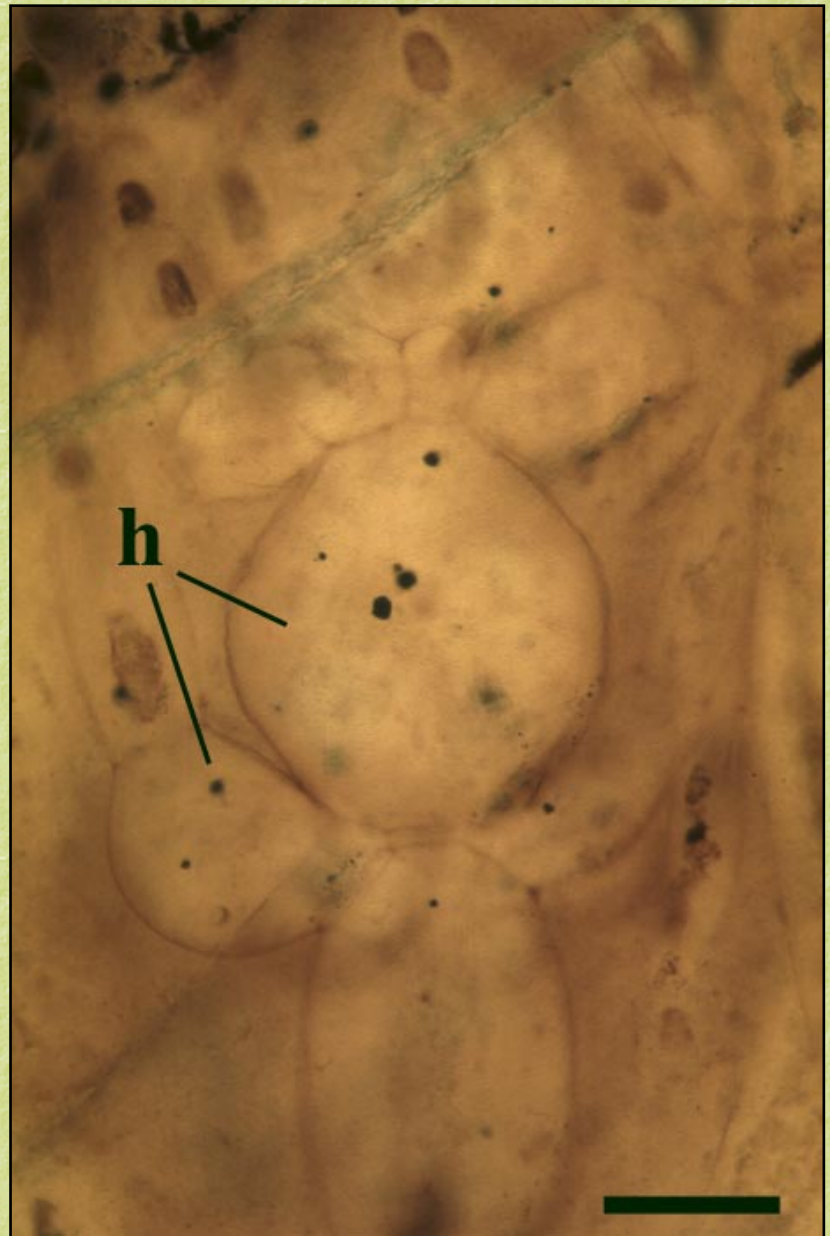
It is clear from understanding mycorrhizae and lichens that symbiosis is an extremely widespread phenomenon, essential to the normal functioning of nearly all modern plant communities and was clearly developed in Early Devonian terrestrial communities.

Parasitism is also evident in the Rhynie chert. Parasitism is where an organism lives in or on a host from which it obtains food, but unlike a predator a parasite does not have to kill its host to gain nutrients. In the Rhynie chert, for example, parasitic aquatic fungi have been found attached to cells of the charophyte *Palaeonitella cranii*, the latter often showing extensive hypertrophy or enlarged, mutated cells as a response to the fungus (Taylor *et al.* 1992) (see inset right).

The Rhynie mites such as *Protacarus crani* and the springtail *Rhyniella*

praecursor as with some of their modern counterparts may have been facultative parasites (organisms that may live as parasites or as independent saprophytes), their stylet-like mouthparts being adapted to puncture the cuticle of plants and imbibe the sap. The hemispherical projections found on the epidermis of *Rhynia gwynne-vaughanii* have been purported to have been a response by the plant to such parasitism ([Kevan et al. 1975](#)).

Right: Longitudinal section of the charophyte *Palaeonitella cranii* showing hypertrophied cells (**h**) in response to parasitism by the fungi *Milleromyces rhyniensis* and *Krispiromyces discoides* (scale bar = 150µm) (Copyright owned by University Münster).



The most likely predators found in the Rhynie chert are the trigonotarbid arachnids and centipedes, since both display morphological characteristics that lend them to a predatory lifestyle, namely the possession of fangs and poison claws respectively; though no unequivocal evidence has been found to date to identify specific prey items. An interesting feature with the trigonotarbids however, is their common association with empty sporangia and plant straws ([Kevan et al. 1975](#)). These may have provided the arachnid with a hiding place from which to capture prey or alternatively may have provided a relatively safe shelter in which the animal could moult its cuticle. Some authors have suggested the Rhynie trigonotarbids may have been facultative herbivores, occasionally feeding on spore protoplasts ([Kevan et al. 1975](#)).

A number of the Rhynie organisms appear to have been wholly or at least partially saprophytic. As mentioned above, the mites and the collembolan were likely to have been partially saprophytic in their ecology. At least some of the Rhynie fungi were also likely to be saprophytic, evidenced by the close association of fungal hyphae with decayed plant material. But perhaps the most unequivocal evidence of

this form of coaction, and detritivory, is the preservation of the gut contents in the myriapod *Leverhulmia mariae*, found to comprise almost entirely spores and macerated plant debris ([Anderson & Trewin 2003](#)). The euthycarcinoid *Heterocrania rhyniensis* and the crustacean *Lepidocaris rhyniensis* were likely to be saprophytes and detritivores as evidenced by their morphology, particularly in their mouthparts, and more speculatively from the contents of coprolites, found in close association, that may have been produced by these organisms.

Evidence for Reaction

The evidence for reaction in the Rhynie chert (i.e.: the evidence for the biota affecting the inorganic environment) is less clear than that for evidence of coaction, and perhaps more speculative. Perhaps the best evidence for reaction is the contribution of the biota, particularly the flora to soil formation.

Many of the composite, plant-bearing chert beds exhibit sand-rich layers or earlier sinter surfaces that had subsequently been colonised by plants. Early colonisers such as *Rhynia gwynne-vaughanii* (primarily in drier areas) and *Horneophyton lignieri* (primarily in wetter areas), followed by later colonisation by other Rhynie plants, would have had a significant organic contribution to these sinter and sandy substrates, particularly by the accumulation of decaying plant litter. The accumulation of organic matter together with the 'recycling' activity of saprophytes such as fungi, mites and collembolans would have made a significant contribution to formation of humus-rich soils (see inset right).

A number of the cyanobacteria found in the Rhynie chert, including *Archaeothrix* possess heterocysts. Heterocysts are used by modern photosynthetic bacteria in the fixation of atmospheric nitrogen. It is very likely,



Above: A composite bed of laminated and massive

therefore that many of the Early Devonian cyanobacteria played an important roll in fixing atmospheric nitrogen into soils at Rhynie 400 million years ago.

chert. The dark laminae, particularly towards the base of the bed, represent compacted, coalified organic matter incorporated into cherty sandstone. This in part may represent a silicified soil horizon.

Evidence for Action

Evidence for action in the Rhynie chert is rather subjective, particularly since we cannot see the Rhynie biota as living organisms. It would be expected, considering the presence of an active hydrothermal complex at Rhynie 400 million years ago, that the 'inorganic environment' would have had some affect on the biota. However, we know that a number of different 'sub-environments' existed within this complex.

For example, we have seen in certain chert beds containing a rich biota of crustaceans, euthycarcinoids, charophytes and various forms of chytrid fungi, algae and cyanobacteria, that these particular beds were deposited in localised pools and ephemeral bodies of standing water. It is not likely that these pond-dwelling organisms were particularly specialised for a hot-water environment. With the exception of cyanobacteria, most 'modern equivalents' of these organisms would not tolerate high water temperatures. It is possible, therefore, that these 'aquatic assemblages' may have represented a background biota that in life was not adapted to life in hot springs, but were killed and preserved by the sudden invasion of their living environment by hot spring fluids.

However, it has been noted in modern hydrothermal areas that in certain areas in proximity to hot-springs and geysers that the flora may be specialised and some forms stunted, reflecting variations in available water, water temperature, pH and nutrients. It remains a matter of debate as to whether some of the Rhynie flora were also specialised in this way or if they represented the background flora living at the time. Current studies on spore assemblages from the cherts and interbedded sediments may help to answer this question.

CONTENTS PAGE



The Ancient Environment and Modern Analogues



Above: Sawmill geyser in eruption, Yellowstone National Park.

[Introduction](#)

[Modern Analogues](#)

Introduction

By combining all the aspects of the Rhynie geology from the structural setting and sedimentology to the palaeontology and palaeobotany we can interpret the environment in the Rhynie area some 400 million years ago. As we have seen previously, the cherts and associated sediments were deposited in a narrow northeast-southwest trending basin or half-graben with a hinterland of Dalradian metamorphic and Ordovician basic igneous rocks (see [Geology and Setting](#)). The basin sediments and rocks indicate a continental setting; generally an **alluvial plain** with an **axial river system**, **floodplains** and **localised ponds and lakes**. There appears to have been contemporaneous volcanic activity with the deposition of tuffs and the localised extrusion of andesitic lavas. We know, beyond a doubt, that the chert beds represent the surface expression of an active hydrothermal system which appears to have been fed by conduits along an active fault zone bounding the north western edge of the basin. From the suite of textures and the differing biota within individual chert beds it appears that many different sub-environments were present during the deposition of the chert, but how do we deduce these sub-environments?

We do not base our conclusions of the fossil environments on observations of the Rhynie chert alone. To help us better understand the **palaeoenvironments** represented by the cherts at Rhynie, modern analogues or comparative environments are particularly instructive.

Modern Analogues

We are fortunate in that there are a number of hydrothermally active areas in virtually all of the world's volcanic regions that can be studied as possible analogues to the Rhynie chert, though only a few have the necessary requirements for geyser activity. The better known areas where geysers are seen include Rotorua in New Zealand and Yellowstone National Park in the USA. Although the structural and volcanic setting is rather different in both these areas compared with that of Rhynie, not to mention the differences in contemporary biotas, in terms of the actual surface processes and sub-environments Rotorua and particularly Yellowstone provide quite good modern analogues. By studying the sub-environments associated with these areas, the type of biota and the sediments and their textures, we can compare and contrast with similar features seen in the Rhynie chert and thus begin to interpret the ancient palaeoenvironments (e.g. [Trewin *et al.* 2003](#)).

For the purposes of this resource, we can look at these modern analogues in two main ways; in terms of 'large-scale features' such as the spatial arrangements of biota, their associations and style of preservation with respect to the hot springs and their deposits, and also in terms of 'micro-features' such as the textures formed in the modern sinters as observed under a microscope:

- [Large-scale features](#)
- [Micro-features](#)

CONTENTS PAGE



Significance to Science?

Since its discovery the Rhynie chert has proved to be of great significance to science. In particular this enigmatic deposit has been (and still is!) of interest to botanists, zoologists and geologists alike.

Click on the tags below to find out why:

[Botanical Significance](#)

[Zoological Significance](#)

[Geological Significance](#)

CONTENTS PAGE



Glossary

Words and terminology which may be unfamiliar to you are presented here within the glossary section. Suggestions for further inclusions in later versions of this module are welcomed.

Abscission: The rejection of plant organs, such as the shedding of leaves during the autumn.

Adventitious: Growing from an unusual position.

Allochthonous: Material, particularly within sediments and sedimentary rocks, that has been transported; including organic debris, mineral and rock fragments.

Alluvial environment: A generalised term for a sedimentary environment where sediment (alluvium) is deposited by rivers and streams.

Andesite: A dark coloured extrusive igneous rock composed of sodic plagioclase minerals (e.g. andesine), and mafic minerals that may include biotite, hornblende or pyroxene. **Phenocrysts** are often common and may comprise one or more of these minerals. Quartz is also often present in the matrix or 'groundmass'.

Antheridium, antheridia: The reproductive structure that produces male **gametes**.

Apical meristem: The embryonic tissue at the 'growing tips' of stems and roots of plants.

Apodous: Not possessing legs or appendages.

Arcari: An order of the Class Arachnida (Subphylum Chelicerata) comprising the mites and ticks. The oldest fossil arcarid *Protocarus crani* occurs in the Rhynie chert.

Archegonium, archegonia: The reproductive structure that produces female **gametes**.

Arthropod: Any invertebrate possessing jointed limbs and a segmented exoskeleton. Belonging to the phylum Arthropoda, the group includes crustaceans, arachnids (e.g.: spiders, scorpions and mites), myriapods (e.g.: millipedes and centipedes) and insects.

Autochthonous: Material, particularly within sediments and sedimentary rocks, that has formed or grown *in situ* and has not been transported.

Autolysins: Enzymes capable of breaking down the cell walls in microbes.

Biostratigraphy: The organisation of sedimentary rocks into units on the basis of the fossils they contain (see also [biozone](#)).

Biozone: A subdivision of the rock record based on the presence of particular fossils, one of which is designated the [zone fossil](#).

Breccia: A rock type comprised of often large angular fragments of pre-existing rock and set within a finer-grained rock matrix or cement.

Calcite: A common rock forming mineral of calcium carbonate (CaCO_3), found primarily in limestones but also commonly forming a diagenetic cement in many other rock types and as a [gangue mineral](#) in many ore deposits.

Carotenoid: Orange, yellow or red-coloured accessory photosynthetic pigments, related to vitamin A, found in higher plants and photosynthetic bacteria. Carotenoids protect cells from strong UV radiation, and therefore cyanobacterial mats often appear more orange than green in colour during bright summer months.

Chloroplast: A cell with a complex internal structure of stacked, photosynthetic pigment-bearing, membranous discs set in a matrix. The chloroplasts of various algae also possess areas of starch formation (see [pyrenoid](#)).

Circinate vernation: A condition observed in plants (esp. ferns) where a leaf bud is curled up.

Clastic: A general term used in sedimentology to describe mineral and rock fragments in sediments/sedimentary rocks that have been derived from pre-existing rock. Rock and mineral fragments in this context may be referred to as clasts.

Clypeus: The area of the facial wall between the labrum and the frons (upper anterior portion of the head) in insects, usually separated from the latter by a groove.

Collophore: A peculiar tube-like structure found in collembolans or 'springtails' situated on the ventral side of the first abdominal segment.

Cortex: Plant tissue found between the epidermis and vascular tissue and comprised primarily of [parenchyma](#) cells.

Cross-stratification: Beds or strata inclined at an angle to the main bedding or stratification. Most is formed by the migration of bed-forms such as ripples and dunes.

Cutan: Complex waxy polymers that form cuticle.

Cuticle: 1. Impermeable layer made of cutan on the outer surface of the [epidermis](#) of plants. 2. Hard protecting layer covering the epidermis of arthropods.

Dichotomous branching: A simple type of branching in plants where the [apical meristem](#) splits or bifurcates at various intervals.

Enations: Non-vascularised leaf-like structures grown out from the [epidermis](#) on some early land plants. In the case of *Asteroxylon mackiei*, vascular traces extend from the stele to the base of the enations.

Endarch: Where the maturation and development of the xylem strand is centrifugal or 'from the inside outwards'. In this case the small xylem cells that are the first to differentiate and mature (the protoxylem) are surrounded by the later developed, longer metaxylem cells.

Epidermis: 1. The exterior tissue of leaves, roots and young stems of plants usually comprising a single layer of cells. 2. The outer layer of cells of an invertebrate (esp. arthropods).

Eukaryote: An organism whose cells contain a distinct nucleus.

Exarch: Where the maturation and development of the xylem strand is centripetal or 'from the outside inwards'. In this case the small xylem cells that are the first to differentiate and mature (the protoxylem) are peripheral to the later developed, longer metaxylem cells.

Exine: The outer, decay-resistant coat of a pollen grain or spore.

Gametangia: General term for the reproductive structures in plants.

Gamete: A haploid germ cell (e.g.: a spermatozoon or ovum) that fuses with another germ cell during fertilisation.

Gametophyte: The haploid stage in the life cycle of a plant, in species that show alternation of generations, that produces the [gametes](#).

Gangue mineral: A mineral of no economic value, often associated with metalliferous ore deposits.

Graded bedding: Bedding in which internally the sediment shows a vertical gradual and progressive change in particle or grain-size. "Normal grading" is most common in which the particle size "fines-upwards", and frequently forms as a result of a gradually waning sediment-laden current, depositing progressively finer material as the current velocity decreases.

Gyrogonites: Dispersed fossil charophyte [oogonia](#).

Half-graben: Term used in geology to describe a sedimentary basin where one side is bounded by an extensional or 'normal' fault.

Hydroid: An elongate, non-lignified water conducting xylem cell in some bryophytes. Analogous with [tracheids](#) in vascular plants.

Internodal cells, internodes: The long single cells on main axes, branches and branchlets in charophytes separating clusters of [nodal cells](#).

Labrum: A sheet of cuticle on the ventral side of the head in arthropods, projecting in front of and protecting the mouthparts.

Lignin: Complex woody polymers found in vascular plants.

Lithostratigraphy: The organisation of sedimentary and volcanic rocks into distinctive named units on the basis of their lithologic character and stratigraphic position in relation to other units (compare with [biostratigraphy](#)).

Macerates: Insoluble organic residues left, for example, after dissolving sandstone samples in hydrofluoric acid.

Mesarch: Where the maturation and development of the xylem strand is both centripetal and centrifugal or 'from the outside inwards' and 'from inside outwards'. In this case the small xylem cells that are the first to differentiate and mature (the protoxylem) are embedded in the later developed, longer metaxylem cells.

Microphyll: A leaf with a single vascular strand, characteristic of lycophytes. Lycophyte leaves appear to have evolved independently from leaves seen in other vascular plants which exhibit more than one vascular strand (megaphyll).

Monopodial branching: A type of branching where lateral branches grow from a main stem.

Mycorrhizae: Symbiotic or parasitic fungi that live within intracellular and/or intercellular cavities in a plant.

Nodal cells, nodes: The short cells on the main axes and branches of charophytes from which branches, branchlets and gametangia may grow. Clusters of nodal cells are separated by long [internodal cells](#).

Norite: A basic, coarsely crystalline plutonic igneous rock containing the plagioclase mineral labradorite as the main component and differing from gabbro by having orthopyroxene as the main ferromagnesian mineral present.

Ontogeny: The series of growth stages of a particular organism.

Oogonium, oogonia: The reproductive structure in charophytes that produces female [gametes](#) (see also [gyrogonites](#)).

Outlier: An area or group of rocks that are surrounded by rocks of an older age.

Palynology: Generally the study of all acid-insoluble organic material extracted from sedimentary rocks by acid solution techniques (see also [palynomorphs](#)), though more specifically concerned with the study of spores and pollen.

Parenchyma: Thin-walled cells in plants that may have various functions and morphologies.

Palynomorphs: Acid-insoluble organic remains, often microscopic, found in maceration residues. May include spores, pollen, acritarchs, dinoflagellates and arthropod cuticle fragments.

Permineralisation: The preservation of organisms where a mineral in-fills intercellular and intracellular cavities, but cell walls are not replaced.

Petrifaction: The preservation of organisms where a mineral in-fills intercellular and intracellular cavities and also replaces the organic material of cell walls.

Phenocrysts: Term used for relatively large conspicuous crystals set in a finer crystalline matrix in an igneous rock. These large crystals have typically grown at a much earlier stage and at a deeper level in the Earth's crust than the finer matrix in which they are set. Igneous rocks containing phenocrysts exhibit a **porphyritic texture**.

Phloem: The photosynthate conducting tissue in vascular plants.

Prokaryote: A primarily unicellular organism in which the cells lack a true nucleus.

Pseudomonopodial branching: A type of branching where the apical meristem appears to divide to form two branches, one of which is dominant resulting in an upright main axis with distinct side branches.

Pyrenoid: An area of starch formation found in the chloroplasts of certain algae.

Pyrite: A common metallic mineral comprising iron disulphide (FeS_2). Crystallizing in the isometric system, pyrite is opaque and has a pale brass-yellow colour, metallic luster, and commonly occurs as cubic or octahedral crystals. Pyrite may occur as nodules or as finely disseminated crystals in sedimentary rocks, and may also replace fossils.

Quartz: A common rock-forming mineral of crystalline silica (SiO_2) composed of silicon-oxygen tetrahedra in a 3D network. In sedimentary rocks quartz is a common detrital mineral, it also occurs in cherts as a result of the diagenesis of amorphous, hydrated forms of silica such as opal and chalcedony.

Retuse, retusoid: Showing a rounded apex with a central depression.

Sclerenchyma: Plant tissue where cells possess walls thickened and hardened with [lignin](#) thus helping to support the plant.

Sheet floods: Flooding events, particularly from rivers, where the flow of water is primarily unconfined (i.e.: not channelised) resulting in transported sediment being deposited as a broad 'sheet'.

Sinter: A porous deposit formed in hydrothermal areas by the precipitation of amorphous opaline silica from silica-saturated waters erupted from geysers and derived from hot springs.

Sporangium, sporangia: The structure in certain plants and fungi in which spores are produced.

Sporophyte: The diploid stage in the life cycle of a plant, in species that show alternation of generations, that produces asexual spores.

Stoma, stomata: A pore in the epidermis of vascular plants used for gaseous exchange and transpiration. It is flanked by two guard cells which allow the pore to open and close.

Tapetum: The nutritive layer of cells in the sporangia of plants.

Terete: Smooth, cylindrical and tapering. Often used in describing vascular cells in plants (esp. [xylem](#) cells).

Tracheid: A water-conducting [xylem](#) cell that is thickened and hardened by [lignin](#), contributing to the support of the plant.

Tuff: Term used for volcanic ash that has been consolidated and cemented.

Vascular tissue: The area of the plant comprising the conducting cells: the [xylem](#) and the [phloem](#).

Vesicles: In solidified lavas this is a term used to describe 'frozen' gas bubbles. When lavas are erupted, the drop in pressure allows gases to separate and form bubbles in the molten rock. If the lava solidifies before the gas bubbles escape the 'bubbles' or vesicles are preserved in the rock. When vesicles are later in filled with a mineral they are called **amygdales**.

Xylem: Plant tissue through which all water and dissolved nutrients are conducted (see also [tracheid](#) and [hydroid](#)).

Zone fossil: A fossil that is characteristic of a [biozone](#) or biostratigraphic unit, and from which the biozone takes its name.

Zosterophyll: A plant belonging to an extinct group of tracheophyte plants, the Zosterophyllophytina, typified by having [pseudomonopodial](#) or [dichotomous](#) branching; lateral, stalked, reniform [sporangia](#) with a marginal dehiscence mechanism; and a [terete](#), [exarch xylem](#) strand.

CONTENTS PAGE

Bibliography

This page lists most of the texts and articles written on the Rhynie chert; the geology, palaeoenvironments and biota as well as some other related articles referred to in this resource. Suggestions for further inclusions in later versions of this module are welcomed.

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CONTENTS PAGE



Links

The following are links related to research on the Rhynie chert and associated subjects. Suggestions for further links to be included in later versions of this module are welcomed.

Universities

[Palaeobotanical Research Group, University of Munster, Germany](#)

[Centre for Palynology, University of Sheffield, UK](#)

[Department of Earth Sciences, Cardiff University, UK](#)

Museums and other organisations

[British Geological Survey](#)

[Dynamic Earth](#)

[Elgin Museum](#)

[The Geologists' Association](#)

[The Hunterian Museum, Glasgow](#)

[The International Code of Zoological Nomenclature](#)

[Joint Information Systems Committee](#)

[The Natural History Museum, London, UK](#)

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[The Paleobiological Fund](#)

[The Paleonet Pages](#)

[The Palaeontological Association \(UK\)](#)

[PSIgate \(Physical Sciences Information Gateway\)](#)

[Scottish Geology](#)

[Scottish Natural Heritage](#)

[The Tree of Life project](#)

[University of California, Berkeley](#)

Geyser and hot spring sites

[GOSA \(The Geyser Observation and Study Association\)](#)

[Matt McLean's pages](#)

[PMEL \(Pacific Marine Environmental Laboratory\) Vents Program](#)

[USGS \(United States Geological Survey\) geyser definition](#)

Other palaeontology sites

[Alan Channing \(plant silicification\)](#)

[Hans Steur's Rhynie chert pictures](#)

[Jack Mount's paleontology links](#)

[Jason Dunlop's Fossil Arachnids page](#)

[Links for Palaeobotanists \(University of Würzburg\)](#)

[Lyall Anderson's Fossil Surgery](#)

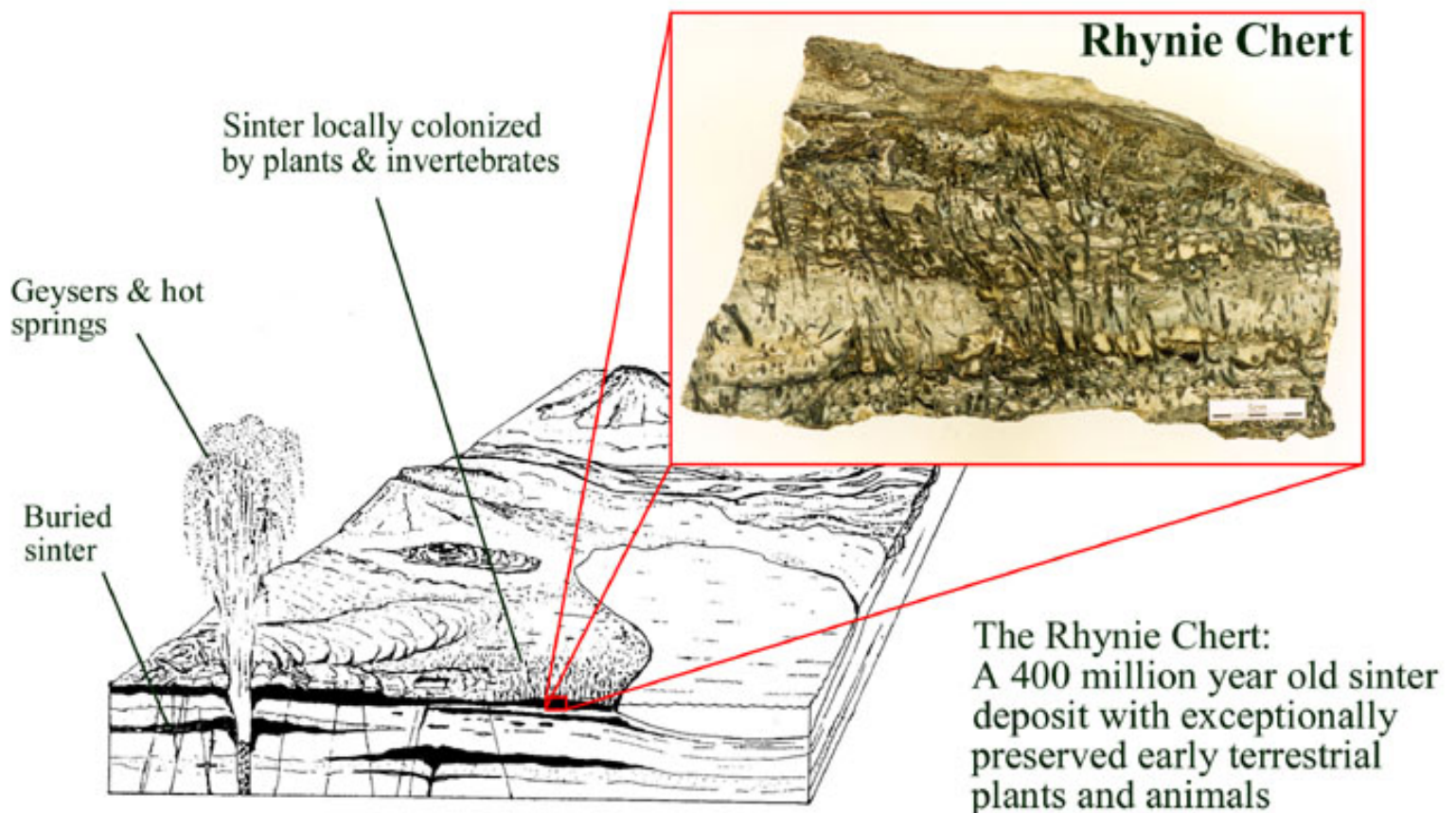
[Palaeos - The trace of life on Earth](#)

CONTENTS PAGE

The Biota of Early Terrestrial Ecosystems:

The Rhynie Chert

(A Teaching and Learning Resource)



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The Proceedings of [The Rhynie Hot-Spring System: Geology, Biota and Mineralisation conference have now been published.](#)

In July 2004 we exhibited at the Royal Society's Summer Science Exhibition! Our exhibit was entitled ['410 million years ago in Scotland: Fossils from the Rhynie chert'](#).

A summary of the 17 - 20 September 2003 conference: [The Rhynie Hot-Spring System: Geology, Biota and Mineralisation](#)

About this site

This web site is designed as a learning and teaching resource based on the Rhynie chert, a rock formation from northeast Scotland that contains a superbly preserved 400 million year old terrestrial and freshwater flora and fauna. The site is designed to be of greatest value for Honours Geology students but can be used by anyone with an interest in earth or life sciences. The site comprises **two main components**:

1. The Learning Resource

The first is primarily a **resource site** for students and teachers covering many aspects of the present knowledge of this unique geological deposit and its scientific significance. It also includes glossary and bibliography pages, as well as a page containing links to many other Rhynie chert websites and related sites of interest (to enter this site click on the icon above left).

2. Suggestions For Tutors

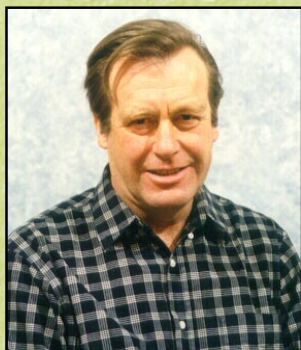
The second part provides guidance for teachers in this subject area. It is primarily aimed at a university Honours degree level but can be utilised at any level. The content is primarily of value in geology teaching, but has relevance to botany, zoology, ecology and history of science (to enter this site click on the icon above right).

Partnerships

This teaching and learning resource has been funded by the [Joint Information Systems Committee](#). It has been authored by the Rhynie chert Research Group, University of Aberdeen, UK (see list of authors below) with contributions and support by the [Palaeobotanical Research Group, University of Münster, Germany](#), the [Centre for Palynology, University of Sheffield, UK](#), [The Natural History Museum, London, UK](#) and [The Royal Museum, National Museums of Scotland](#).



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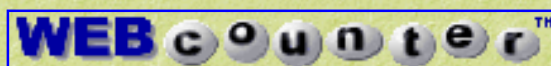
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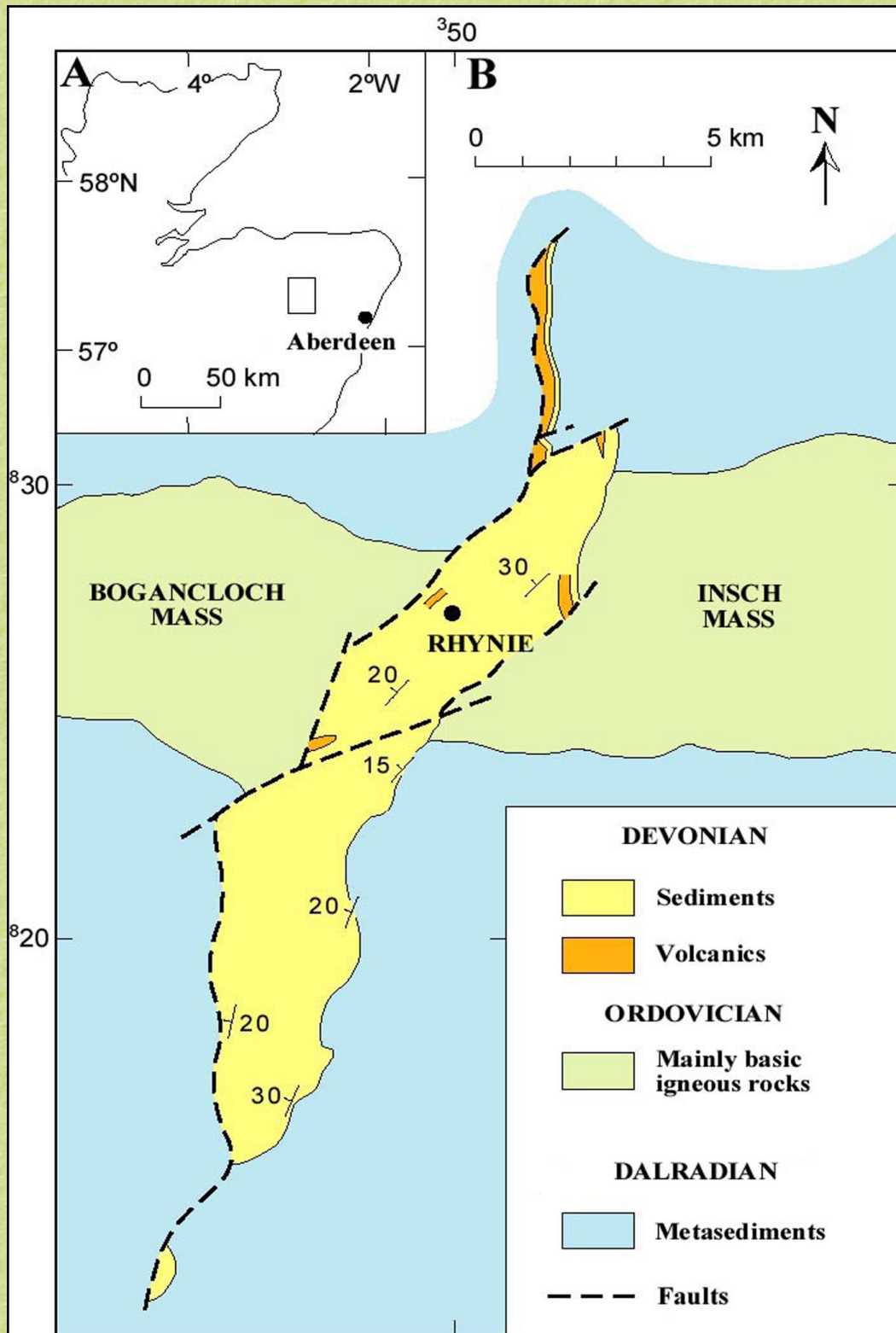
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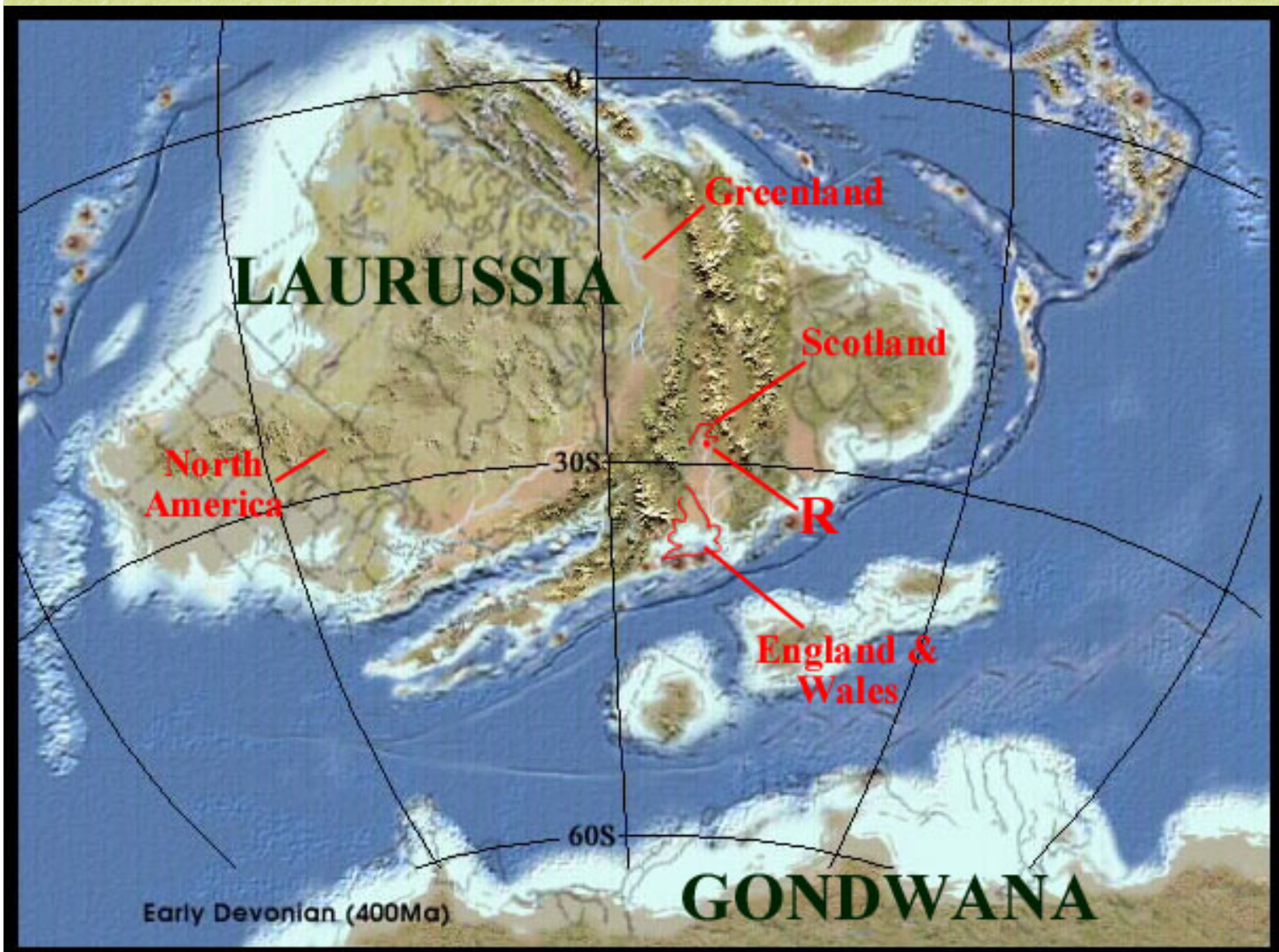


Above: Locality map showing the simplified geology of the Rhynie area.

BACK



Early Devonian Palaeogeography



Above: Palaeogeographic map of Laurussia, the 'Old Red Continent' during the Early Devonian around 400Ma. At this time Rhynie (R) was situated approximately 28° south of the equator (Copyright owned by Dr Ronald Blakey, Northern Arizona University).

BACK



Above: Close up of the splash textures on a block of the 'Windyfield chert'. Compare this with splash textures seen around a modern geyser vent (below).




BACK



The Rhynie Hot Spring System: Geology, Biota and Mineralisation

17 – 20 September 2003





Above: Photograph of the delegates who attended the Rhynie conference, taken in the grounds of King's College, University of Aberdeen, 18th September 2003.

Over forty delegates attended this international conference and workshop, which provided a forum for discussion of all aspects of research on the Early Devonian Rhynie hot spring complex, Aberdeenshire Scotland. As well as from UK and European universities, delegates also came from the US, Australia and New Zealand.

A wide variety of areas of research were covered by oral and poster presentations, and are listed at the bottom of this page. Palaeontological aspects included both review papers and descriptions of new elements of the biota from the Rhynie and Windyfield cherts. Other areas covered included a history of Rhynie research, geology, mineralisation and dating of the Rhynie deposits. Various topics relating to modern hot spring analogues were also explored. These included taphonomy and preservation of biota, sinter formation and facies variation in hot spring environments, silica maturation and sinter diagenesis, together with the role of microbes in silicification, sinter formation and the precipitation of metals.

For the conference, with permission from Scottish Natural Heritage, a trench was excavated through part of the Rhynie chert-bearing unit, revealing a 12 metre sequence of cherts and chert-cemented sandstones interbedded with weathered carbonaceous sandstones, siltstones and shales (see inset below right). For the first time oriented blocks of chert were recovered from *in situ* chert beds, and will provide material for future work on the palaeoecology of the deposit. The trench was visited by the conference delegates on Saturday 20th September as the main part of a field excursion looking at the geology of the Rhynie area

Transactions of the Royal Society of Edinburgh - Rhynie special publication:

The papers resulting from the conference and accepted by Transactions of the Royal Society of Edinburgh will shortly be published as Part 4 of Vol 94 (2004) of the Transactions.

Public open day at Rhynie

On Sunday 21st September, Drs. Nigel Trewin and Clive Rice gave a talk on the geology and palaeontology of the Rhynie hot spring complex at the school in Rhynie, which was attended by over two hundred people from the village and the surrounding area! Following the presentation members of the public were invited to view the trench excavated through part of the Rhynie chert-bearing sequence (see inset right).

We would like to thank Scottish Natural Heritage, who own the Rhynie chert SSSI (Site of Special Scientific Interest) for their cooperation and allowing the excavation to take place. Jim Duncan is also thanked for his help in excavating the trench.

Right: Members of the public viewing the trench excavated through part of the Rhynie chert-bearing sequence at Rhynie.



Conference Presentations

The following contributions were given during the conference, and the abstracts may be viewed [here](#).

Oral Presentations

History and framework geology

[*History of research on the geology and palaeontology of the Rhynie area, Aberdeenshire, Scotland.*](#) N. H. Trewin
(University of Aberdeen)

[*Geological setting of the Rhynie Hot Spring System.*](#) C. M. Rice and W. A. Ashcroft (University of Aberdeen)

[*Absolute age and underlying cause of hot spring activity at Rhynie.*](#) S. F. Parry (University of Aberdeen) and S. R. Noble (N. I.G.L., Keyworth)

Palaeontology

[*A review of the sporophytes of embryophytes in the cherts at Rhynie.*](#) D. Edwards (University of Cardiff)

[*Rhynie chert gametophytes.*](#) H. Kerp and H. Hass (Westfälische Wilhelms Universität, Munster) and N. H. Trewin (University of Aberdeen)

[*Rhynie chert plants and adaptations to their substrates.*](#) H. Hass and H. Kerp (Westfälische Wilhelms Universität, Munster)

[*Assimilation and transpiration capabilities of rhyniophytic plants and implications for palaeoatmospheric carbon dioxide concentration.*](#) W. Konrad and A. Roth-Nebelsick (Institut für Geowissenschaften der Universität Tübingen)

[*Dispersed spore assemblages from the Lower Devonian sequence of the Rhynie outlier, Scotland.*](#) C. H. Wellman (University of Sheffield)

[*Fungi in the Rhynie chert: a view from the dark side.*](#) T. N. Taylor (University of Kansas), H. Hass (Westfälische Wilhelms Universität, Munster), M. Krings (University of Kansas), S. D. Klavins (University of Kansas) and H. Kerp (Westfälische Wilhelms Universität, Munster)

[*Charophyte algae from the Rhynie Chert.*](#) R. Kelman (University of Aberdeen), M. Feist (Université de Montpellier), N. H. Trewin (University of Aberdeen) and H. Hass (Westfälische Wilhelms Universität, Munster)

[*A review of the palaeoenvironments and biota of the Windyfield chert.*](#) S. R. Fayers and N. H. Trewin (University of Aberdeen)

[*A harvestman \(Arachnida: Opiliones\) from the Early Devonian Rhynie Cherts, Aberdeenshire Scotland.*](#) J. Dunlop (Humboldt Universität, Berlin), L. I. Anderson (National Museum of Scotland), H. Kerp and H. Hass (Westfälische Wilhelms Universität, Munster)

[*A crustacean with cladoceran affinities from the Early Devonian \(Pragian\) Rhynie chert.*](#) L. I. Anderson, W. R. B. Crichton (National Museum of Scotland) and H. Hass (Westfälische Wilhelms Universität, Munster)

[*The feeding habits of Lower Devonian terrestrial fauna; evidence from an assemblage of coprolites preserved in the Rhynie chert.*](#) K. Habgood (Praxis Critical Systems, Bath)

Rhynie analogues - Modern hot springs

[*Experimental taphonomy: silicification of plants in Yellowstone hot spring environments.*](#) A. Channing (National Museum and Galleries of Wales)

[*Windows on silica sinter maturation, preservation and depositional environments, North Island, New Zealand.*](#) K. A. Campbell, B. Y. Smith, P. R. L. Browne and T. F. Buddle (University of Auckland)

[*Modern silicification of microbes in hot spring settings: implications for interpretation of ancient silicified microbes.*](#) B. Jones (University of Alberta), R. W. Renaut (University of Saskatchewan) and M. R. Rosen (USGS, Carson City)

[*Morphology, facies and development of sinter terraces.*](#) R. W. Renaut (University of Saskatchewan), B. Jones (University of Alberta) and R. B. Owen (Hong Kong Baptist University)

[*Exploration of possible metal precipitation pathways resulting from microbial communities present in metalliferous hot springs in New Zealand.*](#) Jennifer A. Haddow, Andy Meharg, James Prosser and Clive M. Rice (University of Aberdeen)

[*Bacterial silicification: Experimental field and laboratory studies.*](#) Liane G. Benning (University of Leeds) and Bruce W. Mountain (Wairakei Research Centre, Taupo, New Zealand)

Posters

[*Meet Medusa: silicification of arthropods in a modern-day, terrestrial, hot-spring system.*](#) L. I. Anderson (National Museum of Scotland), A. Channing (National Museum of Wales), N. H. Trewin (University of Aberdeen) and S. Sturtevant

(Billings, Montana).

[*A geothermal wetland dominated by unconsolidated chemically precipitated silica sediment: A window on silica deposition in Palaeozoic geothermal environments?*](#) A. Channing (National Museum and Galleries of Wales) and S. Sturtevant

(Billings, Montana)

[*Rhynie chert: Department of Palaeontology, Natural History Museum, London, Collection.*](#) P. G. Davis (Natural History Museum)

[*A new crustacean from the Pragian Rhynie chert, Rhynie, Aberdeenshire, Scotland.*](#) S. R. Fayers and N. H. Trewin

(University of Aberdeen)

[*The Rhynie chert - a web-based teaching and learning resource.*](#) N. H. Trewin, S. R. Fayers (University of Aberdeen) and L. I. Anderson (National Museum of Scotland)

[*IGCP 491: Devonian Disaster ~ lahars and lagoons in northern New Brunswick.*](#) S. Turner and R. Miller (New Brunswick Museum, Canada)

[*Geothermal and magmatic-hydrothermal systems in Cenozoic arc basalts, South Shetland Islands, Antarctica.*](#) Robert C. R. Willan (BAS, Cambridge), Adrian J. Boyce and Tony E. Fallick (SUERC, Glasgow)

[*Correlation between 3 boreholes, drilled within the Rhynie SSSI, Aberdeenshire, Scotland.*](#) E. Wilson and N. H. Trewin (University of Aberdeen)

[*Old Red Sandstone Life Beyond the Litter: Devonian Terrestrial Arthropods Outside of Rhynie and Gilboa.*](#) Heather M. Wilson (University of Maryland)



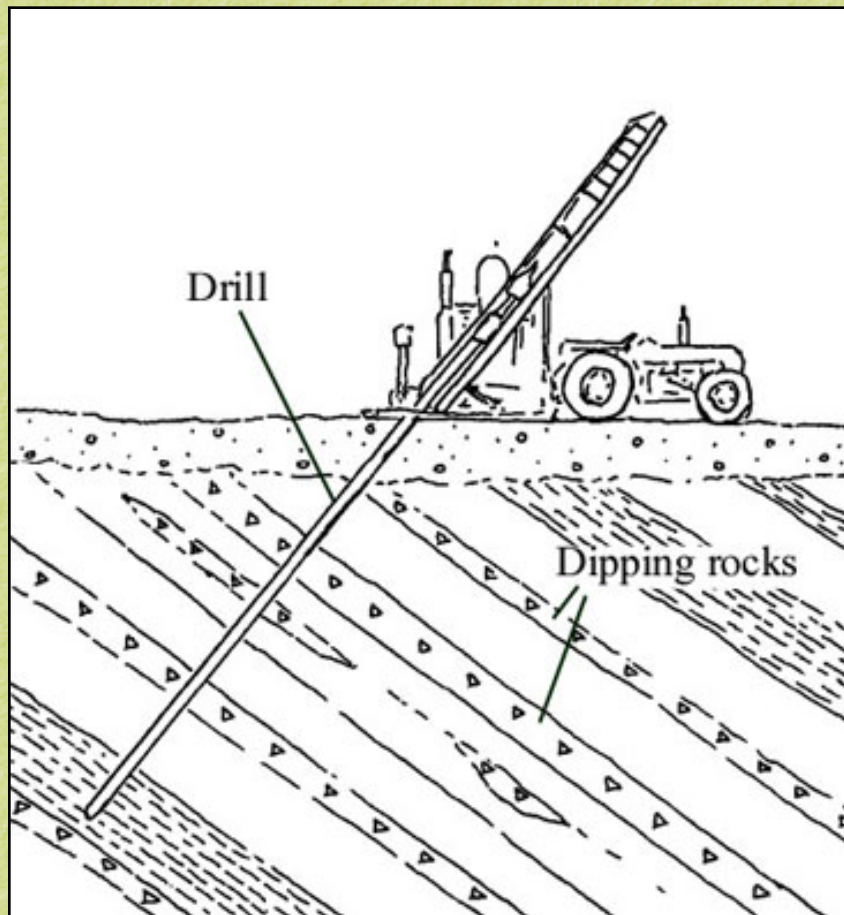


Drilling at Rhynie



Above: Drilling rig at Rhynie in 1997. The drilling crew on the left are removing a section of core barrel which encloses a 50mm diameter length of rock or 'core' taken from the Rhynie chert sequence.

One of the methods employed to sample the Rhynie chert together with the interbedded sedimentary rocks is to 'core' the rocks beneath the surface using a drilling rig (see inset above). If it is known, from previous work, the orientation in which the sedimentary rocks in the subsurface are tilting or 'dipping', the drill can be set at an angle that will be at or near to 90° to the dip of the rocks. This allows the maximum coverage of the sedimentary sequence cored (see inset below).



Above: Diagrammatic section of a drilling rig set at an angle to recover 'rock core' at 90° to the dip of the sedimentary rocks in the subsurface.

Once recovered, the 'cores' of rock are marked with the respective drilling depth and are then transferred (in depth order) into specially designed boxes for storage and future study (see inset below).



Above: Cores of the Rhynie sequence recovered by drilling have been carefully marked and transferred into core boxes for storage and study back in the lab.

Other reasons for drilling?

From studying the cores of rock we can analyse not only the chert beds that may be present, but also the sedimentary rocks between the chert beds. In studying various aspects of the **sedimentology** we can assess many things, from the environment in which the sediments were deposited, to what happened to them after they were buried.

Drilling results help us to understand the **stratigraphy** of the sediments in the area - both in terms of the age and the 'sequence' in which the sediments were deposited. Another useful aspect of drilling a series of cores over a defined area, is that if we encounter the same chert beds within successive coring operations we can also assess the distribution or **lateral continuity** of the cherts over that area - in other words where individual chert beds occur and where they die out.

Over the years many cores have been taken through the sedimentary sequence at various localities in the Rhynie area. The drilling projects have provided hundreds of metres of rock core, much of it from the **Dryden Flags Formation** that contains the Rhynie chert. Drilling has also provided information on the other rock units in the area and on the geological structure of the area ([Rice et al. 2002](#)) (see the section on the [Site Geology and Setting](#)).

We would like to thank Hays Business Services for housing the cores taken from the Rhynie area at their core store in Aberdeen

CONTENTS PAGE



Trenching at Rhynie

The Rhynie chert is nowhere exposed naturally at the surface, being found primarily as loose 'float' blocks in the fields. Apart from drilling, the only means available to see the chert and interbedded sediments *in situ* is to dig trenches. The photograph on the left illustrates one of a series of trenches excavated in August 1963. Here the trench has intersected one of the chert beds (the light coloured rock just above left of center and bottom right) where it is interbedded mainly with dark shales and minor muddy sandstones. The beds are dipping quite steeply to the northeast (right as viewed).

By observing the cherts *in situ* we can better understand their geometry (e.g. whether they occur as tabular beds or lenses), lateral continuity, and distribution in relation to the sedimentary rocks in which they occur.

Try clicking on the cherts in the picture for a close-up!



Above: Photograph of one of the trenches dug in 1963 showing a chert bed dipping steeply to the northeast (to the right in photograph).

In 1997, trenching to the north-east of the Rhynie chert locality in the vicinity of Windyfield Farm revealed the only known *in situ* occurrence of the Windyfield chert (see section on [Geology and Setting](#)).

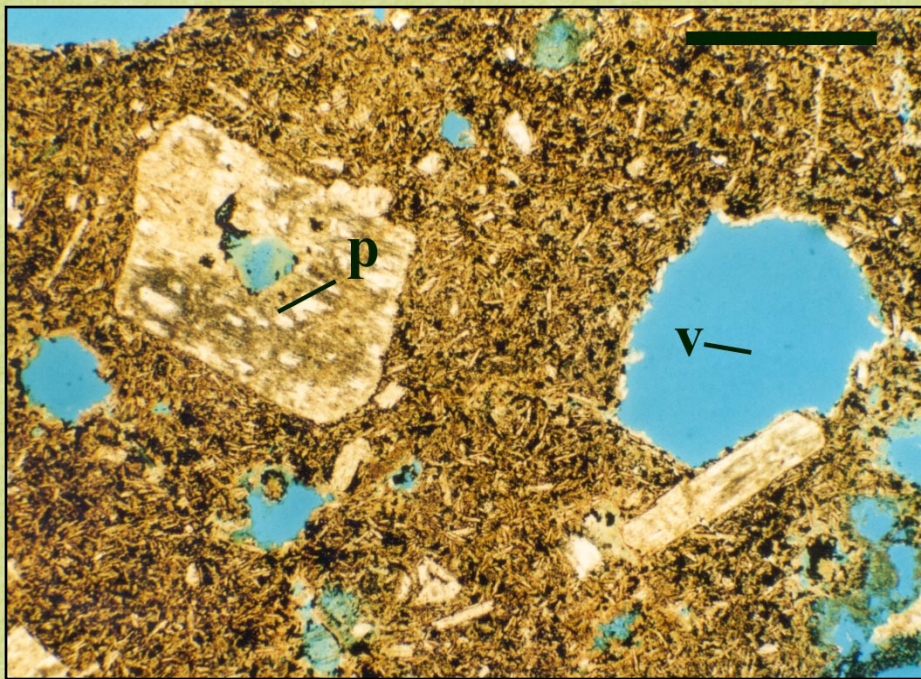
More recent trenching, since 2000, in the northern part of the Rhynie Basin away from the Rhynie chert locality has helped to constrain the sedimentary sequence, stratigraphy and structural geology of the area (see [Rice *et al.* 2002](#); [Rice & Ashcroft in press](#)).

CONTENTS PAGE



Tillybrachty Sandstone Formation

This lithostratigraphic unit comprises the lower part of the sequence of the basin fill and is laterally variable in character. In much of the basin the unit is dominated by coarse-grained [clastic rocks](#), primarily locally derived sandstones and conglomerates. In the area of Rhynie itself much of the unit appears to comprise a significant thickness of [tuffs](#) with interbedded sandstones ([Rice et al. 2002](#)). Some of the tuffs appear to represent direct air-fall deposits, but most appear to have been water-lain and were probably derived from eroding ash cones.



Concurrent volcanic activity is also recorded in the rocks of the Tillybrachty Sandstone Formation in the form of extrusive [andesite](#) lava flows. The andesites show many primary textures that were preserved at the time the lava cooled and solidified such as [vesicles](#) and [phenocrysts](#), however, due to later passage of hot fluids through the lavas the original minerals that make up the rock have been highly altered (see inset left).

Above: Thin section of andesite showing vesicles (v) and plagioclase phenocrysts (p). Most of the plagioclase and mafic minerals have been hydrothermally altered (scale bar = 1mm). *Note: The blue colour in the vesicles is dyed epoxy resin to show void space in the thin section.*

The sedimentary rocks of the Tillybrachty Sandstone Formation appear to represent localised deposition

in an [alluvial environment](#). The conglomerates and coarse-grained sandstones were probably initially deposited as alluvial fans at the basin margins with sediment being distributed further into the basin by [sheet flood](#) events. Localised volcanic activity is also evident by the presence of andesitic lava flows and tuffs.

CONTENTS PAGE



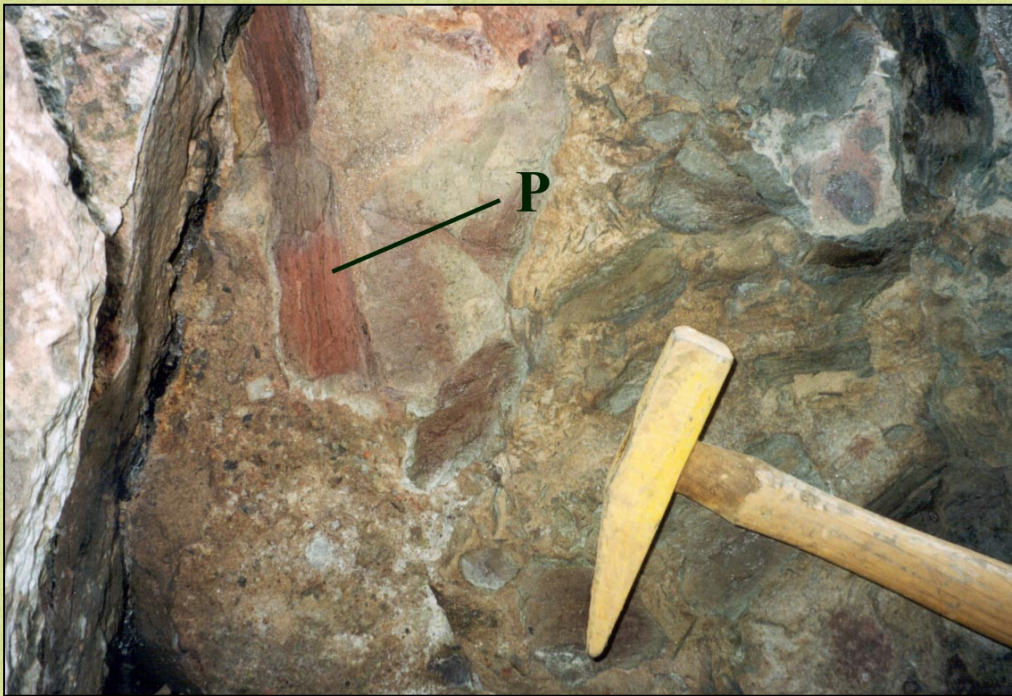
Quarry Hill Sandstone Formation

This lithostratigraphic unit succeeds the Tillybrachty Sandstone Formation. It occurs throughout much of the basin and is particularly distinctive in the south west of the area where it outcrops in the disused sandstone quarries on Quarry Hill (see inset below). This formation primarily comprises stacked, well bedded, current rippled, laminated and **cross-stratified** sandstones rich in feldspar grains. In this particular area these sandstone beds form large-scale channelised deposits commonly exhibiting erosive bases with mud rip-up clasts and are occasionally interbedded with scoured thin shale horizons.



Above: Exposure of the Quarry Hill Sandstone Formation at Quarry Hill, Rhynie. The hammer (arrowed) is 40cm long.

In the Quarry Hill area the sandstones locally yield casts of transported plant debris, some of which are particularly large (see inset below).



Above: Base of a sandstone bed in the Quarry Hill Sandstone Formation at Quarry Hill, Rhynie, showing fossilised plant debris (P).

Of these plant remains, and perhaps one of the most enigmatic, may tentatively be assigned to the genus *Prototaxites* (belonging to an extinct group of Palaeozoic plants called the [nematophytes](#)). When the area was actively being quarried in the late 19th and early 20th centuries, these plant fossils were occasionally found in the form of logs preserved as sandstone casts. One specimen, recorded by [Newlands \(1913\)](#) as "a plant fragment" and nearly 1.3 m in length, is now housed in the collection of the Department of Geology and Petroleum Geology, University of Aberdeen (see inset below).

Above: Sandstone cast of a probable nematophyte 'log' from the quarries at Quarry Hill, Rhynie, as reported

by [Newlands \(1913\)](#) (scale bar = 10cm).

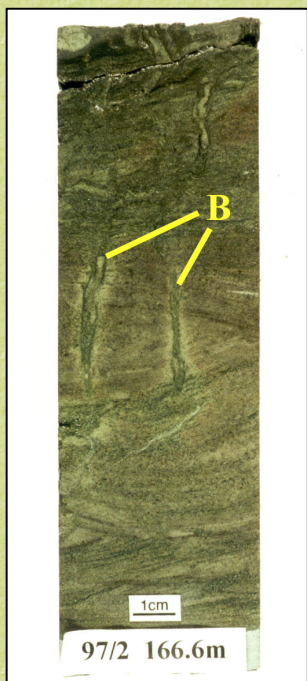
Trace fossils have also occasionally been found on bed surfaces including *Diplichnites*, a preserved trackway about 5cm wide, probably created by a large myriapodous [arthropod](#) (see inset below).



Above: The under surface of a sandstone bed from Quarry Hill showing the trace fossil *Diplichnites*. This is the cast of a trackway, most likely made by a large myriapodous arthropod, such as a millipede or arthropleurid. The shape of the footprints suggests the direction in which the animal was moving was from left to right in this picture (click on image for a close-up!).

The "White Sandstones Unit" encountered in Borehole 97/2, north west of Rhynie village, is a 50m interval of hydrothermally altered white, laminated, rippled and cross-stratified sandstones with minor shale interbeds. It is thought to represent at least part of the formation in this area (see insets below). Locally the sandstones are heavily cemented by calcite. In this borehole its basal contact is with a hydrothermal breccia above the main fault zone and, with increasing shale content, passes upwards into the more mud-rich beds of the [Dryden Flags Formation](#).

Typical features of the White Sandstones Unit in Borehole 97/2:



Above: Vertical burrows (B) cutting ripple laminated sandstone.



Above: Current ripples (C) in sandstones with dark carbonaceous debris.



Above: Graded sandstone bed with sharp erosive base (S) fining upwards into more argillaceous current rippled sandstone (C).



Above: Ripped-up mud clasts (M) at the base of a cross-stratified bed.

The overall environment that seems to be represented by this unit is one dominated by shallow fluvial channels of a river system flowing towards the northeast along the axis of the basin. The occasional shale horizons may in part represent poorly preserved overbank and floodplain deposits.

The lateral change from the more stacked, well-bedded sand-rich lithofacies at Quarry Hill to the dominantly thinly bedded sands and minor shales in the area northwest of Rhynie village suggests the presence of larger-scale fluvial channels in the Quarry Hill area.

CONTENTS PAGE



Dryden Flags Formation

The Rhynie cherts occur within the Dryden Flags Formation which forms the upper part of the of the sequence of the basin fill. It is a sequence of thinly bedded micaceous sandstones (traditionally termed 'flags') and shales, that were previously recognised as the Dryden Flags and Shales and in part may represent a lateral equivalent to the Quarry Hill Sandstone Formation (see [Rice *et al.* \(2002\)](#) for details of the stratigraphy described below).

The succession of the Dryden Flags Formation in the Rhynie area, following the drilling programmes by the University of Aberdeen and recent studies, can now be divided lithologically into four discrete units. The lowest unit, informally termed the "**Shales and Muddy Sandstones Unit**" grades up from the "White Sandstones Unit" below and comprises primarily thickly bedded (up to 1m thick), erosively based massive muddy sandstones interbedded with thin shales and siltstones which show abundant soft-sediment deformation features. This unit passes upwards into a thick sequence of dark shales with thin fluidised and disrupted sand and silt laminae, informally termed the "**Lower Shales Unit**" (see inset below left).



Above: Laminated shales with fluidised and disrupted sandy and silty laminae in the "Lower Shales Unit" (Dryden Flags Formation).

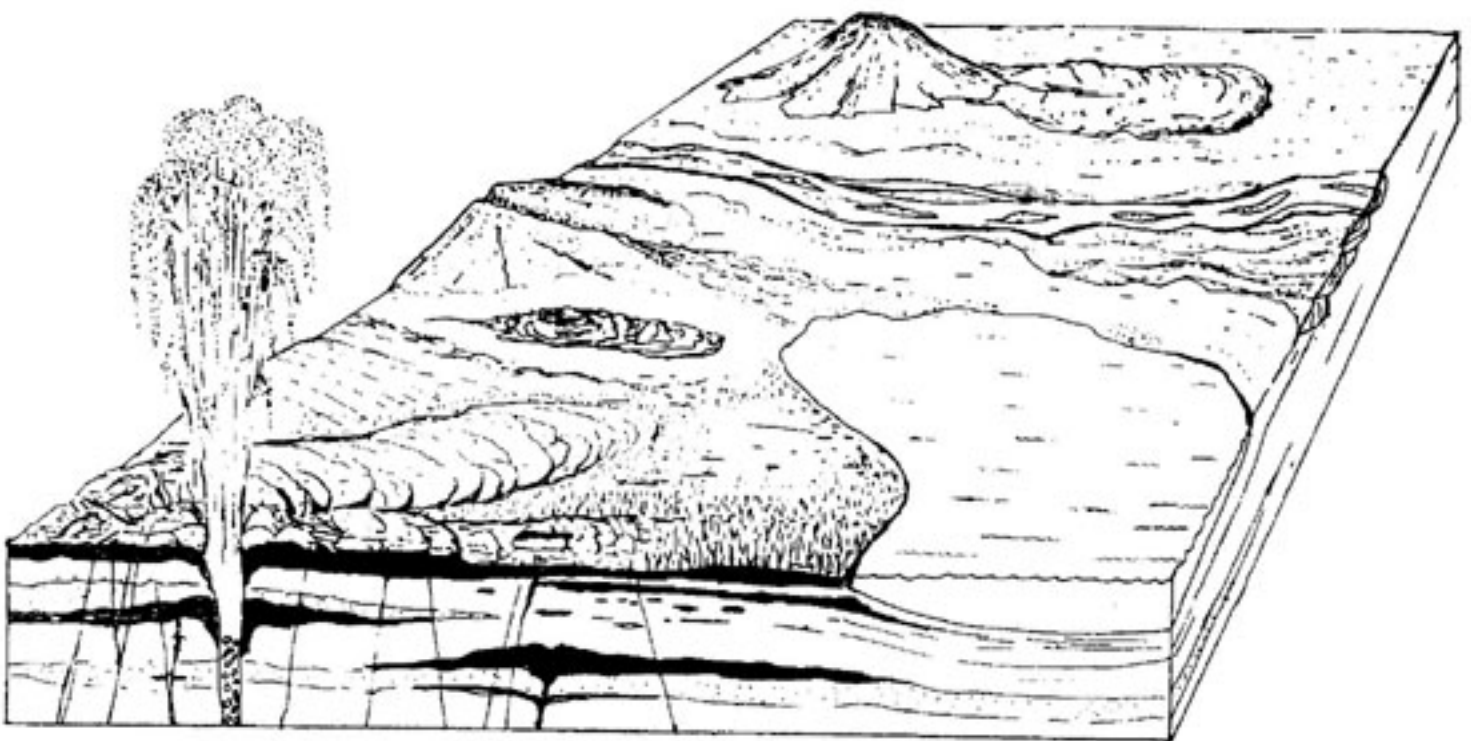


Above: Massive chert with very well preserved axes of *Aglaophyton major* (A) in the "Rhynie cherts Unit" (Dryden Flags Formation).

Above the shales lies the chert-bearing part of the sequence, informally termed the "**Rhynie Chert Unit**". Comparing borehole and trench data the chert beds (see inset above right) are laterally impersistent ([Trewin & Wilson 2004](#)). One borehole (19c) studied by Clare Powell exhibited 53 individual chert beds over a depth interval of 26m, many of which are plant-bearing ([Powell et al. 2000b](#)) (for a more detailed review of the chert morphologies and textures see the following section on [Chert Textures](#)). The chert horizons are variably interbedded with silicified compacted sandstones with organostylolites, together with thin shales and siltstones similar in lithology to the units below and above. By comparing the biota content and textures of the discontinuous plant-bearing chert beds of the Rhynie Chert Unit with Recent plant-bearing sinters and modern hot spring environments at Yellowstone National Park, USA, [Trewin and Wilson \(2004\)](#) suggest that much of the Rhynie chert succession represents sinter deposition on the distal, cooler reaches of a hot spring outwash apron.

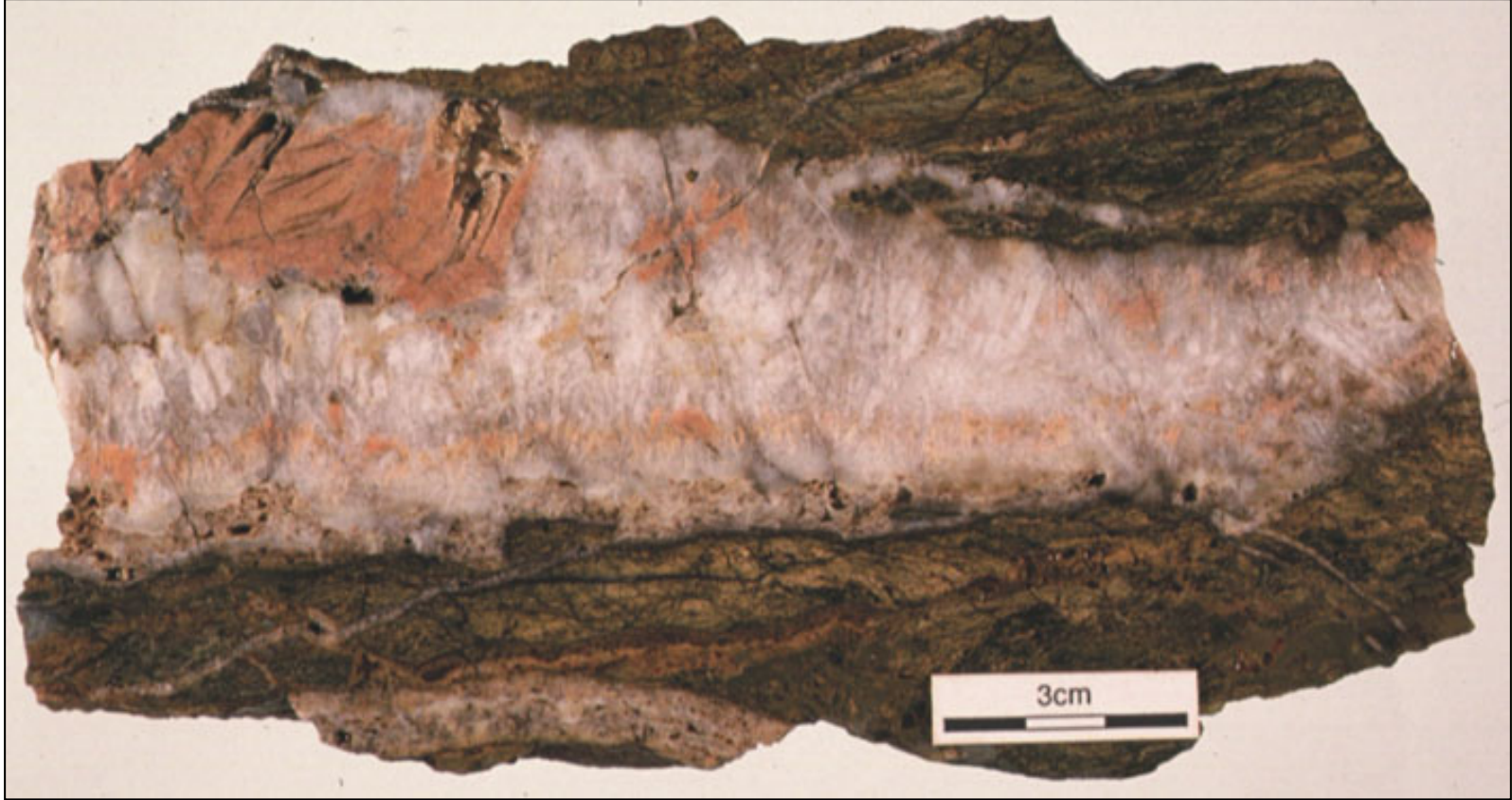
The uppermost lithological unit in the Dryden Flags Formation is informally termed the "**Upper Shales Unit**" and is at least 13m thick. It comprises primarily green-coloured laminated shales (locally exhibiting desiccation cracks) variably interbedded with impersistent thin sandstone beds that often display sharp to erosive bases, mud rip-up clasts, current ripple laminae and **graded bedding**. Patchy calcite cementation is present in the sandstones. Similar lithologies host the **Windyfield chert**, some 700 m to the northeast of the Rhynie chert locality, and therefore it has been suggested the Windyfield chert probably occurs within this younger unit ([Rice *et al.* 2002](#); [Rice & Ashcroft in press](#)).

The overall environment represented by the rocks of the Dryden Flags Formation appears to be an alluvial plain setting with mainly overbank deposition on floodplains and in ephemeral lakes with occasional **sheet-flood** events. The cherts and their interbedded sediments representing localised deposition of subaerial and subaqueous sinters from hot spring and geyser activity and the accumulation of soils on floodplains (see inset below).



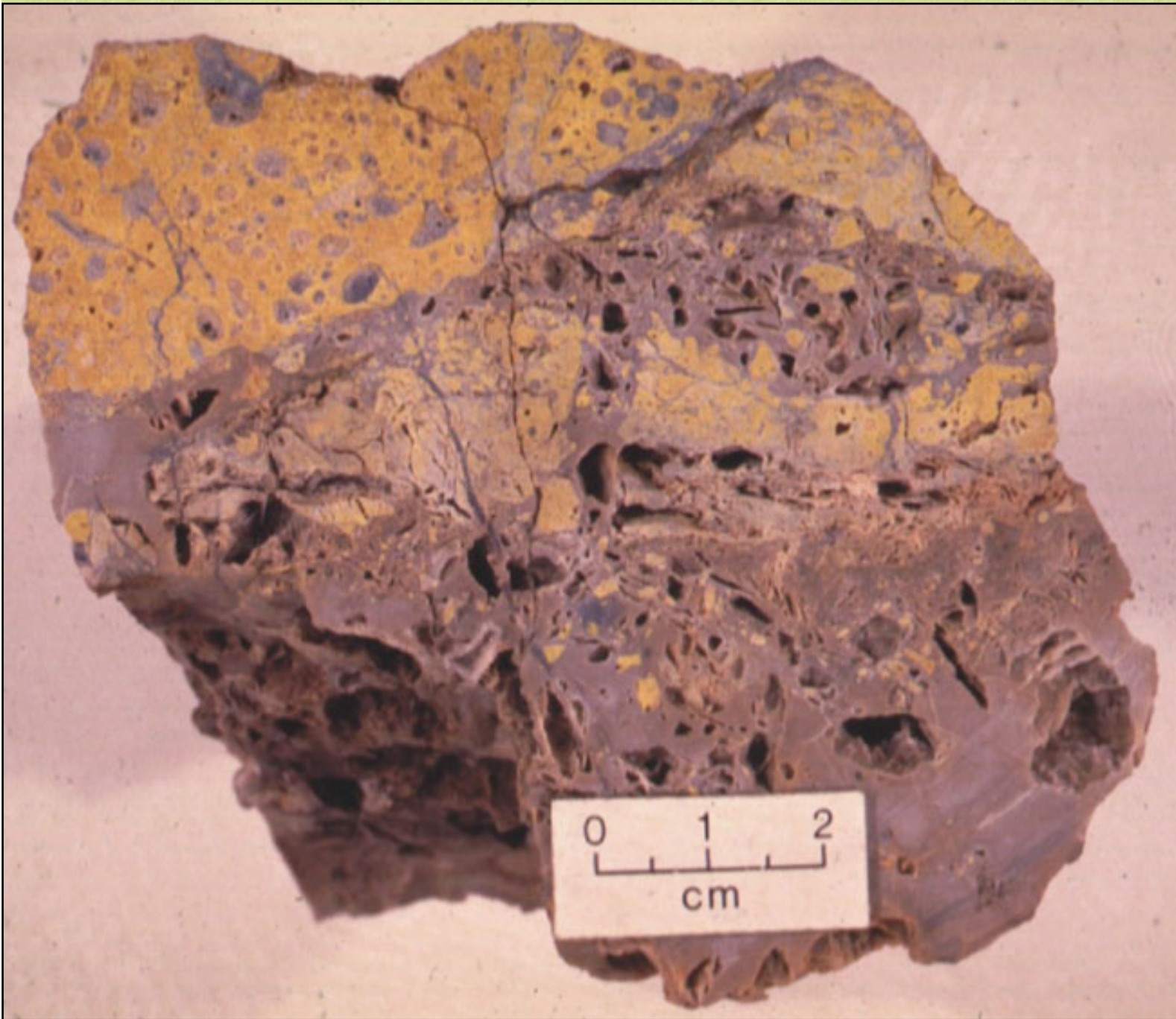
Above: Environmental reconstruction of the Rhynie area during the deposition of the Dryden Flags Formation. The background setting is an alluvial plane with an axial river system (middle distance), floodplain with patchy soil development and plant growth (center foreground), shallow ephemeral lakes (right foreground) and local eroding volcanic ash cones (far distance). An active geyser vent is seen in cross-section (left foreground) with sinter deposits and localised freshwater ponds. Black bands represent earlier, buried sinters, sealed vents and fractures (after [Trewin 1994](#)).

CONTENTS PAGE



Above: Close-up of a quartz and K-feldspar vein in sandstone from the basin margin fault zone at Rhynie.

BACK

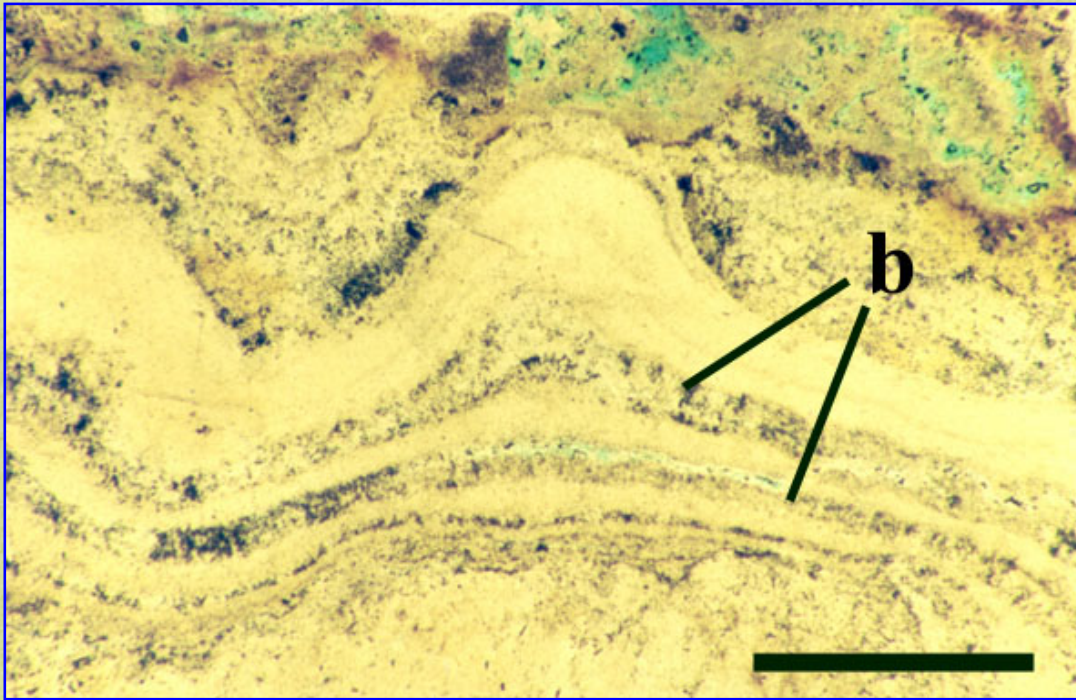


Above: Close-up of altered, brecciated andesite from the basin margin fault zone at Rhynie. The andesite has been altered to quartz and K-feldspar (adularia). To highlight the differences in mineralogy the K-feldspar has been stained yellow using sodium cobaltinitrate solution

BACK



Cyanophytes



Above: Cross section through crenulated 'stromatolitic' laminae. The darker layers (**b**) contain relic filaments that may represent cyanobacteria (click on picture for a close-up!). This section is taken from the block of Windyfield chert displaying the geyser vent splash texture seen in previous sections (scale bar = 500 μ m).

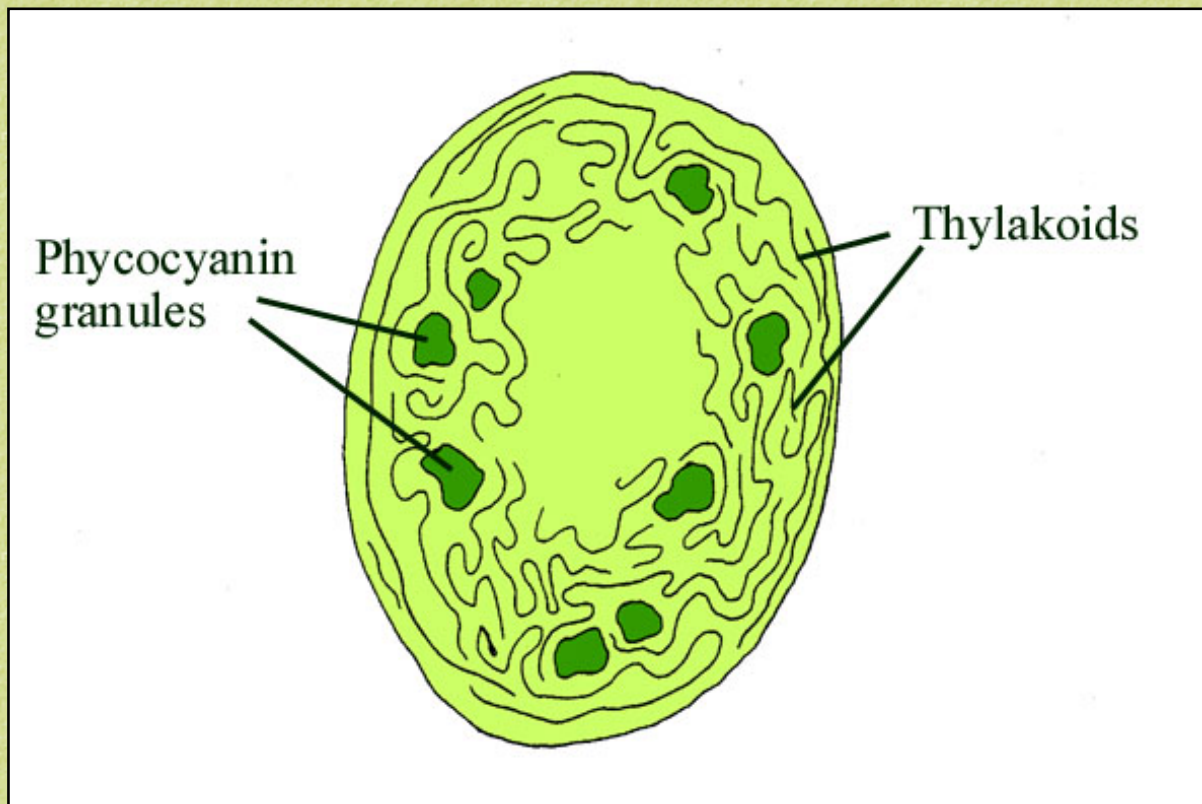
[Introduction](#)

[Fossil Record](#)

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Introduction

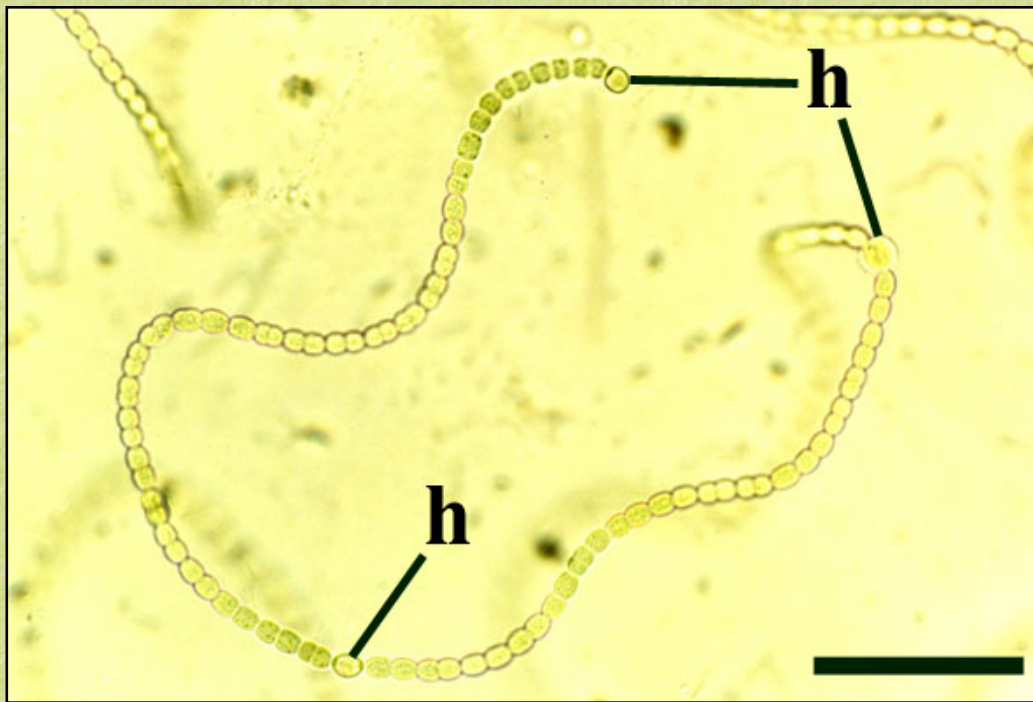
Cyanophytes are an enigmatic group of **prokaryotic** organisms that comprise what were formerly known as the 'blue-green algae'. Strictly speaking these are only termed 'algae' because they are organisms that can undergo photosynthesis. They are in fact a large and varied group of bacteria, the **cyanobacteria**, that possess a type of chlorophyll (chlorophyll *a*) and are able to photosynthesise in the presence of air and sunlight and produce oxygen. Cyanobacteria, unlike chlorophytes, do not possess chloroplasts. In fact the chloroplast in the cells of eukaryotic algae and plants is actually a symbiotic cyanobacterium. In cyanobacteria the chlorophyll is carried on specialised membranes within the cells called **thylakoids** (see inset below).



Above: Diagrammatic section through a prokaryotic cell.

Many cyanophytes are important in the fixation of atmospheric nitrogen. This process can only occur in the absence of oxygen, therefore certain cyanobacteria possess specially thickened cells or **heterocysts** which contain an anaerobic microenvironment in which this can take place (see inset below).

Cyanobacteria may be unicellular or filamentous and may or may not be colonial (see inset below).



Above: Modern freshwater cyanobacteria forming a chain-like colony of single cells, showing occasional larger, thick-walled heterocysts (**h**) (scale bar = 100 μ m).

Modern cyanobacteria live in many different environments ranging from marine to freshwater habitats and also in soil, on rocks and on plants. A few types of cyanobacteria have a symbiotic relationship with fungi forming lichens.

Certain cyanobacteria help to form rigid biogenic structures such as **pisoliths** and **stromatolites**. Both are formed by the organisms growing on a particular surface or substrate to which they gradually bind consecutive layers of very fine sediment and precipitated minerals, eventually forming (especially in stromatolites) a stacked sequence of smooth, wavy and crenulated laminae, often forming mounds. Pisoliths usually form by growth around a moveable object such as a sand grain or shell fragment which may be periodically turned over by current action thus creating an almost concentric layer of laminae.

Stromatolites and pisoliths are locally common in the geological record and in certain areas of the world are being formed today such as at Shark Bay in western Australia. Thermophillic cyanobacteria also produce stromatolitic textures in hot spring areas where they bind detrital grains and precipitated opaline silica to the substrate (see inset below, and section on [The Ancient Environment and Modern Analogues](#)).



Above: Cyanobacterial mat on a sinter apron (in this case the bacterium *Phormidium*) in West Thumb Basin, Yellowstone National Park. The dominantly orange colour is due to the presence of [carotenoids](#) in the photosynthetic bacteria. The view is approximately 1 m across.

Fossil Record

Cyanobacteria comprise the earliest forms of life, their fossils having been found in Archaean Precambrian rocks in western Australia dated at almost 3500 million years old. Some of the best preserved fossil cyanobacteria have been found in cherts (including the Early Devonian Rhynie chert) such as in the Late Proterozoic Bitter Springs Chert in Australia. In many cases it is the structures formed by these organisms, primarily pisoliths and stromatolites, that are often preserved in the fossil record, particularly in limestones and carbonate rocks. Both are common and locally well-developed, for example, in the Carboniferous limestones of Ireland and Derbyshire in England and also in the Upper Jurassic Purbeck

Limestones of southern England.

The Early Devonian Rhynie chert yields a number of fossil micro-organisms and sedimentary textures that may be attributable to cyanobacteria. Most of the latter occur as well-developed stromatolitic structures that are highly comparable with those formed by the growth of cyanobacterial mats on modern sinter terraces and in hot springs (see heading photograph and sections on [Chert Textures](#) and [The Ancient Environment and Modern Analogues](#)). However, because of the paucity of well-preserved diagnostic features, only a few probable cyanobacteria have been formally described and named by [Kidston and Lang \(1921b\)](#), [Croft and George \(1959\)](#) and [D.S. Edwards and Lyon \(1983\)](#); *Archaeothrix contexta*, *Archaeothrix oscillatoriformis*, *Kidstoniella fritschii*, *Langiella scourfeldii*, **Rhyniella vermiformis* and *Rhyniococcus uniformis*. Many other unicellular and multicellular forms of probable cyanobacterial origin are also present but for the lack of sufficient diagnostic features have not been formally described and named.

For the purposes of this resource we will concentrate on the genus described by Kidston and Lang ([1921b](#)), *Archaeothrix*, the morphology of which is outlined below.

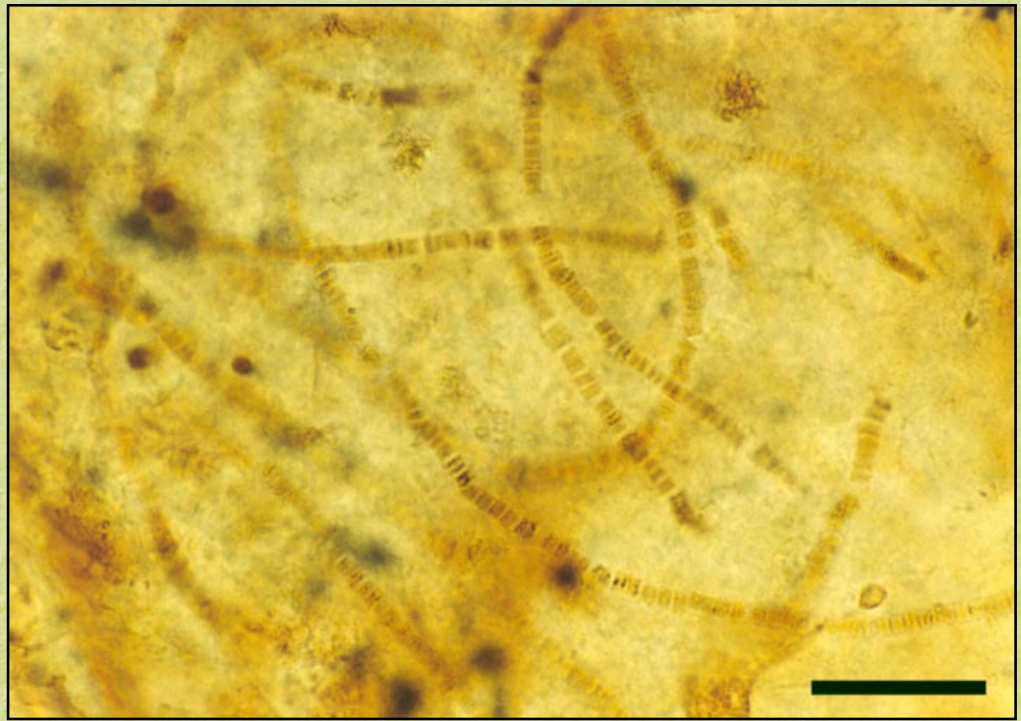
**Note: For the species of probable cyanobacteria described by Croft and George (1959), Rhyniella vermiformis, the generic name was already occupied by the collembolan Rhyniella praecursor.*

Morphology

Archaeothrix

Two species of *Archaeothrix* were originally described by [Kidston and Lang \(1921b\)](#); *Archaeothrix contexta* and *Archaeothrix oscillatoriformi*. Both consist of simple unbranched filaments comprising discoid cells and possessing probable heterocysts. The difference between the two species is mainly in the diameter of the cells. In *A. oscillatoriformi* the cells range from 3µm to 4µm in diameter whereas in *A. contexta* the cells are narrower being approximately 2µm in diameter.

Neither of these cyanobacteria are especially common; *A. oscillatoriformi* has been found within partially decayed stems of *Rhynia* (see inset right) and *A. contexta* has been occasionally found as large masses lying loose within the chert matrix.

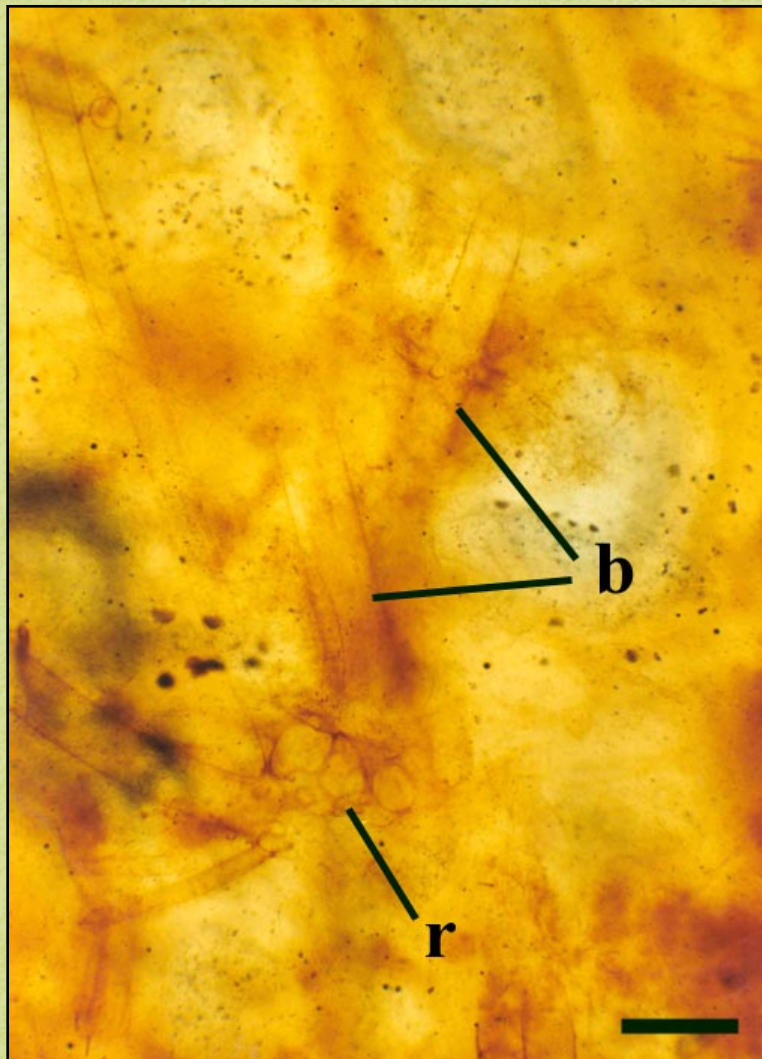


Above: Filaments of *Archaeothrix oscillatoriformi* within a stem of *Rhynia gwynne-vaughanii* (scale bar = 50 μ m).

CONTENTS PAGE



Charophytes



Above: Thin section of Windyfield chert showing branches (**b**) and rhizoids (**r**) of *Palaeonitella cranii* (scale bar = 250 μ m).

[Introduction](#)

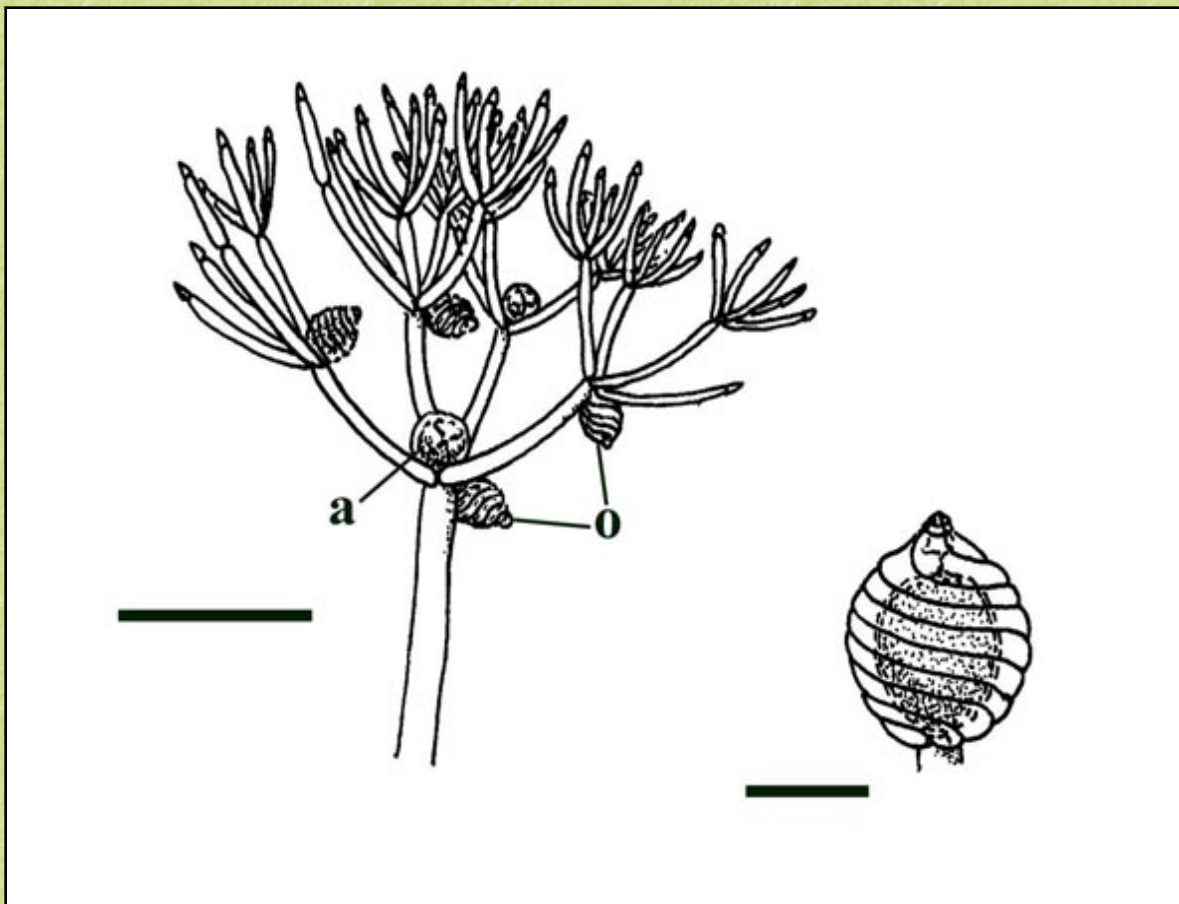
[Fossil Record](#)

[Morphology](#)

Palaeoecology

Introduction

Charophytes or stoneworts are one of the largest and most structurally complex of the green algae, and are thought to be part of the evolutionary lineage that lead to vascular plants ([Kenrick 1994](#)). As green algae, charophytes are sometimes classed within the Chlorophyta but are often classed as a distinct group, the Charophyta. These plants are aquatic, and modern forms are found in many freshwater to brackish habitats such as ponds, lakes, lagoons and streams. The main axes of mature plants comprise a series of multicellular **nodes** interspersed by relatively long single cells or **internodes**. Branches and branchlets grow from individual nodal cells in a whorled arrangement (see inset below). The **gametangia**, or fertile elements of the plant are quite characteristic in charophytes. The female gametangium or **oogonium** is formed from a number of divided cells that grow out from one of the nodes; the outer most cells are elongate and spiral around the oogonium forming a protective sheath (see inset below). The male gametangium or **antheridium** also grows from a nodal cell and is a complex spherical structure usually comprising eight shield-cells, each one enclosing a stalked cell bearing tiny rounded head-cells which in turn bear filaments comprising the cells which produce the spermatozoids. The position of the gametangia on the plants is variable with different charophyte species and can be diagnostic.



Above: Line drawings of a fertile axis of the extant *Nitella gracilis* showing oogonia (o) and antheridia (a) (left) (scale bar = 1mm) and close-up of an oogonium (right) (scale bar = 250µm) (based on [Groves & Bullock-Webster 1920](#)).

As fossils, charophytes can be quite in sediments deposited in suitable environments. It should be noted that the oogonia may be [allochthonous](#) or easily transported, but in instances where the axes of the plant are also preserved it is likely these are more-or-less *in situ* or [autochthonous](#).

Fossil Record

Charophytes are quite well represented in the fossil record from the Tertiary, Cretaceous and Jurassic where they are locally abundant, particularly in limestones and marls deposited in brackish or freshwater settings. In these rocks it is usually the fossilised oogonia that are found (commonly called [gyrogonites](#)). This is because the oogonia are often calcified and are easily preserved as a mineral of calcium carbonate, typically [calcite](#). In some instances, for example in the Upper Jurassic/Lower Cretaceous Purbeck Limestones of southern England, fossil charophyte oogonia are so common, diverse and widespread they can be used as [zone fossils](#) for [biostratigraphy](#) (e.g. [Feist et al. 1995](#)). The

preservation of whole plants is not common, but they can be quite exquisite in their detail (e.g. [Martín-Closas & Diéguez 1998](#)).

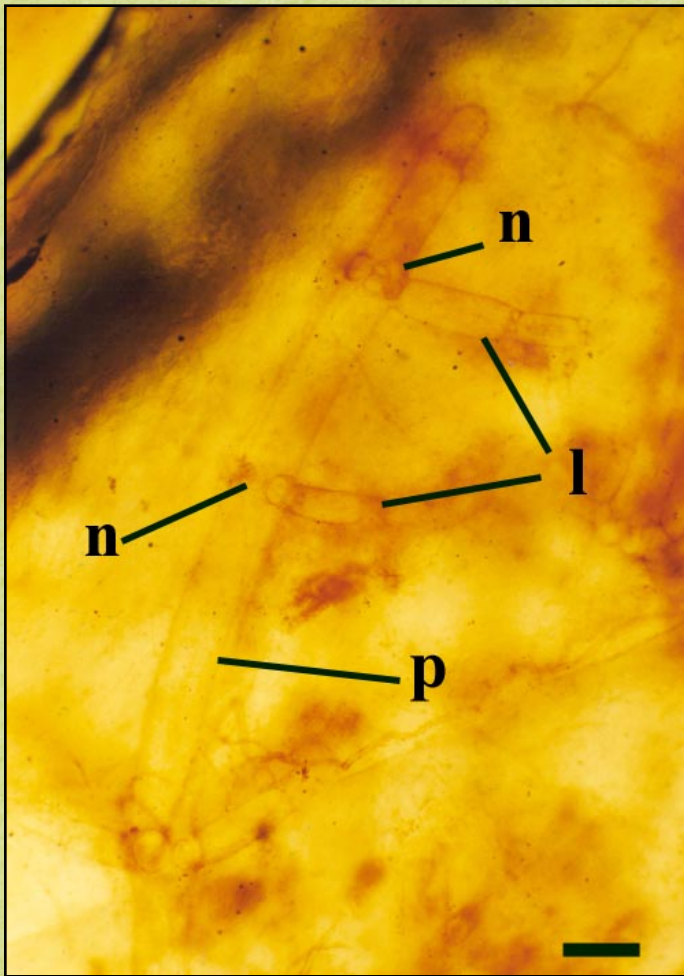
The earliest fossil charophytes have been recorded from the Upper Silurian, though whether or not these are true charophytes is still debated. Early Devonian charophytes have been found exquisitely preserved in the Rhynie chert and were first recorded and described by [Kidston & Lang \(1921b\)](#). The Rhynie charophytes show many similarities with the extant charophyte group, the Nitelleae, and have been assigned to the species *Palaeonitella cranii*. The morphology of *Palaeonitella* is outlined below.

Morphology

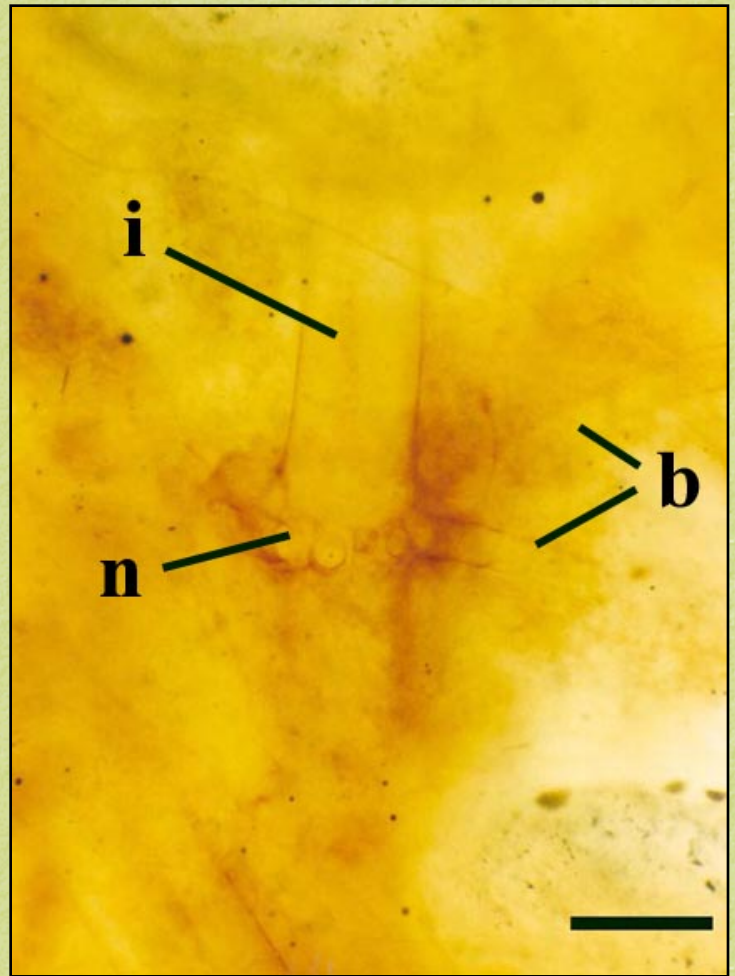
The morphology of *Palaeonitella* is relatively simple, its structure being closely comparable to that of modern Nitelleae (see inset above). An entire reconstruction of the alga has not been published, though much of the plant is known, primarily the branch whorls, rhizoid nodes and possible bulbils. The status of *Palaeonitella* has been questioned by [Tappan \(1980\)](#), but recent discoveries of fertile elements in the chert indicate unequivocally that the plant is a charophyte alga ([Kelman *et al.* in press](#)). The fertile elements will be figured here once published.

Axes

The overall size of the plant is not known, but it comprises upright primary axes that bear regularly spaced clusters of nodal cells with whorls of lateral branches. The spacing of nodal cells or rather the length of the internodes does, however, tend to decrease towards the distal end of the axes (see inset below left). These branches in turn may bear secondary branches. The number of branches or rays in a whorl can be variable. Whorls commonly bearing up to ten secondary rays have been observed on the lateral branches. The primary axes are slender generally being up to 200µm in diameter, lateral branches are conspicuously narrower being up to 100µm in diameter with very fine secondary branches being up to 50µm in diameter (see inset below right). Occasionally the nodal and internodal cells appear **hypertrophic**; mutated and swollen where they have been infested by aquatic fungi ([Taylor *et al.* 1992](#)).



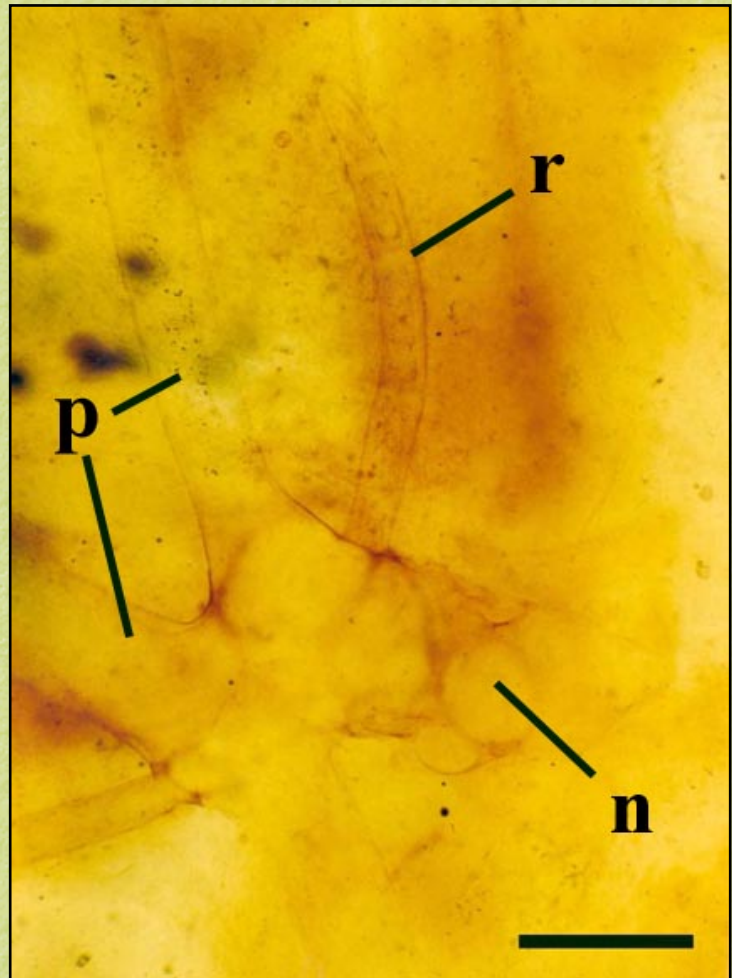
Above: *Palaeonitella cranii* in Windyfield chert showing primary axes (p) with numerous clusters of nodal cells (n) and lateral branches (l) (scale bar = 150µm).



Above: Secondary rays (b) emerging from the nodal cells (n) on a lateral branch of *Palaeonitella cranii*. Internodal cells also shown (i) (scale bar = 150µm).

Rhizoids and Bulbils

At the bases of the primary axes occur tubular cells occasionally displaying oblique septa and nodes. These structures represent the **rhizoids** of *Palaeonitella*. The nodal cells associated with the septa commonly bear small rhizoidal branches (see inset right). These structures are closely comparable to those seen in the rhizoids of extant Nitelleae ([D.S. Edwards & Lyon 1983](#)). Occasionally, conspicuous oval or spherical vesicular structures are seen in connection with these nodal cells. They vary in size, typically ranging between 200µm and 500µm in diameter and represent **bulbils**, another feature seen in some contemporary charophytes.



Right: Close-up of a rhizoid of *Palaeonitella cranii* showing nodal cells (**n**), primary rhizoids (**p**) and rhizoid branches (**r**) (scale bar = 150µm).

Palaeoecology

Palaeonitella was undoubtedly an aquatic plant. It is typically found in chert associated with other aquatic biota, particularly crustaceans, chlorophytic algae and chytrids (tiny aquatic fungi). The enclosing matrix commonly contains coprolites and exhibits a clotted or 'mulm-like' texture. It is likely that the alga was an early coloniser, primarily living in still, relatively shallow freshwater temporary ponds, apparently with rather soft silty and organic-rich substrates. If *Palaeonitella* had a similar ecology to that of most modern Nitelleae it is likely the waters it inhabited were generally quite alkaline. Most extant charophytes tolerate waters with a range of between pH 6 and pH 9. In a few charophyte-

bearing chert horizons, many of the specimens preserved *in situ* exhibit an orientation with axes appearing to be swept or bent over in a particular direction. This probably represents current alignment ([Fayers and Trewin in press](#)); maybe *Palaeonitella* could also tolerate areas of slow moving water, perhaps colonising rather sheltered areas in the cool distal reaches of run-off channels from hot springs.

CONTENTS PAGE



Crustaceans

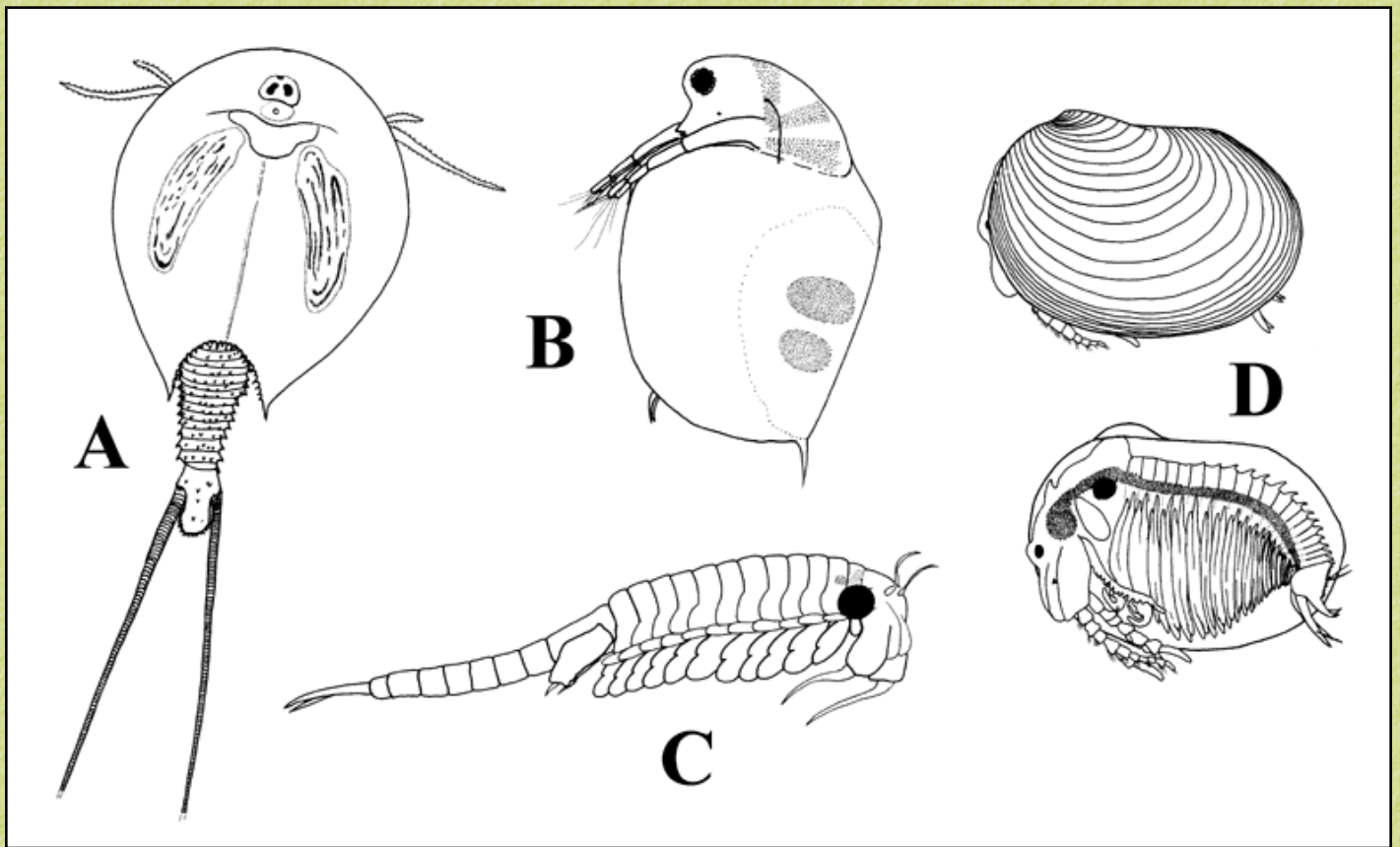
[Introduction](#)

[Relationships](#)

[Identity](#)

Introduction

Several types of aquatic crustaceans are present in the Rhynie chert. Crustaceans are distinguished from all other arthropods by the fact they possess two pairs of antennary appendages in front of the mouth together with the presence of biramous limbs. Crustaceans form a large and highly diverse group of arthropods that have adapted to a number of different environments ranging from deep sea to shallow marine (e.g. shrimp, crab and lobster) to brackish water and freshwater habitats (e.g. crayfish, waterfleas and tadpole shrimps) and in some instances are fully terrestrial (e.g. the modern woodlouse). The crustaceans found in the Rhynie chert appear to have been aquatic, freshwater-living animals and all appear to belong to the Class Branchiopoda of which the tadpole shrimp *Triops*, the water-flea *Daphnia* and the fairy shrimp (e.g. *Artemia*) are modern examples (see inset below).



Above: Examples of extant branchiopod crustaceans (not shown to scale): **A**: a notostracan or 'tadpole shrimp'; **B**: a cladoceran or 'water flea'; **C**: an anostracan or 'fairy shrimp'; **D**: a conchostracan or 'clam shrimp' (the lower image showing the animal with the left valve or 'shell' removed) (after [McLaughlin 1980](#)).

Branchiopods ('gill-feet'), sometimes called phyllopods ('leaf-feet'), are generally very small crustaceans characterised by having a variable number of delicate foliaceous and lobed, relatively uniform trunk or body limbs; some types possess a single dorsal cephalothoracic shield, or a bivalve shell (see inset above). They also commonly possess numerous somites or body segments. The abdomen lacks limbs and the tail ends in distinct furcal rami. They tend to occur in continental aquatic habitats ranging from fresh to hypersaline waters.

The earliest known branchiopod, *Rehbachella kinnekullensis* ([Walossek 1993](#)), from the Orsten rocks of the Upper Cambrian Alum Shale in Sweden, was a marine crustacean. Non-marine branchiopods are known to range from the Early Devonian to the present day and as such those from the Rhynie chert are among the earliest known representatives of this group.

Relationships

The branchiopods, including those found in the Rhynie chert, second only to another group of marine

crustaceans called the cephalocarids, are considered to be the most primitive of living crustaceans. This is suggested by the generally homomorphic nature of their somites or body segments and multi-filamentous biramous limbs. The Rhynie branchiopods are particularly important since not only do they appear to represent a lineage from the 'early crustacean design' but they also give an insight into the timing of the adaptation of these crustaceans to continental and freshwater habitats.

Identity

Until recently, only one crustacean was known from the Rhynie chert, *Lepidocaris rhyniensis* ([Scourfield 1926](#)). This comprises the only member of the extinct branchiopod order Lipostraca.

Recently, however, a number of new branchiopod crustaceans have come to light, including *Castracollis wilsonae* ([Fayers and Trewin 2003](#)) from the Rhynie chert, a branchiopod closely related to the Calmanostraca (e.g. Tadpole Shrimps); and for the first time branchiopod larvae or **nauplii** have been discovered in the Windyfield chert. Another enigmatic branchiopod-like crustacean, *Ebullitiocaris oviformis*, with a univalve 'carapace' from the Rhynie and Windyfield cherts has recently been described by Lyall I. Anderson and others ([Anderson et al. 2004](#)), and will be added to this resource in due course.

Click on the name to see images and a description of the animal.

- [Lepidocaris rhyniensis](#)
- [Castracollis wilsonae](#)
- [Branchiopod larvae](#)
- [Ebullitiocaris oviformis](#)

CONTENTS PAGE



Rhynie Chert Flora:

Basic Information on the Higher Land Plants

Introduction

There are seven genera of terrestrial macroplants described from the Rhynie chert. Of these, five are considered to be true vascular plants, displaying [tracheids](#) in the water-conducting tissue, but the status of *Aglaophyton* and *Nothia*, which appear to lack tracheids, remains in doubt. [Rhynia](#) and [Aglaophyton](#) are the most abundant, [Asteroxylon](#), *Nothia* and [Horneophyton](#) fairly common, and [Trichopherophyton](#) and [Ventarura](#) scarce. These plants seldom exceed 20cm in height.

Aglaophyton major

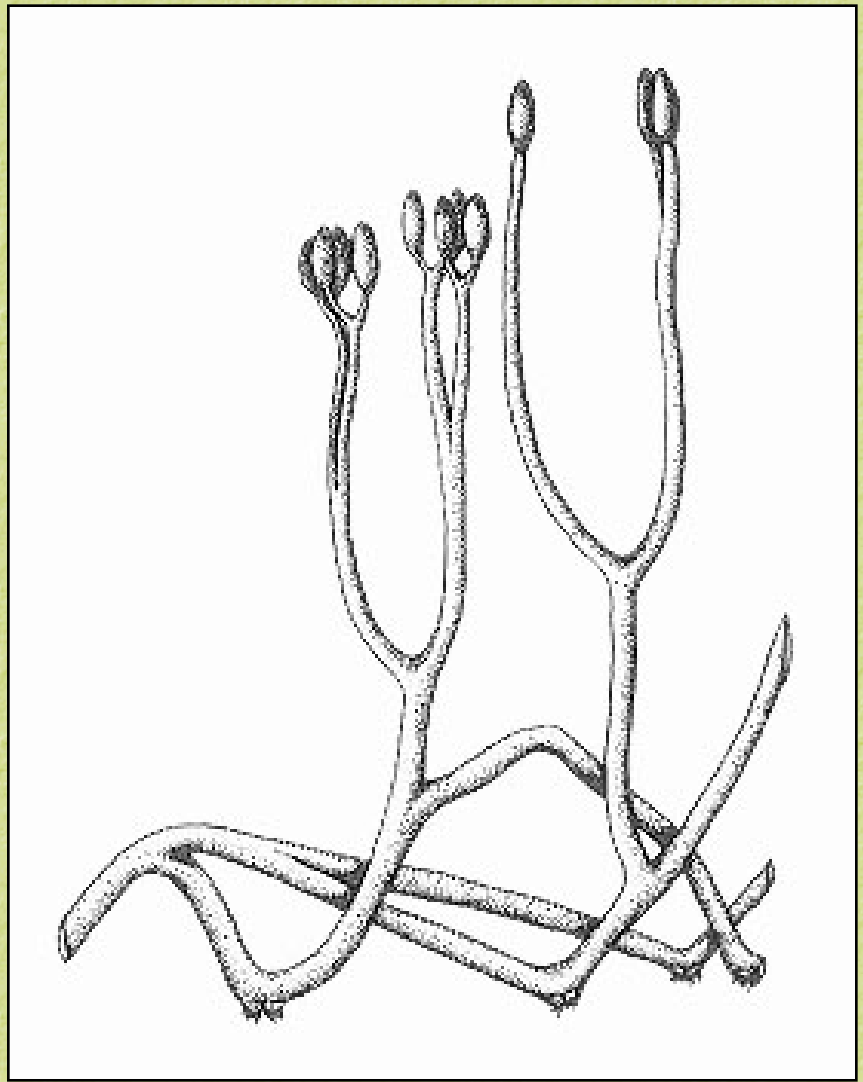
A simple plant with a creeping rhizome and smooth, naked, upright axes. This plant grew to around 15cm in height and its axes were up to 6mm in diameter. The rhizomes occasionally had bulges bearing tufts of rhizoids for taking up water and nutrients. Branching was mainly [dichotomous](#) and fertile axes terminated with pairs of fusiform [sporangia](#) (see inset right). *Aglaophyton* was a [sporophyte](#), the male [gametophyte](#) stage of the plant, called *Lyonophyton rhyniensis*, was much smaller, the upright axis ending in a cup-like structure that bore the [antheridia](#).

The water-conducting cells in this plant did not have thickenings like true vascular plants, being more similar to those seen in

some modern **bryophytes** (a group including mosses and liverworts). The simply branched naked stems are more comparable with the extinct **rhyniophytes** and as such its systematic position remains unknown.

Aglaophyton grew mainly on dry, litter covered, organic-rich substrates, on its own as monotypic stands or with other Rhynie plants, though it seems to have required wet conditions for germination.

Right: Reconstruction of *Aglaophyton major* with fertile upright axes bearing fusiform sporangia (after [D. S. Edwards 1986](#)).



Asteroxylon mackiei

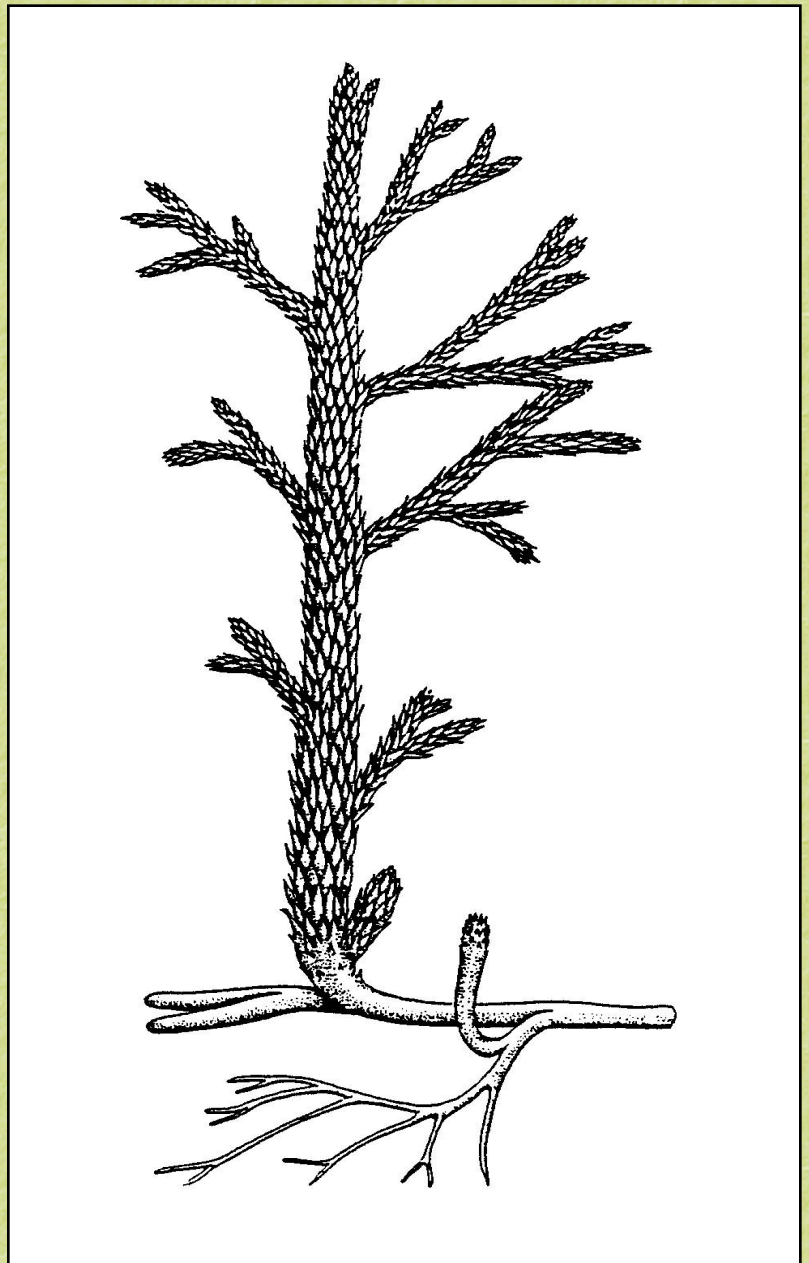
One of the more advanced and complex Rhynie plants, *Asteroxylon* had an extensive subterranean system of branching rhizomes. The aerial upright axes of the plant grew to about 40cm in height with a maximum diameter of 12mm. Branching was **dichotomous** and **monopodial**. The aerial axes possessed scale like 'leaves' or **enations** (see inset right). Fertile axes bore stalked kidney-shaped **sporangia** attached between the 'leaves' and the stem.

In cross-section the water-conducting strand of this plant forms a characteristic star-shape pattern from which smaller strands radiate to meet the base of the 'leaves'.

Asteroxylon is a member of a group of plants called the **lycophytes** which includes modern club mosses.

Asteroxylon mainly grew in organic-rich soils as part of a diverse community together with other Rhyne plants and could probably tolerate quite dry habitats.

Right: Reconstruction of *Asteroxylon mackiei* (after [Kidston & Lang 1921a](#)).



Horneophyton lignieri

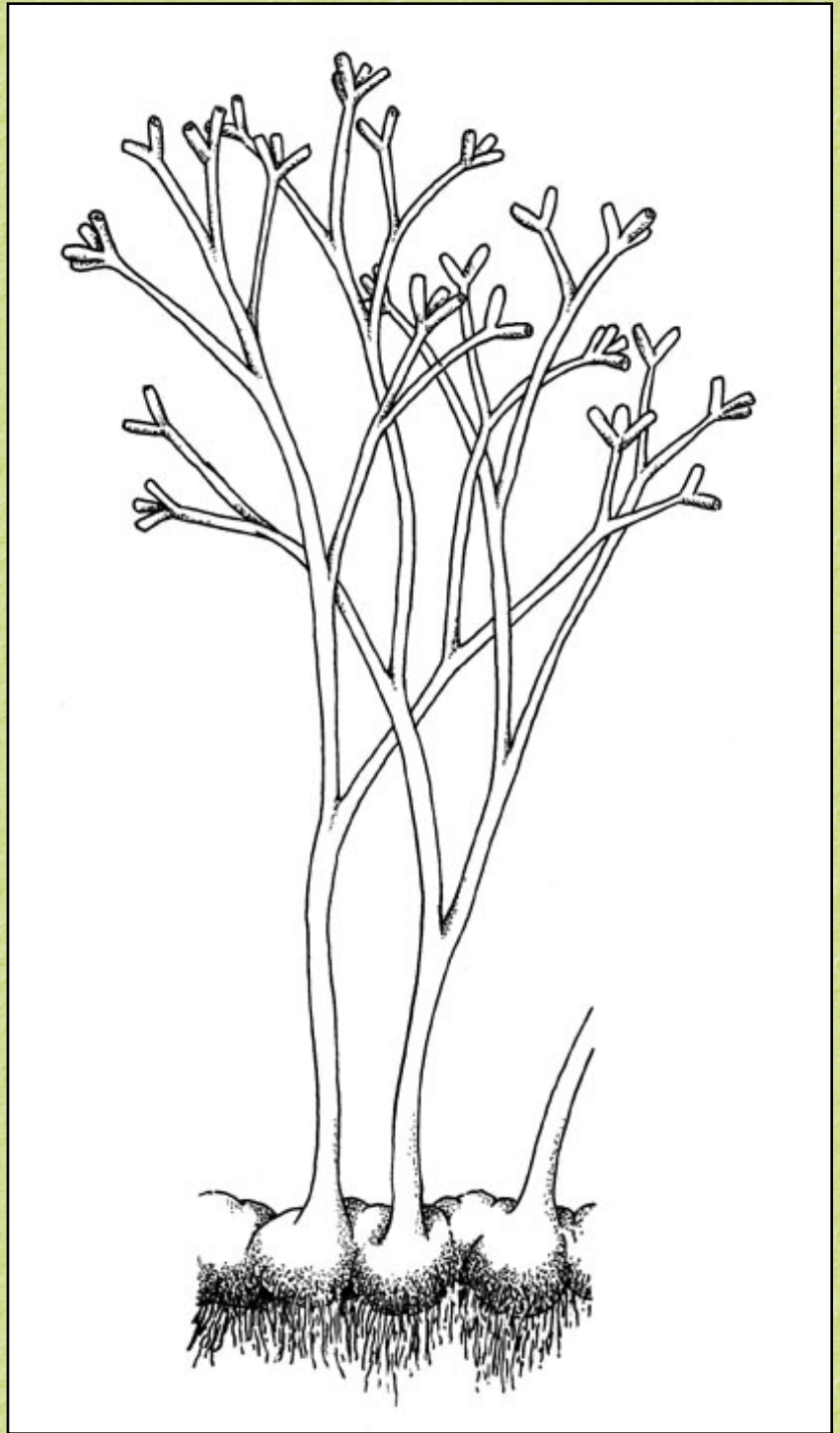
Horneophyton comprised naked upright aerial axes with a subterranean bulbous, corm-like rhizome bearing rhizoid tufts. The aerial axes were smooth and naked, growing up to 20cm in height with a maximum diameter of 2mm. Branching was mainly **dichotomous** and repeated. Fertile axes terminated in branched, tubular **sporangia** (see inset right) that internally possessed a central 'strand' or **collumella**. *Horneophyton* was a **sporophyte**, the female **gametophyte** stage of the plant, called *Langiophyton*

mackiei, was much smaller, the upright axis ending in a cup-like structure that bore the [archegonia](#).

The water-conducting cells in this plant, like true vascular plants, possessed thickenings. However, the presence of a collumella in the sporangia shows similarities with **bryophytes** (a group including mosses and liverworts). As such the systematic position of this plant remains uncertain.

Horneophyton preferred to grow on sandy and organic-rich substrates, often on its own as monotypic stands and probably flourished in damp to wet conditions.

Right: Reconstruction of *Horneophyton lignieri* showing bulbous corm-like rhizomes with rhizoids; dichotomously branching aerial axes with branching terminal sporangia (based on [Eggert 1974](#)).



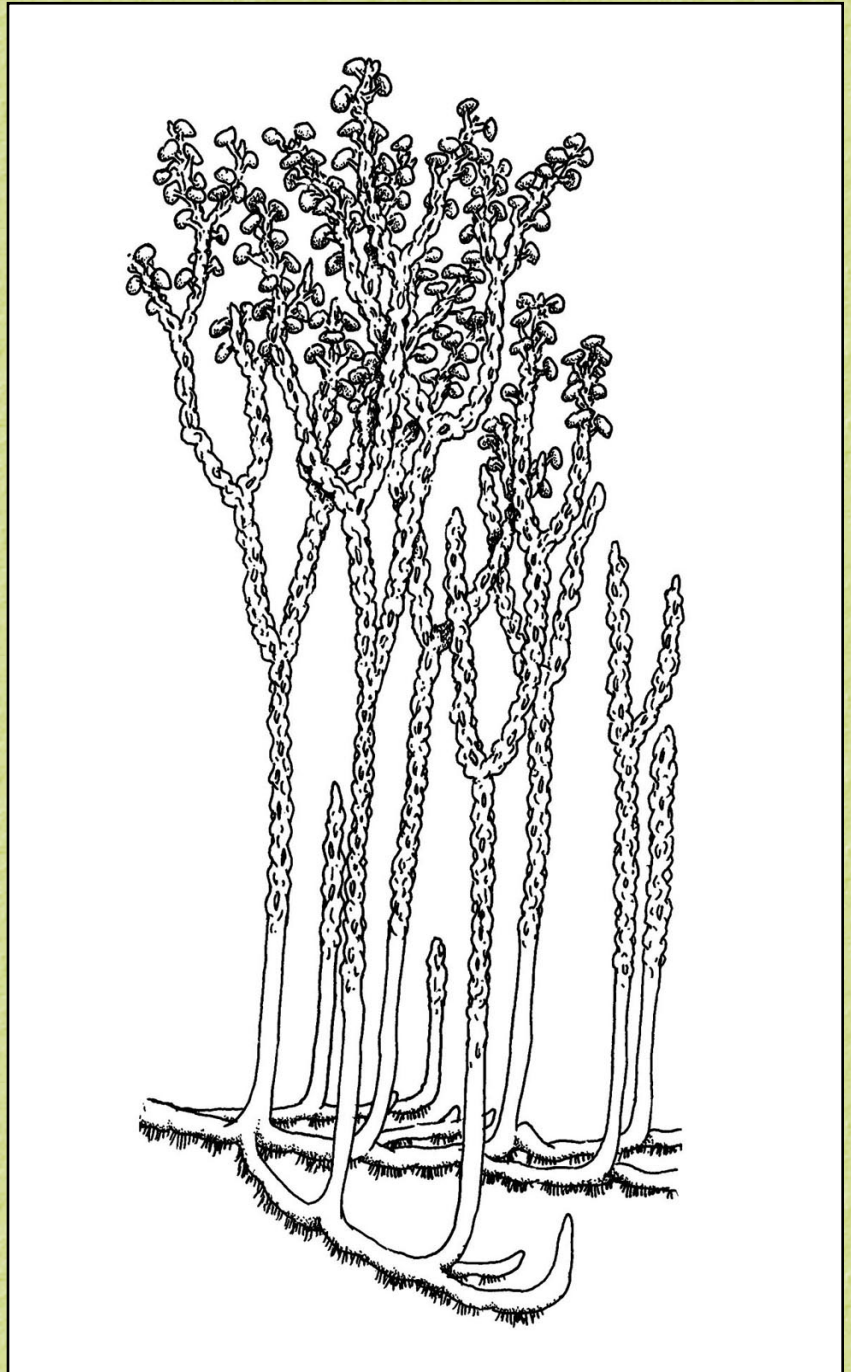
Nothia aphylla

Nothia possessed a laterally extensive, branched subterranean rhizome network, bearing a ventral ridge supporting tufts of rhizoids (see inset right). Locally branches turned upright to form the aerial axes. These axes were naked with a very irregular surface and showed repeated **dichotomous** branching, giving the plant a thicket-like appearance. Fertile terminal axes bore lateral kidney-shaped **sporangia** attached by stalks. *Nothia* was a **sporophyte**, the male **gametophyte** stage of the plant, called *Kidstonophyton discoides*, was much smaller, the upright axis ending in a cup-like structure with tubular outgrowths bearing the **antheridia**.

The water-conducting cells in this plant did not have thickenings like true vascular plants, being similar to those seen in some modern **bryophytes** (a group including mosses and liverworts). The stalked, lateral kidney-shaped sporangia are comparable with **zosterophylls** and the simply branched naked axes with **rhyniophytes** and as such its systematic position remains unknown.

Nothia preferred to grow in sandy soils and plant litter, on its own or with other plants.

Right: Reconstruction of *Nothia aphylla* showing primary rhizomal axes with upright stems passing upwards into aerial axes with distinctive irregular epidermis. Terminal branches locally bearing lateral sporangia (based on [Kerp et al. 2001](#)).



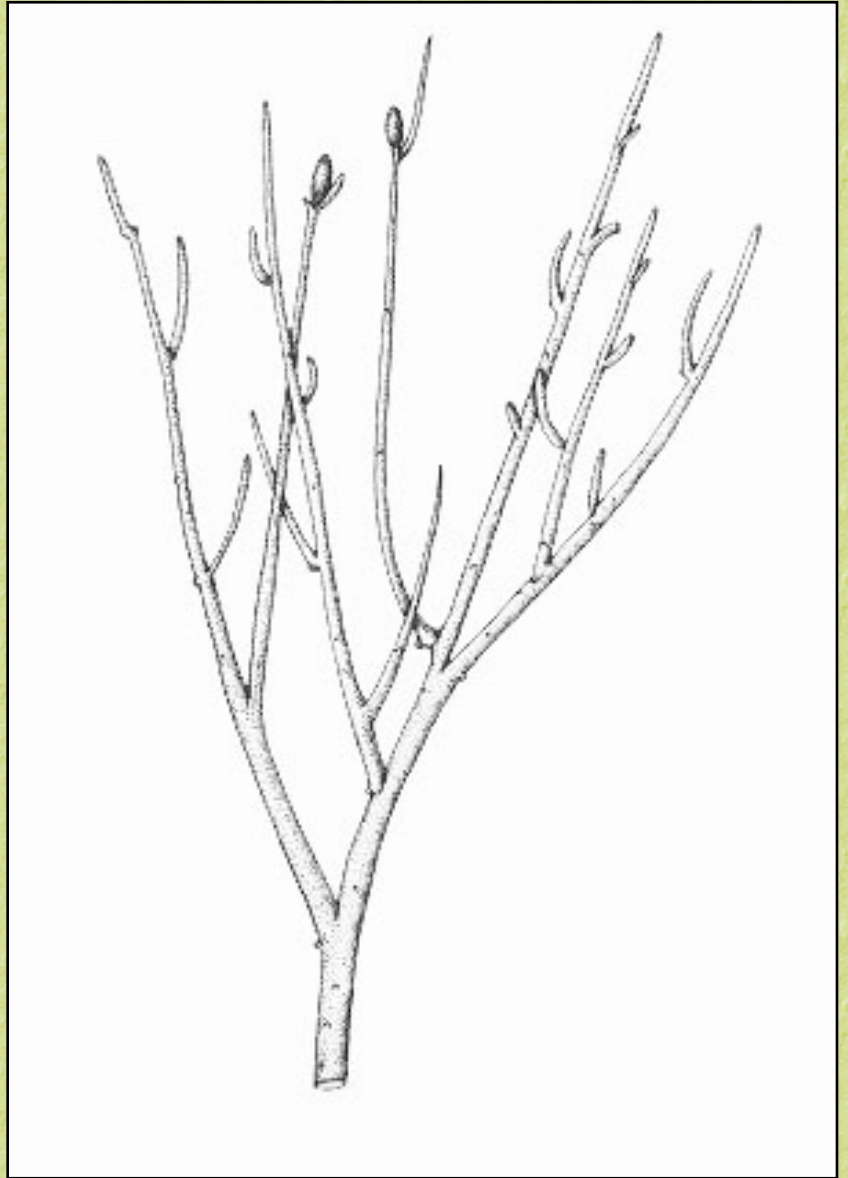
Rhynia gwynne-vaughanii

Rhynia was one of the most common plants in the Rhynie ecosystem. Like *Aglaophyton* it was completely subaerial with creeping, branched rhizomal axes and smooth, naked upright axes (see inset right). The plant grew to a height of about 20cm, individual axes being up to 3mm in diameter. Branching was **dichotomous** and **adventitious** or **monopodial**. The plant possessed curious **hemispherical projections** on its axes, those on the rhizomes bearing tufts of rhizoids. Fertile axes bore terminal fusiform **sporangia**.

Rhynia is a member of an extinct group of primitive plants called the **rhyniophytes**, characterised by their simple branching and naked stems.

Rhynia commonly grew in thickets, typically on its own as monotypic stands and was often an early coloniser of well-drained sinter and sandy substrates. It also grew with other plants and was tolerant of a wide range of habitats.

Right: Reconstruction of *Rhynia gwynne-vaughanii* showing two fertile branches with terminal sporangia (rhizomal axes not shown) (after [D. S. Edwards 1980](#)).



Trichopherophyton teuchansii

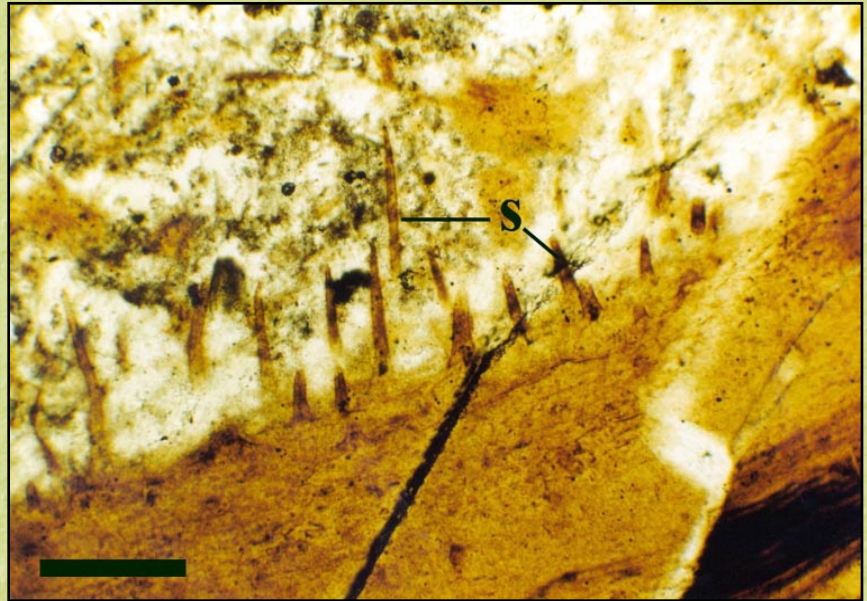
Trichopherophyton was quite a rare plant in the Rhynie ecosystem. The height of this plant is uncertain but the aerial axes had a maximum diameter of 2.5mm. Branching was mainly **dichotomous**. Subterranean rhizomal axes were smooth with small blunt-tipped emergences which probably acted as rhizoids. Aerial axes bore curious **spiny projections** (see inset right) and the tips of the axes displayed a feature called **circinate vernation**. Fertile terminal axes bore lateral, stalked, kidney-shaped **sporangia**, also bearing spiny projections.

The water-conducting cells in this plant, like true vascular plants, possessed thickenings. This together with the shape and position of the sporangia suggest *Trichopherophyton* belongs to a group of plants called the **zosterophylls**.

Trichopherophyton was a late coloniser of organic-rich substrates, always growing with other Rhynie plants as part of a diverse flora.

Ventarura lyonii

Ventarura is the most recently discovered higher land plant from the Windyfield chert. The height of this plant is uncertain but was at least 12cm and the aerial axes had a maximum diameter of 7.2mm. Branching was mainly **dichotomous** and repeated (see inset right). Subterranean rhizomal axes were smooth with small blunt-tipped emergences which probably acted as rhizoids. Aerial axes bore curious **peg-like projections**. Characteristically, internally the axes had a



Above: Longitudinal section of an aerial axis showing conspicuous unicellular spinose projections (s) (scale bar = 500 μ m).

lignified middle layer to the cortex called the **sclerenchyma**. Fertile terminal axes bore lateral, stalked, kidney-shaped **sporangia**.

The water-conducting cells in this plant, like true vascular plants, possessed thickenings. This together with the shape and position of the sporangia suggest *Ventarura* belongs to a group of plants called the **zosterophylls**.

The palaeoecology of *Ventarura* is not fully known, but it probably grew in localised patches, at least in the vicinity of freshwater ponds and probably in sandy and organic-rich substrates.

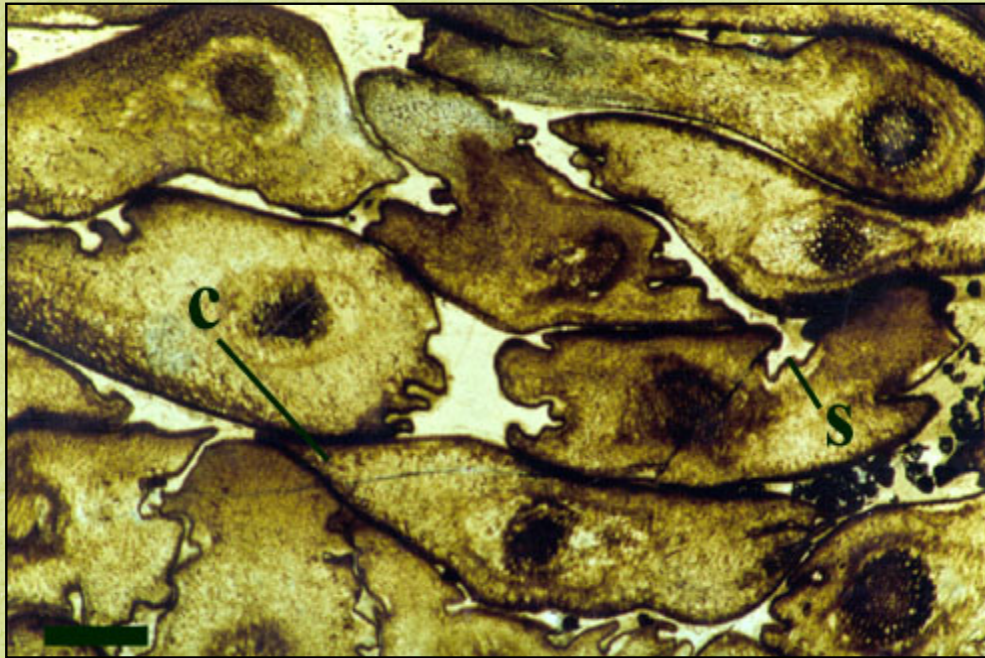


Above: Polished slab of Windyfield chert showing aerial and rhizomal axes of *Ventarura lyonii*. Many of these axes are inverted and therefore not in growth position.

CONTENTS PAGE



Aglaophyton



Above: Slightly oblique transverse section through prostrate stems of *Aglaophyton major*. The stems show partial decay, shrinkage (s) and minor compaction (c) (scale bar = 1mm).

[Introduction](#)

[Morphology](#)

[Relationships](#)

[Palaeoecology](#)

Introduction

Aglaophyton was originally described as *Rhynia gwynne-vaughanii* by [Kidston and Lang in 1917](#). In 1920, however, they split the genus into two species and assigned this plant to the species *Rhynia major*. [D. S. Edwards \(1986\)](#) re-interpreted the plant, based primarily on the lack of thickenings on the xylem cells (a feature originally attributed to

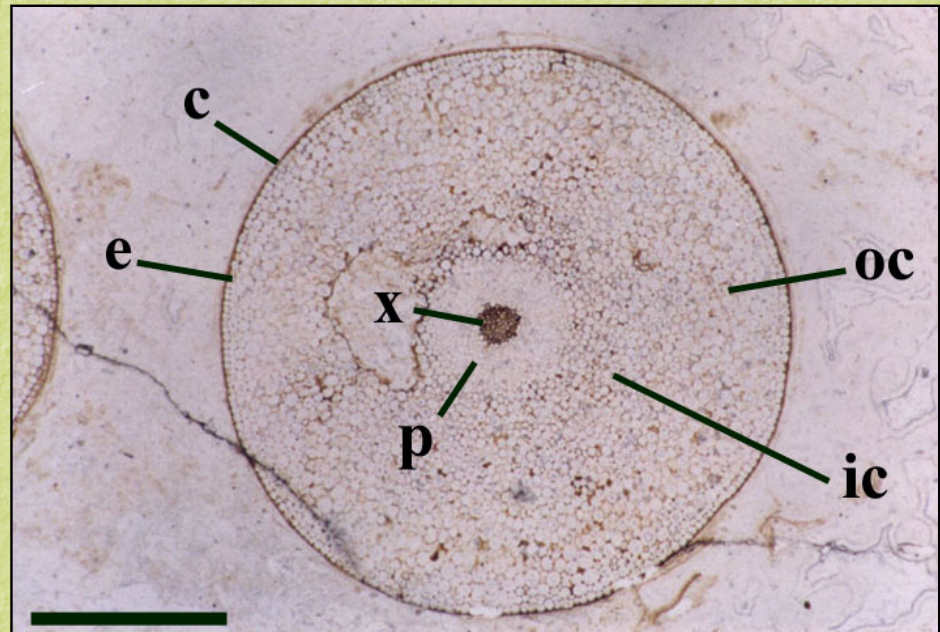
poor preservation by [Kidston and Lang \(1920a\)](#)) and renamed the plant *Aglaophyton major*. Both the male and female gametophytes of *Aglaophyton* have been identified though, to date, only the male gametophyte, *Lyonophyton rhyniensis*, has been formally described and named ([Remy & Remy 1980b](#)). The overall morphology and palaeoecology of *Aglaophyton* is outlined below.

Morphology

'Aerial' Axes

The axes of this plant are superficially similar to *Rhynia gwynne-vaughanii* though there are a number of distinct differences. They exhibit a maximum diameter of 6mm and the plant probably attained a height of around 15cm. Branching in *Aglaophyton* is predominantly [dichotomous](#) (the angle of dichotomy being between 60 and 90⁰) with minor [adventitious](#) branching.

The [epidermis](#) of *Aglaophyton* is smooth and the [cuticle](#) appears deeply flanged. The [stomata](#) are flanked by two reniform or kidney-shaped guard cells. Most of the axis comprises the [cortex](#) (see inset right), this is divided into two, the division occasionally marked by a distinct brown layer.

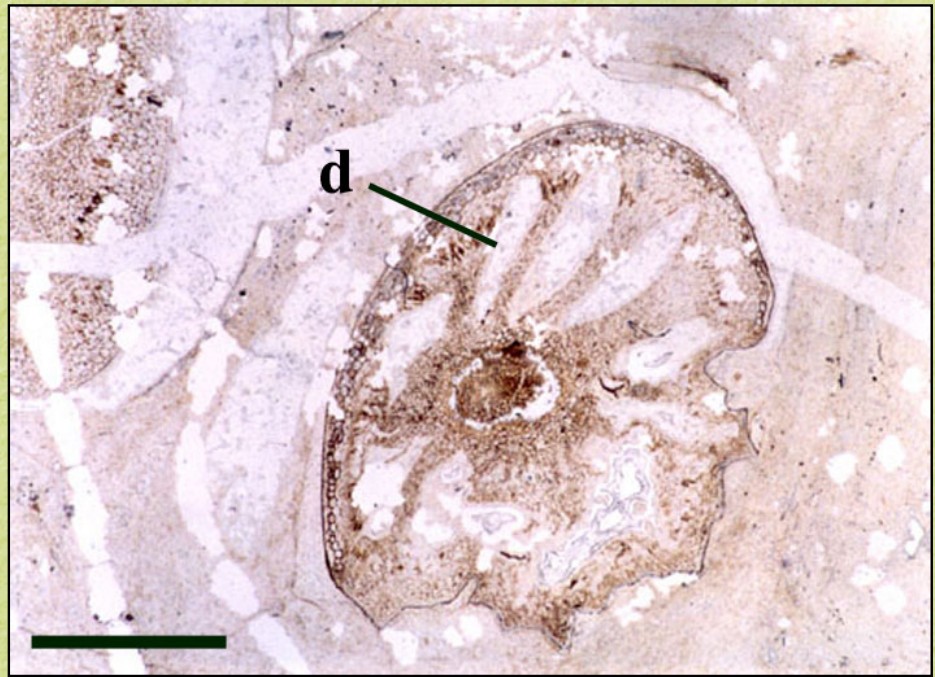


Above: Transverse section through an axis of *Aglaophyton* showing the cuticle (**c**), epidermis (**e**), outer cortex (**oc**), inner cortex (**ic**), phloem (**p**) and xylem strand (**x**) (scale bar = 2mm).

The outer cortex comprises closely packed elongate cells of more or less uniform size. The inner cortex comprises more loosely packed cells with a well-developed inter-cellular air space network. The dark layer is formed by the presence of vesicular arbuscular [mycorrhizae](#) within intracellular air spaces. Partially decayed *Aglaophyton* axes exhibit a characteristic cellular decay pattern in the cortex (see inset right).

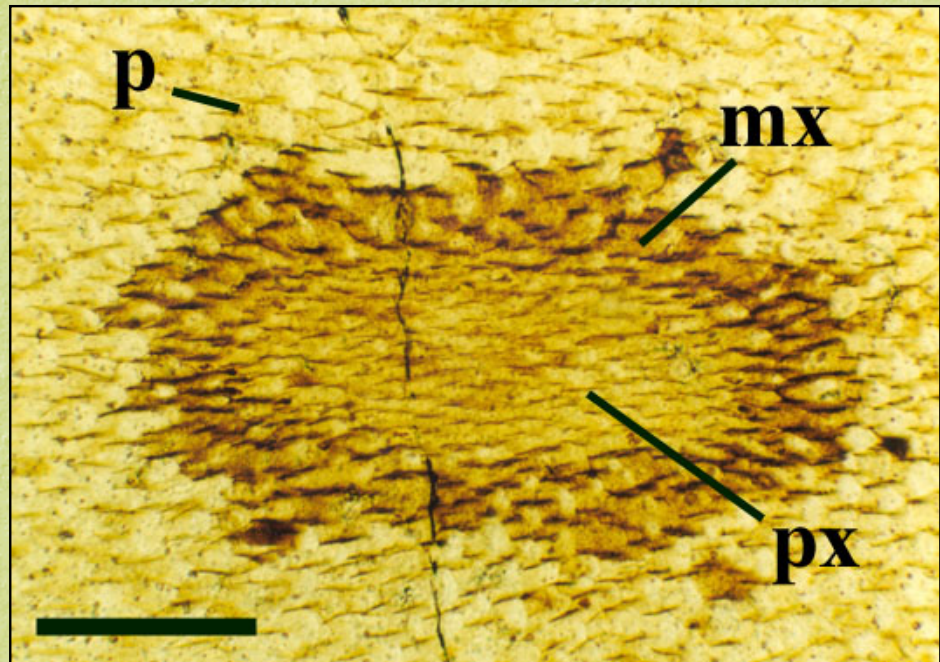
Right: Transverse section through an *Aglaophyton* axis showing the characteristic cellular decay pattern in the cortex (**d**) (scale bar

= 2mm).



The '[vascular strand](#)' of *Aglaophyton* comprises a zone of '[phloem](#)' surrounding a central [xylem](#) strand. The phloem is of uniform thickness, the individual cells showing acute apices. The xylem is [terete](#) and displays an [endarch](#) maturation pattern (see inset right). A significant difference between the xylem in this plant and that in *Rhynia* is the fact that the xylem cells in *Aglaophyton* exhibit no thickenings.

Right: A slightly oblique cross-section through the 'vascular tissue' of *Aglaophyton*. The phloem (**p**) surrounds the central xylem strand which shows the smaller, thin-walled protoxylem cells (**px**) surrounded by larger thicker-walled metaxylem cells (**mx**) (scale bar = 250µm).



Rhizomal Axes

Aglaophyton exhibits creeping rhizomes that in life were subaerial, laying directly on the substrate surface. These branch repeatedly locally turning upwards and passing into the 'aerial' axes described above. The rhizomal axes are cylindrical, naked and generally exhibit a similar morphology and internal anatomy to the upright aerial axes, also bearing stomata. Unicellular rhizoids are present as tufts on 'bulges' on the ventral side of the rhizomes, the bulges formed by elongate cortical cells ([D.S. Edwards 1986](#)).

Right: Rhizoids (**r**) on an *Aglaophyton* rhizomal axis (scale bar = 200 μ m).

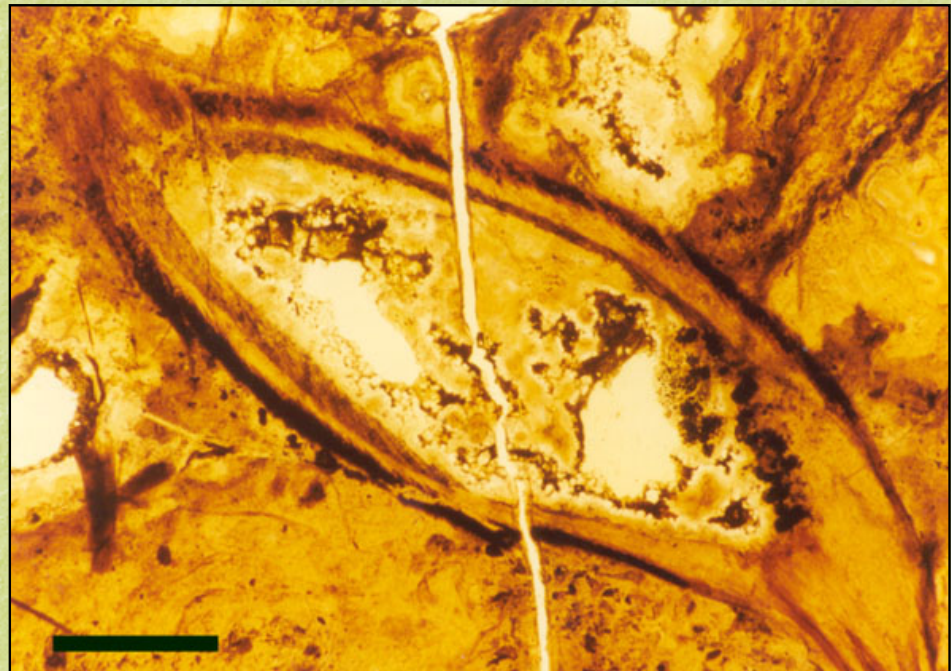


Sporangium

The [sporangia](#) of *Aglaophyton* are elongate and fusiform in shape and relatively large with a maximum size of 12mm by 4mm (see inset right). The dehiscence mechanism was determined by [Remy \(1978\)](#); it would split obliquely along its length.

The disposition of the sporangia is terminal and they usually occur in pairs above the last point of dichotomy (see reconstruction below).

Right: An empty sporangium of *Aglaophyton* (scale bar = 2mm).



The spores of *Aglaophyton* are [retusoid](#) and have smooth walls with a trilete mark located in a thinning of the [exine](#). They are relative large, ranging in diameter from 64 μ m to 85 μ m. These spores are comparable to species of the spore genus *Retusotriletes*. The spores of *Aglaophyton* have often been found preserved at various stages of germination ([Lyon 1957](#)) (see the section on [spores](#) for images of some of these).

Gametophytes

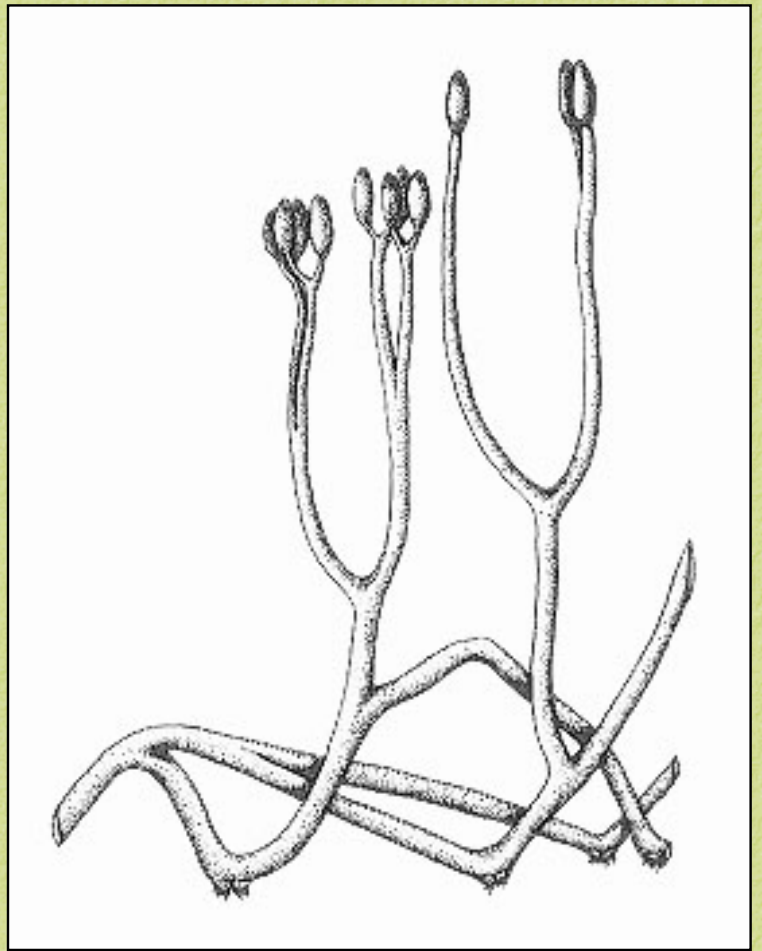
Both male and female gametophytes of this plant have been identified though to date only the male form has been formally described. The male gametophyte has been assigned the name *Lyonophyton rhyniensis* ([Remy and Hass 1980b](#)). This free-living gametophyte of *Aglaophyton* consists of an aerial axis that widens and terminates in a conspicuous cup-like structure which bears the [antheridia](#) (see inset right). Although smaller in size, the axis of the gametophyte is very similar to the sporophyte in its anatomy



Right: Longitudinal section of the male gametophyte *Lyonophyton rhyniensis* bearing antheridia (**a**). Click on the image for a close up! (scale bar = 1mm) (Copyright owned by University Münster).

Reconstruction

Right: Diagrammatic reconstruction of the sporophyte *Aglaophyton major* (after [D.S. Edwards 1986](#)) showing the nature of the creeping rhizome with localised rhizoid tufts; predominant dichotomous branching and fertile axes bearing a number of terminal fusiform sporangia.



Right:
Model of
*Aglaophyton
major*,
sculpted by
Stephen



Relationships

The systematic position of *Aglaophyton*, like a number of other Rhynie plants, remains unresolved because it shows a mixture of anatomical and morphological features that are not typical of any one group of plants. It shows many features characteristic of the **rhyniophytes**, a group of primitive plants, known only from fossils, showing simply branched naked stems of which *Rhynia* is an example. The water-conducting cells of the xylem strand do not show thickenings and as such are more reminiscent of the [hydroids](#) of some **bryophytes** (a group of plants including mosses and liverworts). Since the xylem of *Aglaophyton* does not possess true tracheids, this suggests it is not a true vascular plant.

Palaeoecology

Aglaophyton was a common plant and significant component of the Rhynie ecosystem during the Early Devonian. It appears to have preferred growing on **litter-covered, organic-rich surfaces** and was never a primary coloniser of sinter substrates, though the creeping rhizomal axes of *Aglaophyton* probably allowed it to occupy large surfaces of substrate. It occasionally grew as monotypic stands but is often seen associated with other plants, particularly *Nothia*, *Asteroxylon*, *Horneophyton* and occasionally *Rhynia*.

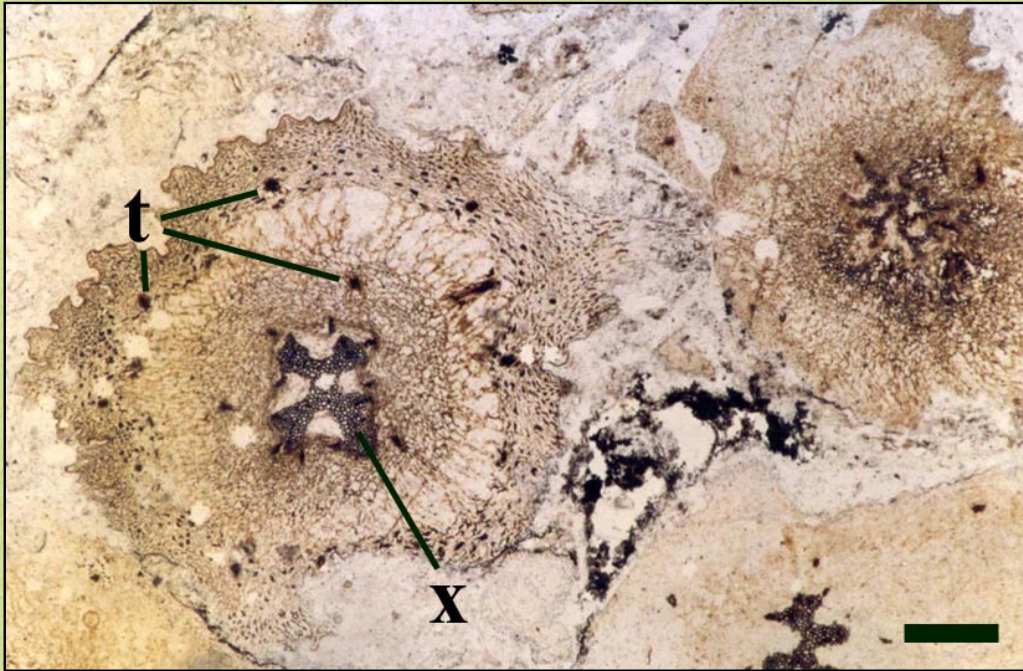
Since *Aglaophyton* exhibits stomata on the rhizomal axes as well as the upright aerial axes, it seems likely that the plant colonised mainly **dry substrates**. The fact that the cuticle and stomata of *Aglaophyton* display adaptations to prevent water loss suggests it could also **tolerate periods of drought** ([Powell 2000b](#)).

However, the matrix of chert beds containing *Aglaophyton* in growth position occasionally contain the charophyte *Palaeonitella*, in association with the freshwater crustacean *Lepidocaris* and the 'aerial' axes of the plant may display infestation by chytrids (**chytridomycetes**) which are a type of tiny, simple fungi that thrive in damp and especially aquatic conditions. Another feature noted by [Remy and Hass \(1996\)](#) is the association of germinating *Aglaophyton* spores with these aquatic elements. Although the plant could probably also tolerate humid or damp conditions, this does not necessarily mean that *Aglaophyton* lived in standing water, perhaps these particular beds represent instances where areas colonised by the plant were occasionally flooded. It does seem likely, however, that **wet conditions may have been necessary for spore germination**.

CONTENTS PAGE



Asteroxylon



Above: Transverse cross-sections through aerial axes of *Asteroxylon mackiei* showing stellate xylem strand (x) and 'leaf traces' (t) (scale bar = 1mm).

[Introduction](#)

[Morphology](#)

[Relationships](#)

[Palaeoecology](#)

Introduction

Asteroxylon, one of the better known Rhynie plants, was originally described by [Kidston and Lang \(1920b\)](#) and assigned the name *Asteroxylon mackiei*. They noted fertile elements probably belonging to *Asteroxylon* within their material; however, the fertile elements of the sporophyte were not finally resolved until [Lyon \(1964\)](#) discovered

sporangia in organic connection with the plant and he concluded that the fertile axes observed by Kidston and Lang were in fact of another new plant, *Nothia aphylla*. To date the gametophytes of *Asteroxylon* remain unknown. The overall morphology and palaeoecology of *Asteroxylon* is outlined below.

Morphology

Aerial Axes

The aerial axes of *Asteroxylon* exhibit a maximum diameter of 12mm and possess characteristic 5mm long scale-like 'leaves' or **enations** surrounding each axis (see inset below right). *Asteroxylon* is perhaps the largest of the known plants from the chert, in life probably attaining a height above ground of about 40cm (it's rhizomes penetrating the substrate to a depth of up to 20cm). Branching is **dichotomous** and **monopodial**.

One of the characteristic features of *Asteroxylon* are the scale like enations that emerge from the **epidermis** in a spiral arrangement around the axes. These are not true leaves since they do not possess a vascular strand (see inset right). The **cuticle** on both axes and enations bear abundant **stomata** with distinctive dark-coloured guard cells. The surface of the epidermis of the enations varies from smooth to papillate whereas that of the axes is smooth.

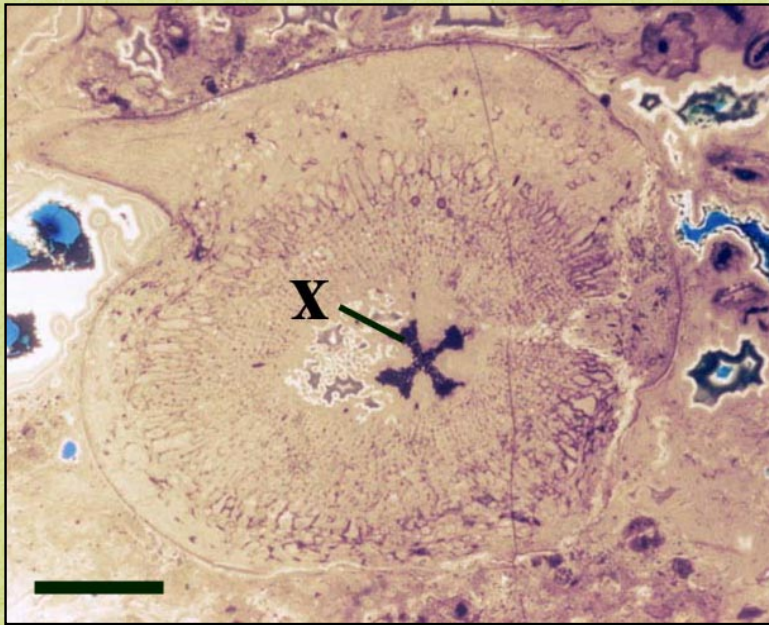


Right: Longitudinal section of the outer cortex and epidermis of an aerial axis of *Asteroxylon mackiei* showing three non-vascularised scale-like enations or 'leaves' (e) (scale bar = 2mm).

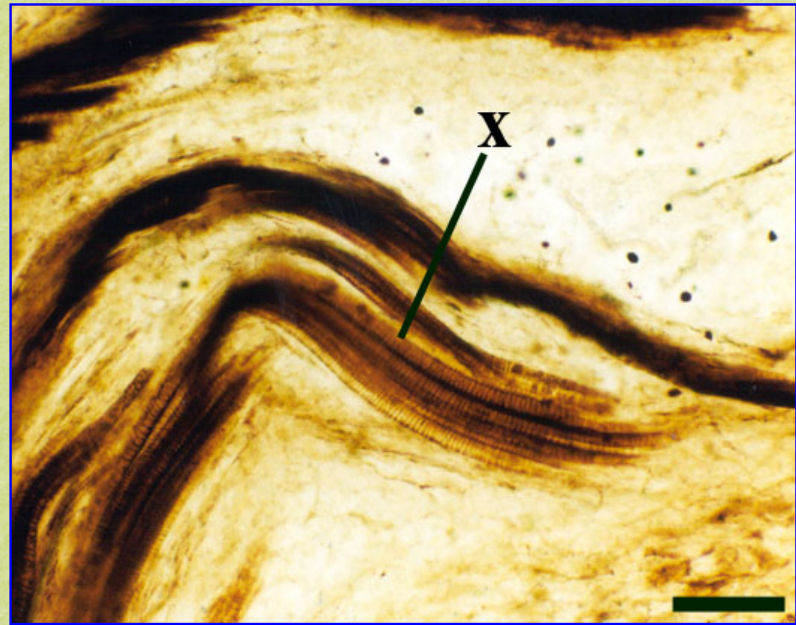
The **cortex** may be divided into a narrow outer zone of closely packed cells and a broader inner cortex that can be further subdivided into three zones: an outer and inner layer of compact cells with a trabecular middle layer of elongate cells with a well-developed inter-cellular air space network. Occasionally the inner zones of the cortex display fungal infestation (see insert below right).

The **vascular strand** is quite distinctive. *Asteroxylon* possess an **actinostele**, in other words the vascular strand

appears star shaped or **stellate** in transverse cross-section (see insert below left and heading photograph). The **xylem** is **exarch** to locally **mesarch** where the protoxylem occurs at the ends of the 'lobes' of the actinostele, and displays spiral thickenings (see insert below right). **Phloem** tissue is best developed between the 'lobes' of the xylem strand. 'Leaf traces' are often seen where vascular tissue splits from the central stele. These traces end at the bases of the enations.



Above: Transverse cross-section through a prostrate aerial axis of *Asteroxylon* showing the distinctive lobed stellate xylem strand (x) (scale bar = 2mm).



Above: Slightly oblique longitudinal cross-section of the xylem strand of *Asteroxylon* (x) showing spiral thickenings. Click on the image for a close up! (scale bar = 500µm).

Rhizomal Axes

The rhizomes of *Asteroxylon* display a diameter of up to 4.2mm, they are naked, lack rhizoids and branch repeatedly. The epidermis of the rhizomes is papillate. The cortex of *Asteroxylon* is divided into three zones; an outer zone of closely packed cells, the inner zones characteristically infected by fungi. The rhizomes exhibit an elliptical exarch xylem strand with spiral thickenings (see inset right).

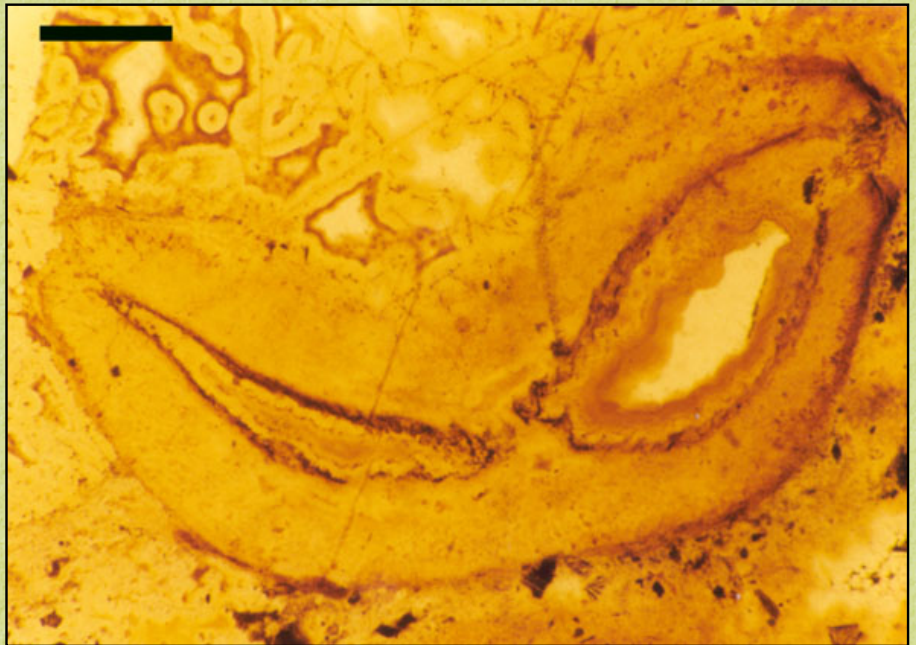
Right: Transverse cross-section through three rhizomal axes of *Asteroxylon* (scale bar = 2mm).



Sporangium

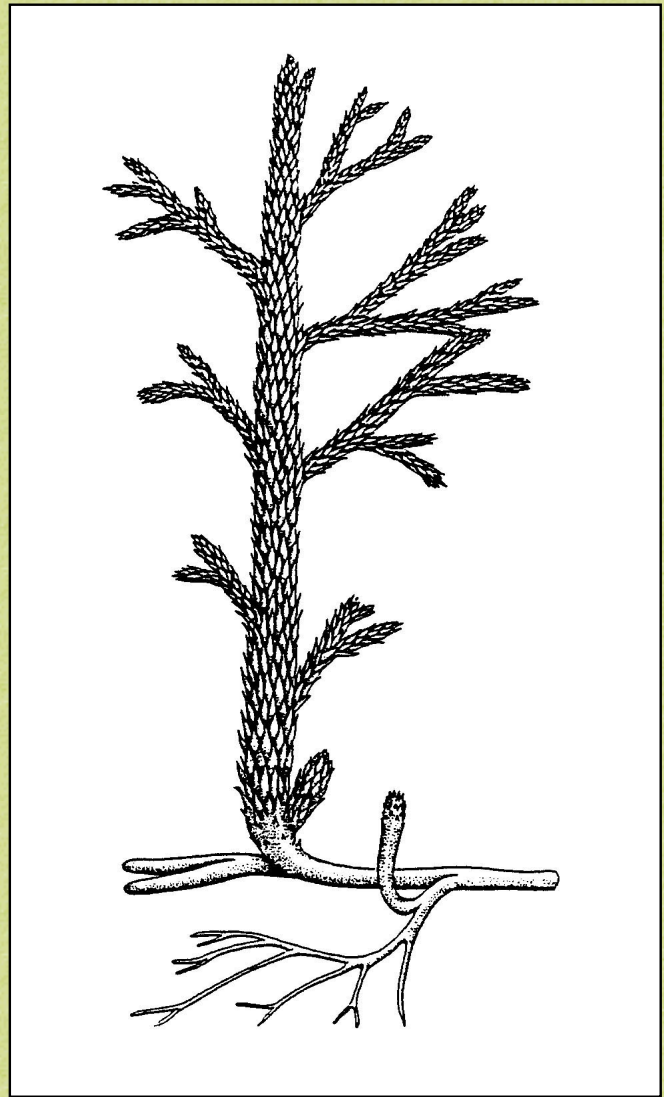
The **sporangia** of *Asteroxylon* were first described by [Lyon \(1964\)](#). Though many anatomical details remain unresolved, the sporangia are reniform (kidney-shaped), rather flattened medially, with a marginal dehiscence mechanism (see inset right). The maximum dimensions for a single sporangium are 7mm by 2.5mm. Their disposition on the aerial axis is rather scattered, each sporangium being laterally attached via a stalk emerging between the angle of an enation and the main stem.

Right: A medially flattened sporangium of *Asteroxylon* (scale bar = 1mm).



Reconstruction

Right: Reconstruction of *Asteroxylon mackiei* by [Kidston and Lang \(1920b, 1921a\)](#) showing aerial axes, dichotomous and lateral branches with scale-like 'leaves' or enations and naked cylindrical rhizomes.





Left: Model of *Asteroxylon mackiei* sculpted by Stephen Caine for the Rhynie Research Group, University of Aberdeen.

Relationships

Asteroxylon is rather more anatomically complex than the other known Rhynie chert plants. The plant is considered a true **lycophyte** (a group of plants which includes the 'club mosses') based on the structure of its **apical meristem** (Hueber 1992) together with the characteristic exarch actinostele and the lateral disposition of the sporangia. The spirally thickened and reticulate cell walls of the xylem cells are also typical of lycophytes (Kenrick & Crane 1991). Modern lycophytes are also characterised by their enations or **microphylls** which possess a single vascular strand. In *Asteroxylon* the vascular trace stops at the base of the enations which may suggest the plant represents an intermediate stage in the evolution of lycopsid leaves.

Palaeoecology

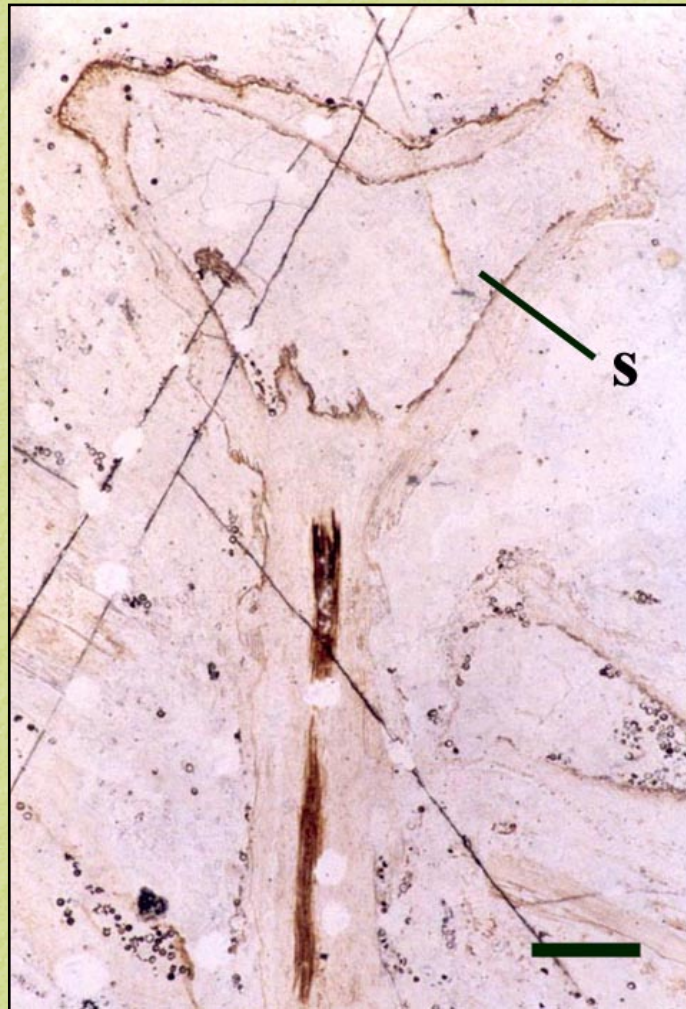
Asteroxylon is quite commonly encountered in a number of chert beds and apparently formed a significant component of the Rhynie flora during the Early Devonian. Its rhizomes are usually found traversing plant litter and the plant is primarily found to occur *in situ* with two or more other genera, commonly *Nothia*, *Rhynia* and *Aglaophyton* and occasionally *Ventarura*. It seems therefore that *Asteroxylon* primarily lived as **part of a diverse plant community** rather than as monotypic stands ([Powell et al. 2000b](#)).

The fact that *Asteroxylon* possesses an extensive, substrate-penetrating 'root' system suggests it was capable of exploiting larger volumes of water and nutrients than the other Rhynie plants. Also the presence of microphylls increase the surface area of the aerial axes. This would have created a larger photosynthetic surface and with the greater density of stomata the plant possesses would also have meant greater efficiency in gaseous exchange and transpiration. It is likely that *Asteroxylon* could tolerate quite **dry habitats** compared with most of the other Rhynie flora..

CONTENTS PAGE



Horneophyton



Above: Aerial axis of *Horneophyton* showing sporangia (s) (scale bar = 1mm).

[Introduction](#)

[Morphology](#)

[Relationships](#)

Introduction

Horneophyton was originally described by [Kidston and Lang \(1920a\)](#) and assigned the name *Hornea lignieri*, however, the generic name was already occupied and it was therefore renamed *Horneophyton lignieri* by [Barghoorn and Darrah in 1938](#). Although one of the better known Rhynie plants, its systematic position is still very much debated. As well as the sporophyte, the female gametophyte of this plant, *Langiophyton mackiei*, has also been described ([Remy and Hass 1991c](#)). The overall morphology and palaeoecology of *Horneophyton* is outlined below.

Morphology

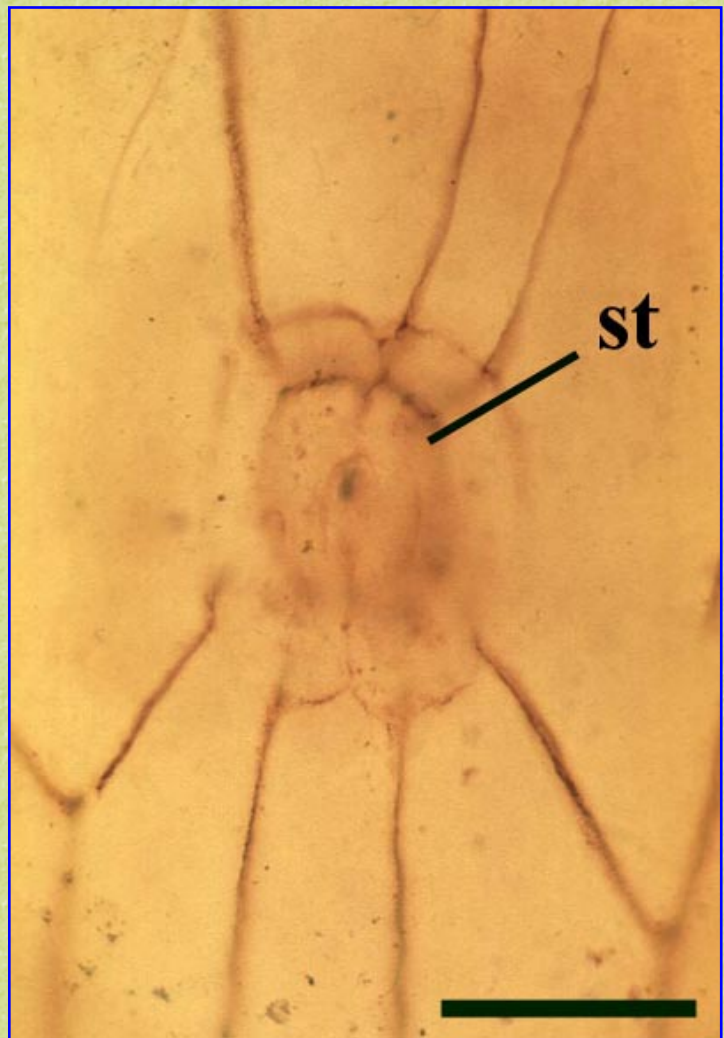
Aerial Axes

The aerial axes of *Horneophyton* display a maximum diameter of 2mm and are cylindrical and naked. The plant probably reached a maximum height of 20cm. The branching of *Horneophyton* is [dichotomous](#) and repeated.

The [cuticle](#) of the [epidermis](#) displays a regular arrangement of elongate cells. [Stomata](#) are relatively rare and are enclosed by distinctly modified cells ([Hass 1991](#)) (see inset right). The [cortex](#) is generally poorly preserved and where present appears to be undivided.

The [vascular tissue](#) comprises an [endarch xylem](#) strand with irregular spiral and reticulate thickenings. This is surrounded by a zone of thin-walled

cells interpreted as **phloem**. The vascular strand becomes less distinct towards the base of the aerial axis (see inset below right).



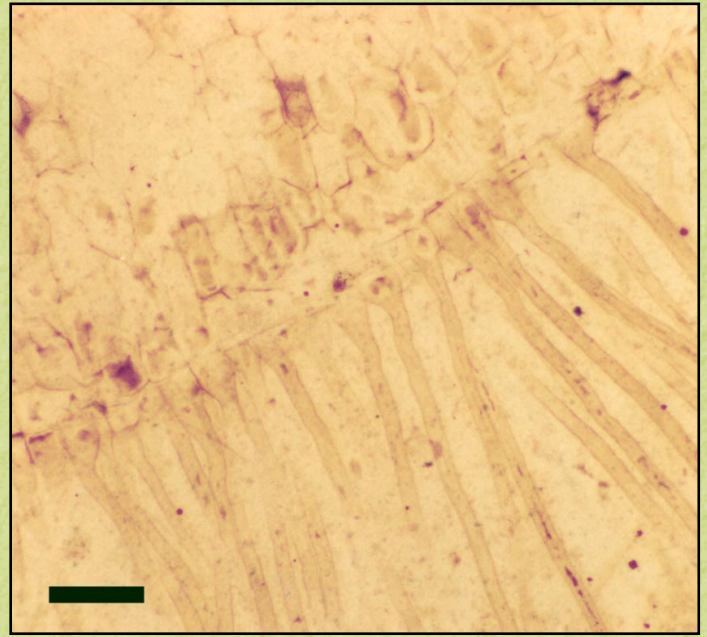
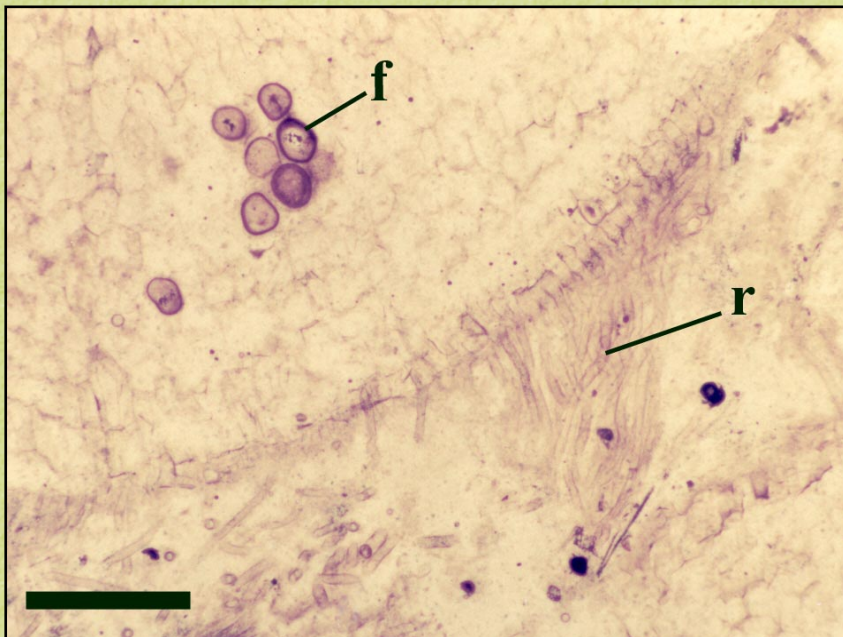
Above: A stoma in the cuticle of *Horneophyton lignieri* (**st**) surrounded by modified cells (click on the image for a cross section!) (scale bar = 20 μ m) (Copyright owned by University Münster).

Rhizomal Axes

The 'rhizomal axes' of *Horneophyton* distinguish it easily from all other Rhynie plants. They comprise a corm-like lobe at the base of the aerial axis with numerous unicellular rhizoids emerging from the epidermis (see insets right and below right). A vascular strand is not present in the rhizome, emerging from **parenchymatous** tissue upwards from the base of the aerial axis.

Occasionally, fungal activity is evident in the cortex of the rhizome (see inset below left).

Right: *Horneophyton lignieri* showing base of an aerial axis with vascular strand (**v**) and the corm-like rhizome (**c**) bearing numerous rhizoids (**r**) (scale bar = 2mm).



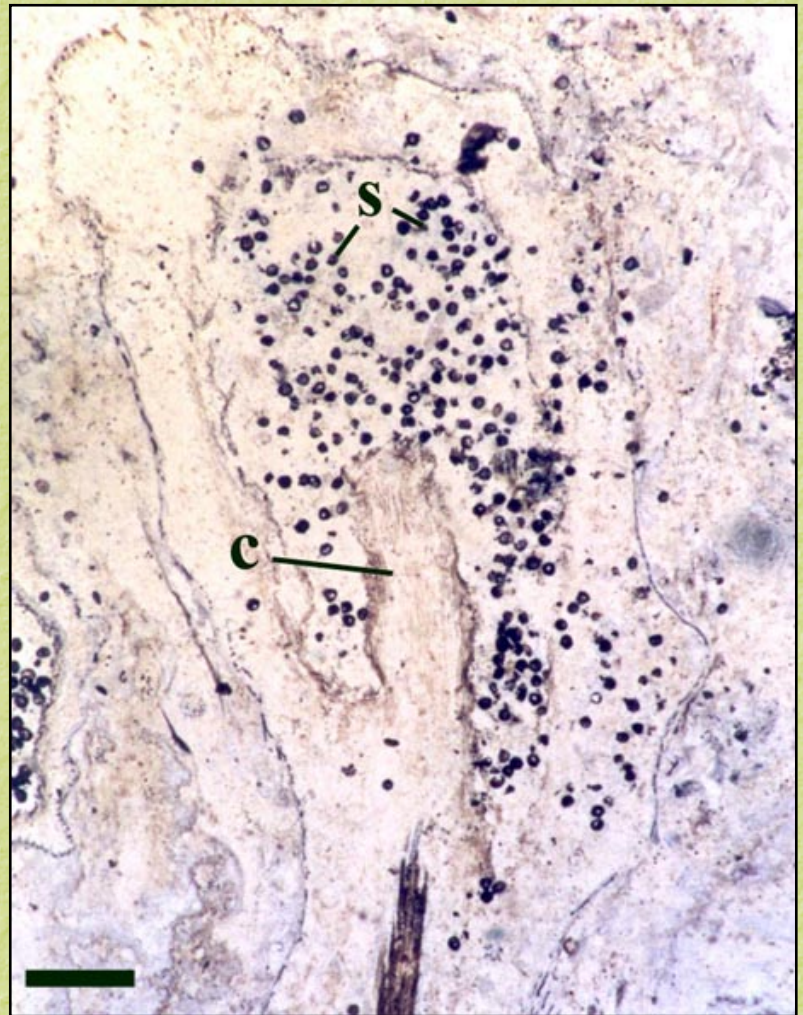
Above: *Horneophyton* rhizome showing fungal cysts in the cortex (f) and rhizoids (r) (scale bar = 500µm).

Above: Close up on the rhizoids of *Horneophyton lignieri* (scale bar = 100µm).

Sporangium

The **sporangia** of *Horneophyton* are very distinctive. Their disposition on the aerial axes is terminal. They are cylindrical to globose in shape and may be branched displaying a number of connected lobes (see heading photograph and reconstruction below); the maximum dimensions of a single sporangium being 7.5mm by 5mm. The dehiscence mechanism is apical and particularly well-developed ([Eggert 1974](#); [El-Saadawy & Lacey 1979a](#)).

One of the more curious features of the sporangia of *Horneophyton* is the presence of a central columella in the sporangial cavity (see inset right).



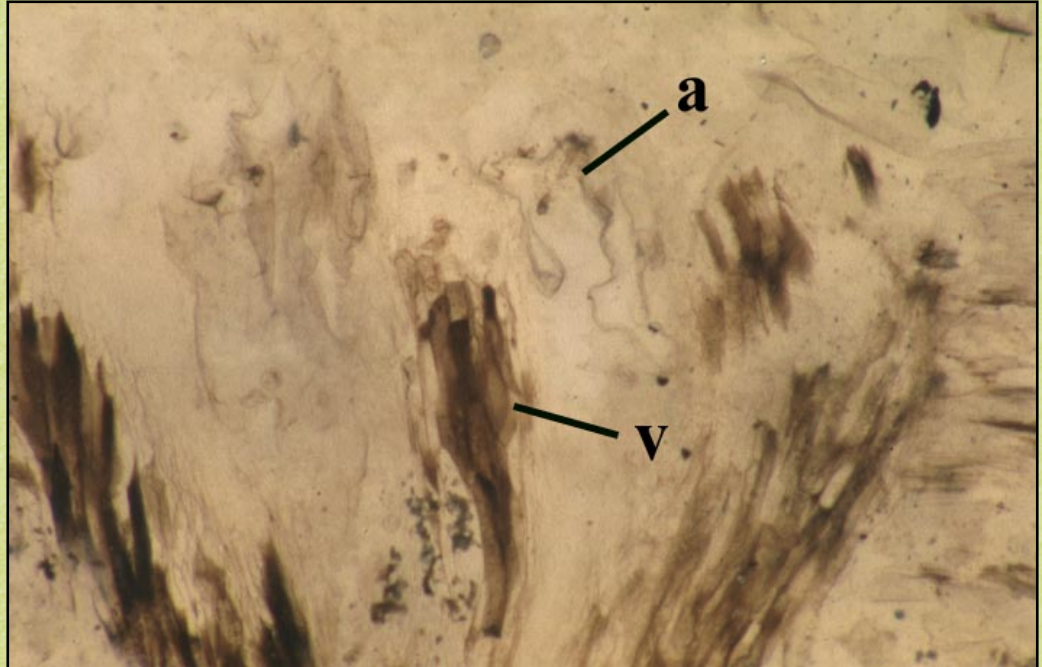
Above: A sporangium of *Horneophyton* showing spores (s) and the central columella (c) (scale bar = 500µm).

The *in situ* **spores** of *Horneophyton* are relatively well known ([Bhutta 1973a](#)) and may be assigned to the spore species *Emphanisporites decoratus*. These vary between 42 and 54µm in size, the proximal face bearing a distinct trilete mark. The proximal face of the spore is also ornamented with radial ribs; the distal face characteristically showing an apiculate ornament, typically of closely spaced micron-sized

spines.

Gametophytes

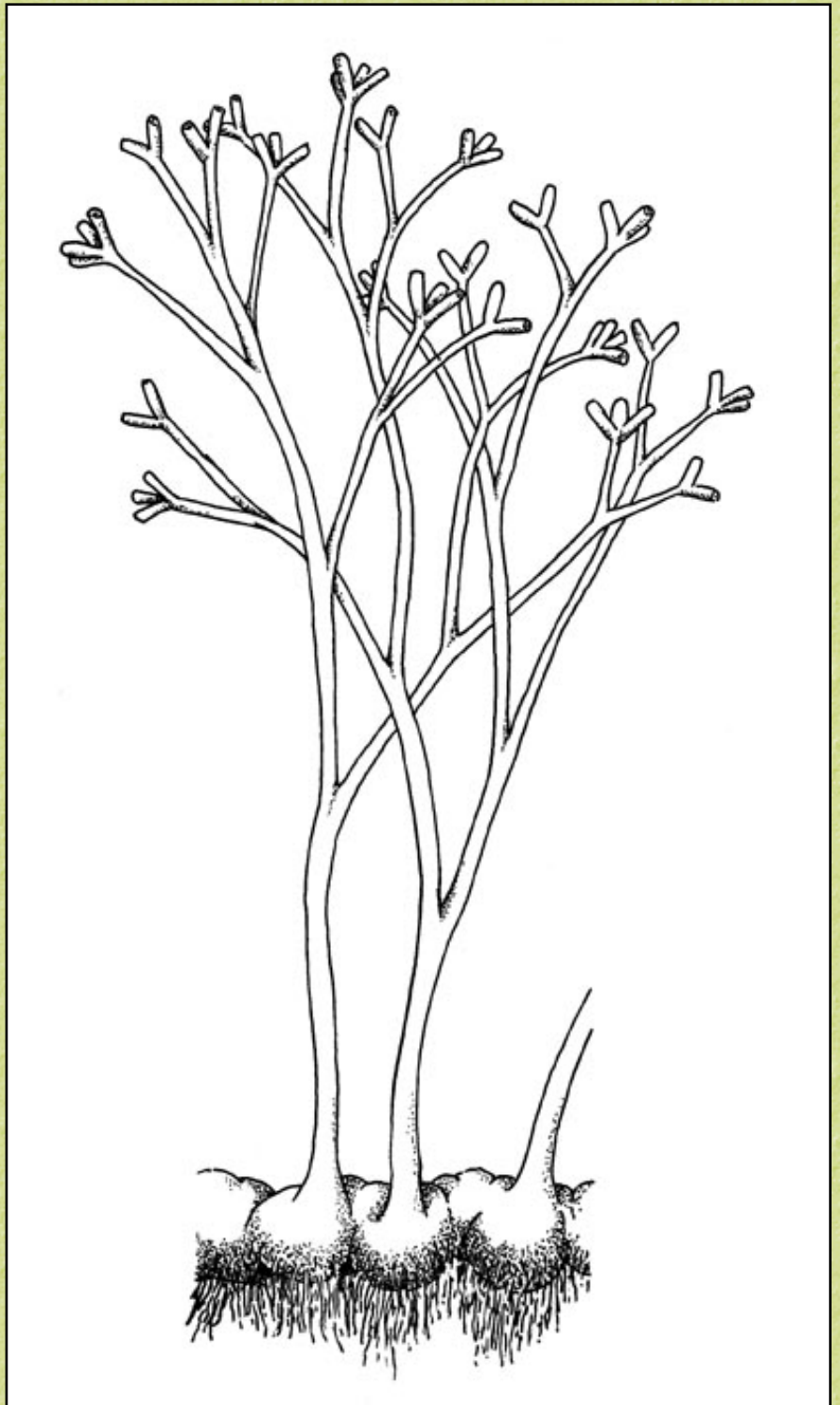
To date the female gametophyte of this plant has been described and has been assigned the name *Langiophyton mackiei* ([Remy and Hass 1991c](#)). This free-living gametophyte of *Horneophyton* probably grew to about 6cm in height, the aerial axis terminating in a conspicuous cup-like structure with numerous tubular outgrowths bearing the [archegonia](#) (see inset right).



Right: Thin section of the female gametophyte *Langiophyton mackiei* showing vascular strand (v) and the tubular outgrowths bearing the archegonia (a) (Copyright owned by University Münster).

Reconstruction

Right: Diagrammatic reconstruction of the sporophyte *Horneophyton lignieri* showing bulbous corm-like rhizomes with rhizoids; dichotomously branching aerial axes and branching terminal sporangia (based on [Eggert 1974](#)).





Left: Model of *Horneophyton lignieri* sculpted by Stephen Caine for the Rhynie Research Group, University of Aberdeen.

Relationships

The presence of a sterile central columella in the sporangia of *Horneophyton* is a feature in extant plants seen only in some **bryophytes** (e.g. mosses) suggesting the plant may have some affinity with the latter, however, the fact that the aerial axes of the plant exhibit a well-developed vascular strand with [tracheids](#) would suggest it is not part of the bryophyte lineage. This mixture of features seen in *Horneophyton*, as with other Rhynie plants, has led to much debate on the systematic position of the plant which still remains in some doubt.

Palaeoecology

Horneophyton appears to have been one of the more common plants in the Early Devonian ecosystem at Rhynie. Where found *in situ* and in life position, *Horneophyton* often occurs at the base of composite chert beds, its subterranean corm-like rhizomes cutting through pre-existing plant litter and its rhizoids probably helped to anchor the plant. It therefore appears that *Horneophyton* preferred **sandy and organic-rich substrates**. The plant is commonly present as **monotypic stands**, perhaps indicating it was also an **early coloniser of sinter surfaces** being able to tolerate environmental conditions unfavourable to many other Rhynie plants ([Powell, et al. 2000b](#)). For example the plant is seldom associated with *Rhynia gwynne-vaughanii* in growth position suggesting the two plant taxa required different optimum conditions for growth.

It is also likely that *Horneophyton* flourished in **damp to wet conditions** ([Powell, et al. 2000b](#); [Remy & Hass 1991c](#)). This seems likely for two main reasons. Firstly, looking at modern sinters, their hygroscopic nature generally means they easily retain water and in some cases the sinter surface where 'early colonising' plants are growing is covered by an intermittent film of water (see also the section on [The Ancient Environment & Modern Analogues](#)). Secondly, Remy and Hass ([1991c](#)) noted that *Horneophyton* was often associated with chytrids (**chytridiomycetes**) which are a type of tiny, simple fungi that thrive in damp and especially aquatic conditions (see also the sections on [Fungi](#) and [Evidence for Plant/Animal Interactions](#)).

CONTENTS PAGE



Nothia



Above: Slightly oblique section through a prostrate aerial axis of *Nothia aphylla* showing irregular surface to epidermis and divided vascular strand (scale bar = 1mm).

[Introduction](#)

[Morphology](#)

[Relationships](#)

[Palaeoecology](#)

Introduction

Nothia was originally described as the probable fertile region of another Rhynie plant, *Asteroxylon mackiei* by [Kidston and Lang \(1920b\)](#). This was assumed to be the case until Geoffrey Lyon discovered the unequivocal fertile leafy shoots belonging to *Asteroxylon* ([Lyon, 1964](#)). In the same paper Lyon gave a preliminary description of this enigmatic new vascular plant and assigned it the name *Nothia aphylla* though no diagnosis was given. [El-Saadawy and Lacey \(1979b\)](#) wrote a more detailed account of *Nothia* and were the first to provide a diagnosis. The most recent work, concentrating on the rhizomal anatomy, has been written by [Kerp et al. \(2001\)](#).

The systematic position of *Nothia* remains unresolved. As well as the sporophyte, the male gametophyte of this plant, *Kidstonophyton discoides*, has also been described ([Remy & Hass 1991b](#)). The overall morphology and palaeoecology of *Nothia* is outlined below.

Morphology

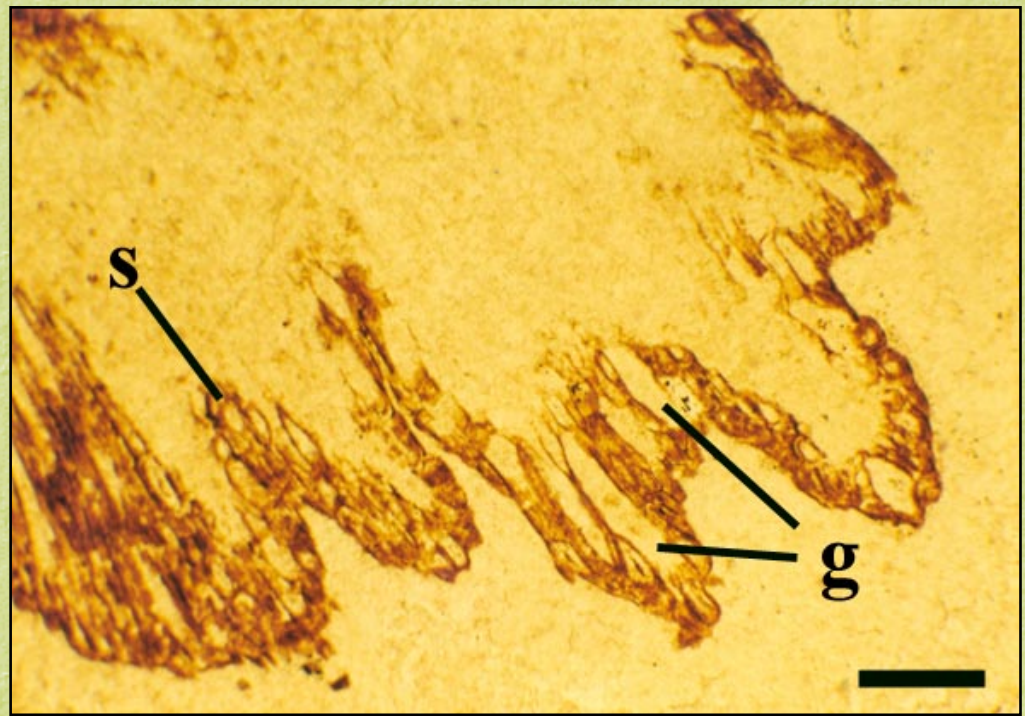
Aerial Axes

The aerial axes of *Nothia* are quite distinctive. They are naked and display a conspicuous, very irregular surface (see heading photograph). The maximum diameter of the axes is 2.5mm and the axes exhibit commonly repeated **dichotomous** branching giving the plant a thicket-like appearance. The plant probably attained a height of about 15cm.

The **epidermis** of *Nothia* shows a characteristic pattern of longitudinally orientated files of short cells alternating with 'giant cells' ([Kerp et al. 2001](#)) (see inset right). It displays elliptical to lenticular stomata-bearing emergences up to 350µm comprising longitudinal files of short cells with up to four intervening 'giant cells'; the files of short cells bearing the **stomata**.

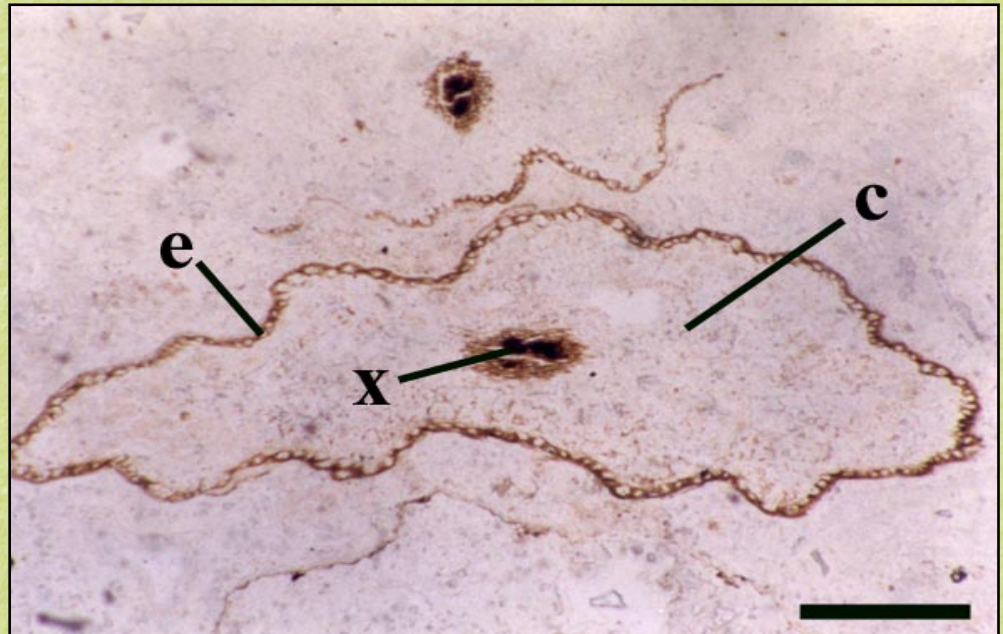
The pores of the stomata are extremely narrow and their two guard cells are usually wider than long. The **cortex** is generally poorly preserved (see inset below right) though an inner and outer

cortex can occasionally be differentiated based on cell shape (Edwards *et al.*, in press), being short in the outer cortex and elongated in the inner cortex. Below the epidermal emergences the intercellular spaces of the outer cortex are large and within the emergences the outer cortex appears spongy (Kerp *et al.* 2001).



Above: Close-up of epidermis of *Nothia* in slightly oblique transverse cross-section showing alternations of short (s) and 'giant' cells (g) (scale bar = 300 μ m).

In many cross-sections the aerial axes of *Nothia* appear to show a double '[vascular strand](#)', reflecting the repeated dichotomy of the plant. In transverse section the [xylem](#) appears elliptical or crescentic in shape (see inset right). It is [sub-terete](#) and [endarch](#) with small central cells being surrounded by larger cells. Unlike most of the other Rhynie plants the xylem does not exhibit thickenings (El-Saadawy & Lacey 1979b) and therefore appears fibrous. Thus *Nothia* does not possess a vascular strand in the strictest sense, a feature it shares with *Aglaophyton*.

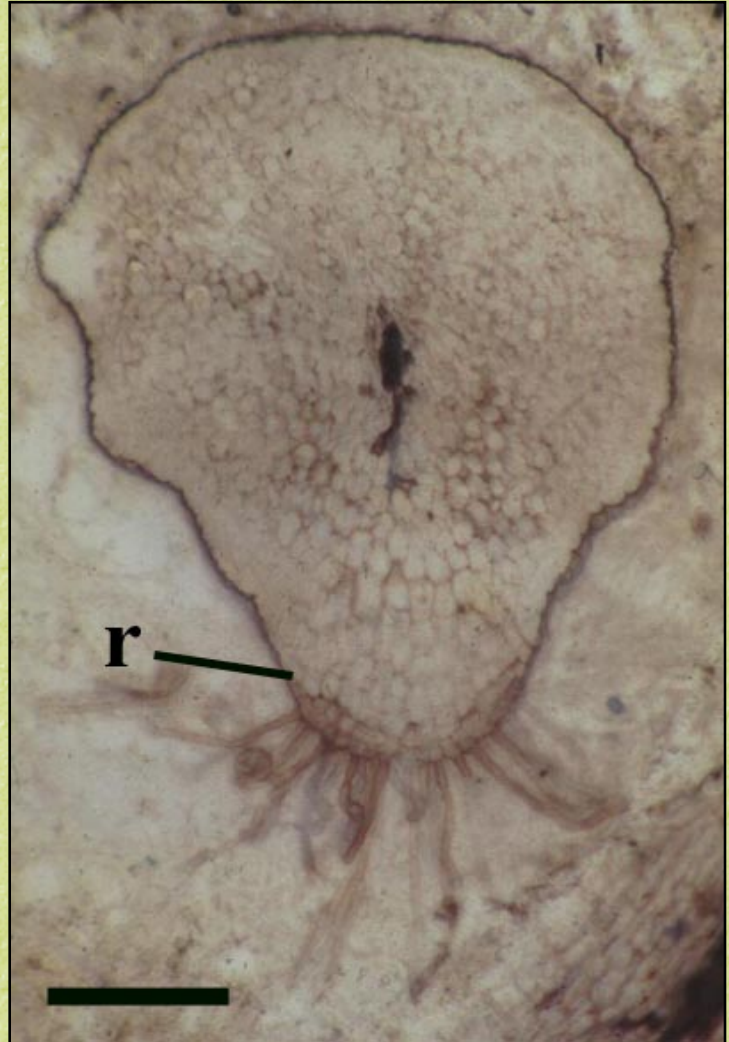


Above: Transverse section through aerial axes of *Nothia aphylla* showing irregular epidermis (e), poorly preserved cortex (c) and split, elliptical xylem strand (x) (scale bar = 1mm).

Rhizomal Axes

The rhizomes of *Nothia* have only recently been adequately described (Kerp *et al.* 2001). Though they have never been discovered in organic connection with the aerial axes, they are assigned to *Nothia* on the basis of their similarity in epidermal and 'vascular' morphology and anatomy. They have primarily been found *in situ* in a number of cherty sandstone beds, exhibiting repeated branching and characteristically show a ridge on the ventral surface that bears the rhizoids (see inset right). These smooth primary axes locally turn upright and are believed to pass upwards into the aerial axes.

Right: Transverse cross section through a primary rhizomal axis of *Nothia aphylla* showing ventral rhizoidal ridge (**r**) with rhizoids (scale bar = 500µm) (Copyright owned by University Münster).



The morphology of epidermal and 'vascular' cells of the rhizome are very similar to that of the aerial axes. The epidermis again consists of alternations of files of short cells and 'giant' cells and the xylem strand exhibits small cells surrounded by larger water-conducting cells. Again the xylem cells do not show partial thickenings and thus have a fibrous appearance. The main differences between the rhizomal and aerial axes is the lack of 'emergences' (the axes consequently appearing 'smooth'), lack of stomata and the thickening of walls in the short cells of the epidermis.

Sporangium

The **sporangia** of *Nothia* have a lateral disposition, each sporangium being attached to the aerial axes by a sporangial stalk (see inset right). The sporangia occur in numerous arrangements, being paired, whorled, as terminal clusters or random ([El-Saadawy & Lacey 1979b](#)). The shape of the sporangia ranges from typically reniform (kidney-shaped) to pear-shaped and they display a well-developed marginal dehiscence mechanism; the maximum dimensions of a single sporangium being 3.1mm by 1.8mm by 1.4mm. Characteristically the sporangial epidermis is very similar to that of the aerial and rhizomal axes showing the alternation of 'giant' cells and files of short cells ([Kerp et al. 2001](#)).



Above: Two empty sporangia of *Nothia aphylla* the left one showing the sporangial stalk (**st**). The dehiscence slit is also evident (**d**) (scale bar = 1mm).

Gametophytes

To date the male gametophyte of this plant has been described and has been assigned the name *Kidstonophyton discoides* ([Remy & Hass 1991b](#)). The aerial axis of the free-living gametophyte show the same general morphology and anatomy as that of the sporophyte, however, the distal end terminates in a distinct cup or disc with tubular projections that bear the [antheridia](#) (see inset right).

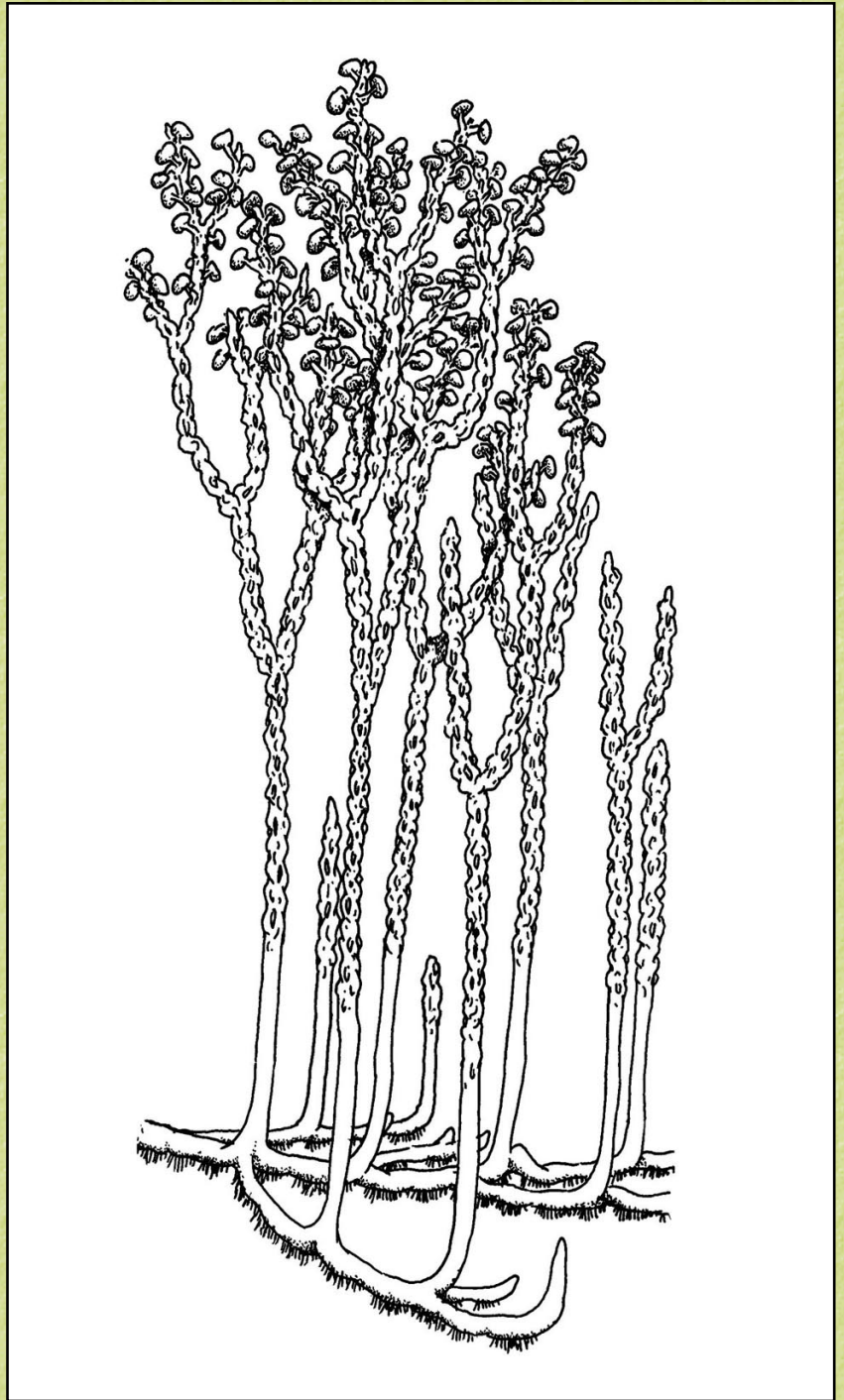


Right: Thin section of the male gametophyte *Kidstonophyton discoides* (scale bar = 1mm) (Copyright owned by University Münster).

Reconstruction

Right: Diagrammatic reconstruction of the sporophyte *Nothia aphylla* showing clonal growth from primary rhizomal axes with

upright stems passing upwards into dichotomously branched aerial axes with distinctive irregular epidermis. Terminal branches locally bearing lateral sporangia (based on [Kerp *et al.* 2001](#)).





Left:
Model of
*Nothia
aphylla*
sculpted
by
Stephen
Caine for
the
Rhynie
Research
Group,
University
of
Aberdeen.



Relationships

Nothia aphylla is yet another Rhynie chert plant whose taxonomic relationship remains unclear, exhibiting morphological and anatomical features characteristic of a number of plant groups. Firstly it shows features characteristic of the **bryophytes**, namely the unthickened water-conducting cells (a feature also seen in the **'hydroids'** of *Aglaophyton major*), a feature which suggests it is not a true vascular plant. Secondly, *Nothia* also shares features with the primitive **rhyniophytes** since its axes are naked and show similar simple branching. Also the sporangia of this plant show similarities with **zosterophylls**, being lateral in their disposition on the axes, reniform in shape with a well-developed marginal dehiscence mechanism.

Palaeoecology

Nothia is a relatively common plant in a number of chert beds occurring in **allochthonous** and **autochthonous** plant litter, though, with the exception of rhizomal axes, not commonly preserved in growth position. In a few horizons rhizomes and aerial axes of *Nothia* occur as monotypic assemblages. In

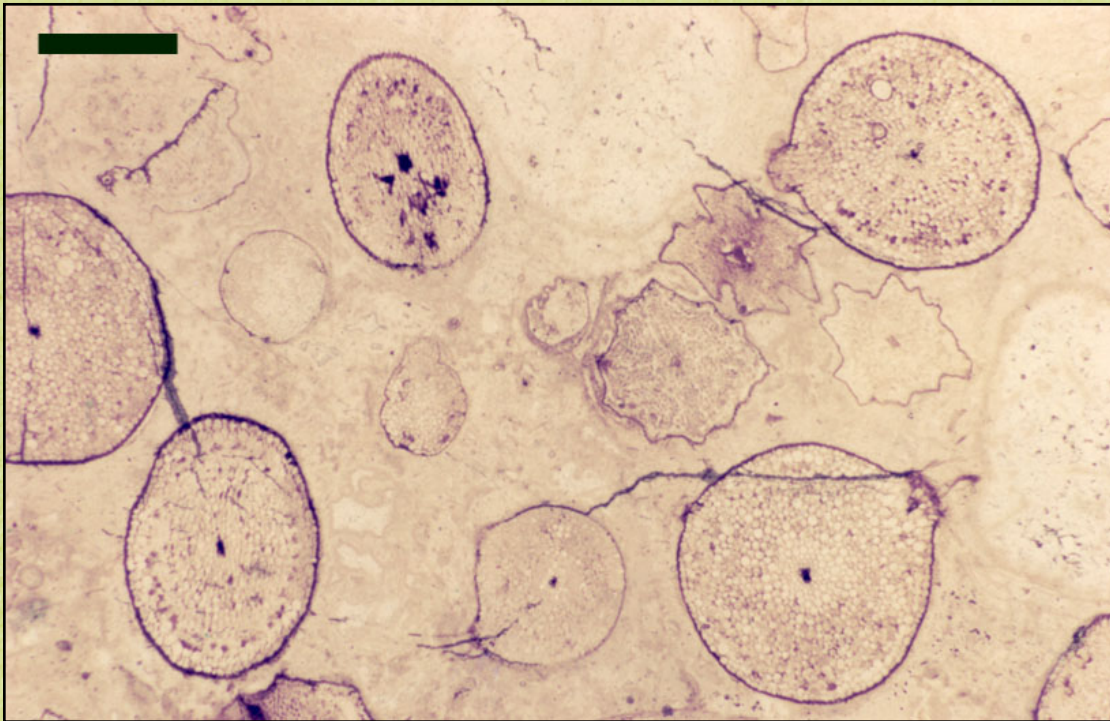
most cases the rhizomal axes of *Nothia* appear to be preserved in cherty sandstone beds along with plant litter. The presence of rhizoids and lack of stomata on the rhizomal axes suggest the rhizomes of *Nothia* were subterranean, apparently preferring **sandy soils**.

In some beds *Nothia* rhizomes appear to have penetrated earlier *Nothia* rhizomes or the rhizomes of other plants (e.g.: *Asteroxylon*) which also suggests they grew within plant litter. The rhizomes or primary axes are always far better preserved and less decayed than the aerial axes, even in the few instances where the latter are found *in situ* in vuggy and massive cherts that usually contain very well preserved axes of other Rhynie plants. These observations tend to suggest a much longer lifespan for the rhizomal (subterranean) axes than the aerial axes the growth of which was perhaps determined by seasonal changes ([Kerp et al. 2001](#)).

CONTENTS PAGE



Rhynia



Above: Transverse sections through axes of *Rhynia gwynnevaughanii*. The star-shaped axes, right of centre, are a result of shrinkage during decay and desiccation of the stems (scale bar = 1mm).

[Introduction](#)

[Morphology](#)

[Relationships](#)

[Palaeoecology](#)

Introduction

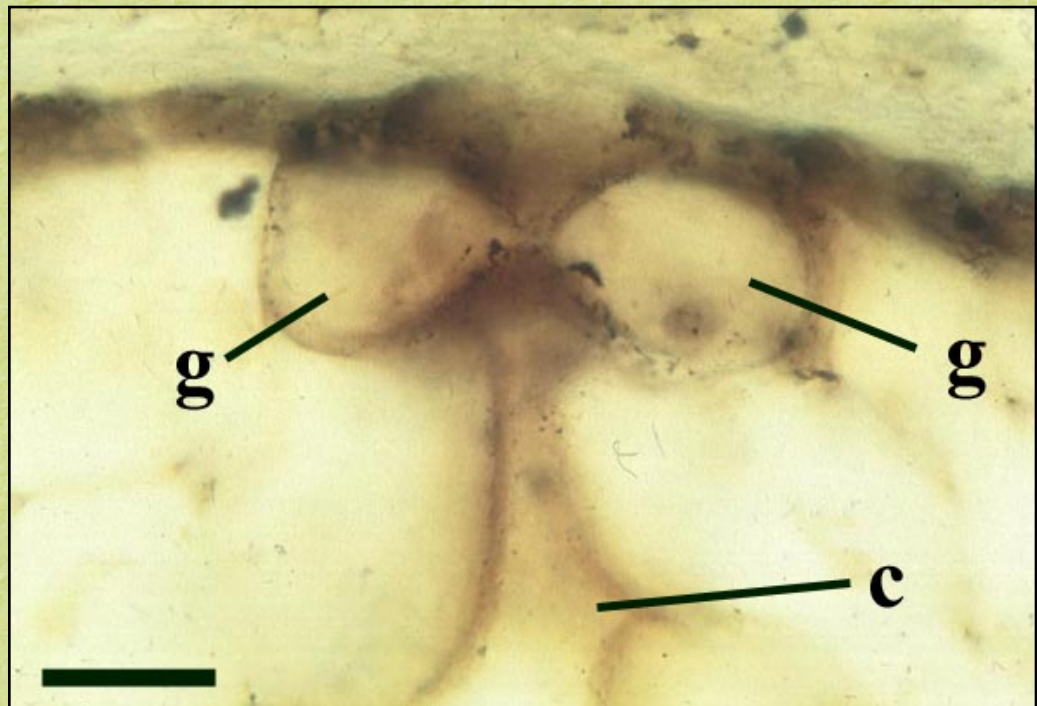
One of the first Rhynie chert plants to be described and perhaps the most abundant is the form *Rhynia*. The plant was originally described and classified by [Kidston and Lang in 1917, 1920a](#) and assigned the species name *Rhynia gwynne-vaughanii*. Another plant now known as *Aglaophyton*, possessing a slightly similar anatomy, was originally described by Kidston and Lang in their 1917 paper as also belonging to *Rhynia gwynne-vaughanii*, but differs significantly in its vascular anatomy and was subsequently reassigned (see also [Aglaophyton](#)). Unequivocal gametophytes of *Rhynia* have recently been discovered ([Kerp et al. in press](#)) and will be illustrated here once published. The overall morphology and palaeoecology of *Rhynia* is outlined below.

Morphology

'Aerial' Axes

The axes of *Rhynia* exhibit a maximum diameter of 3mm and the plant probably attained a height of up to 20cm. The aerial or rather the 'upright' axes are cylindrical, naked and upwardly tapering. The branching of *Rhynia* is both [dichotomous](#) and [adventitious](#) or [monopodial](#), with dichotomy occurring at an angle between 17 and 35° ([D. S. Edwards 1980](#)).

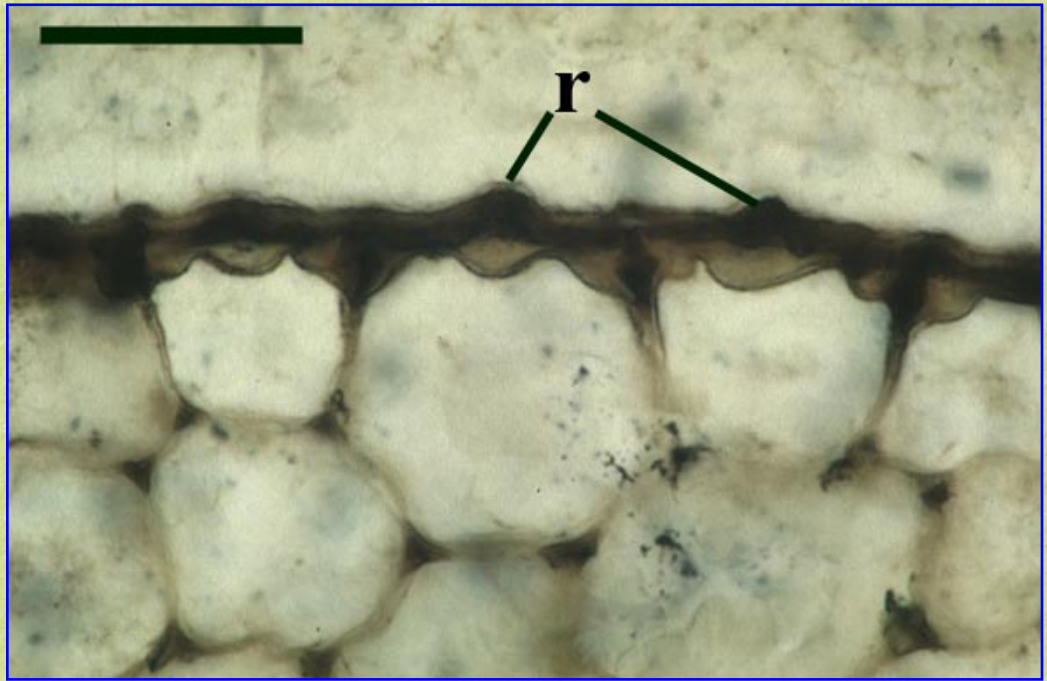
The surface of the axis bear numerous conspicuous emergences or **hemispherical projections** (see insert below right) from the epidermis which are occasionally located beneath stomata and at the base of adventitious branches and in other instances internally display fungal activity and dark necrotic tissue.



Right: Transverse cross section through a stoma showing the two guard cells (g) with the stomatal chamber (c) beneath (scale bar = 20µm) (Copyright owned by University Münster).

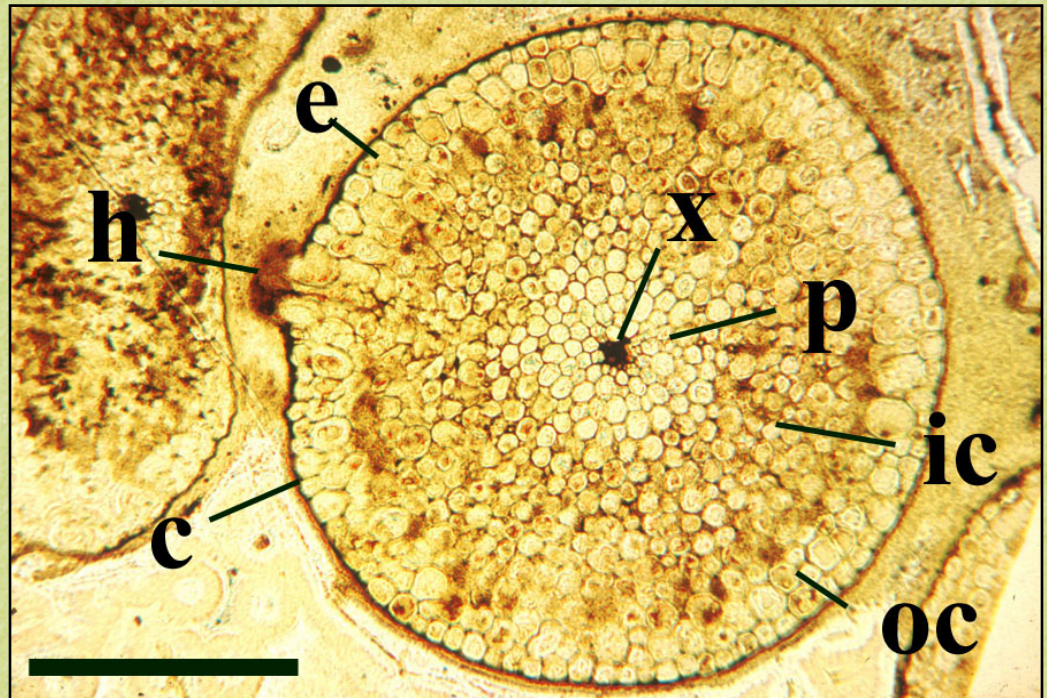
The **stomata** typically appear circular on the cuticle surface and are flanked by two guard cells (see inset above right). The cells of the **cuticle** often exhibit a median ridge giving the cuticle a flanged appearance.

Right: Transverse cross section through the cuticle and epidermis of *Rhynia* showing the median ridges on the cuticle (**r**) (click on the image for a close up!) (scale bar = 100µm) (Copyright owned by University Münster).



The **cortex** is divided into two distinct zones separated by a brown line of amorphous material. The outer cortex comprises closely packed uniform cells, becoming noticeably elongate below the hemispherical projections. The inner cortex comprises uniform cells with a well-developed inter-cellular air space network and commonly exhibits vesicular arbuscular mycorrhizae. The **vascular tissue** or stele comprises a zone of '**phloem**' of uniform thickness surrounding a central **xylem** strand. The phloem cell walls exhibit what appear to be pores (Satterthwait and Schopf 1972, Kenrick and Crane 1991).

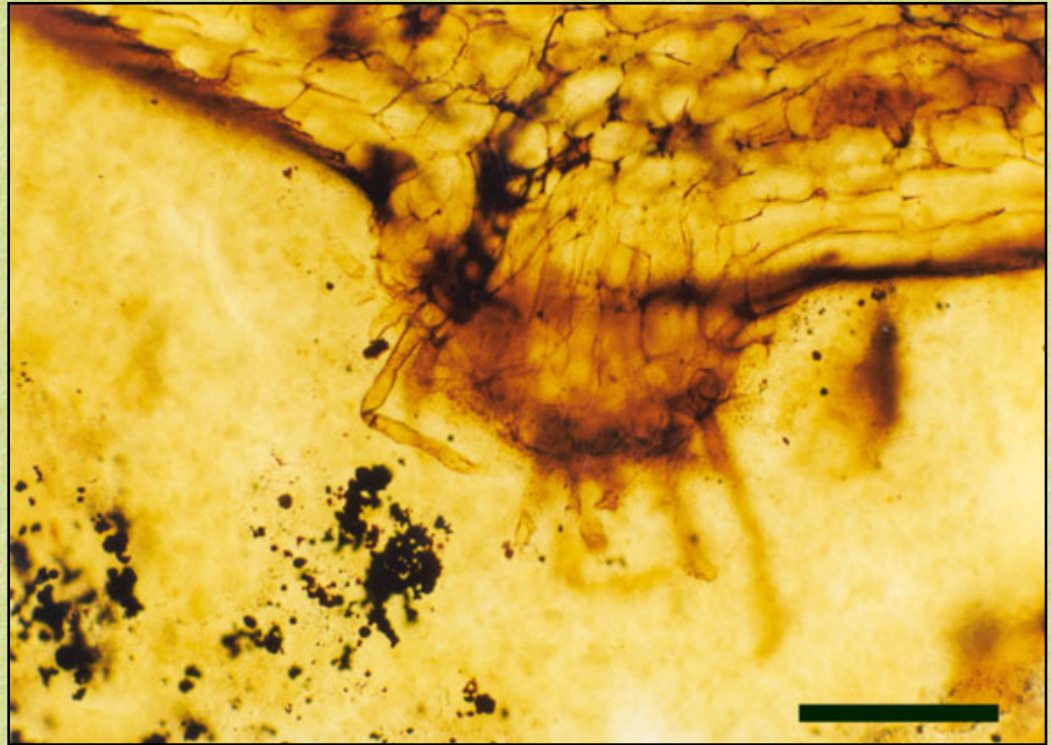
The xylem strand is **terete**, exhibiting **endarch** cell development. The xylem cells also exhibit annular and rare spiral thickenings.



Above: Transverse section through a *Rhynia* axis showing xylem (**x**), 'phloem' (**p**), inner cortex (**ic**), outer cortex (**oc**), epidermis (**e**), cuticle (**c**) and a small hemispherical projection (**h**) (scale bar = 1mm) (Copyright owned by University Münster).

Rhizomal Axes

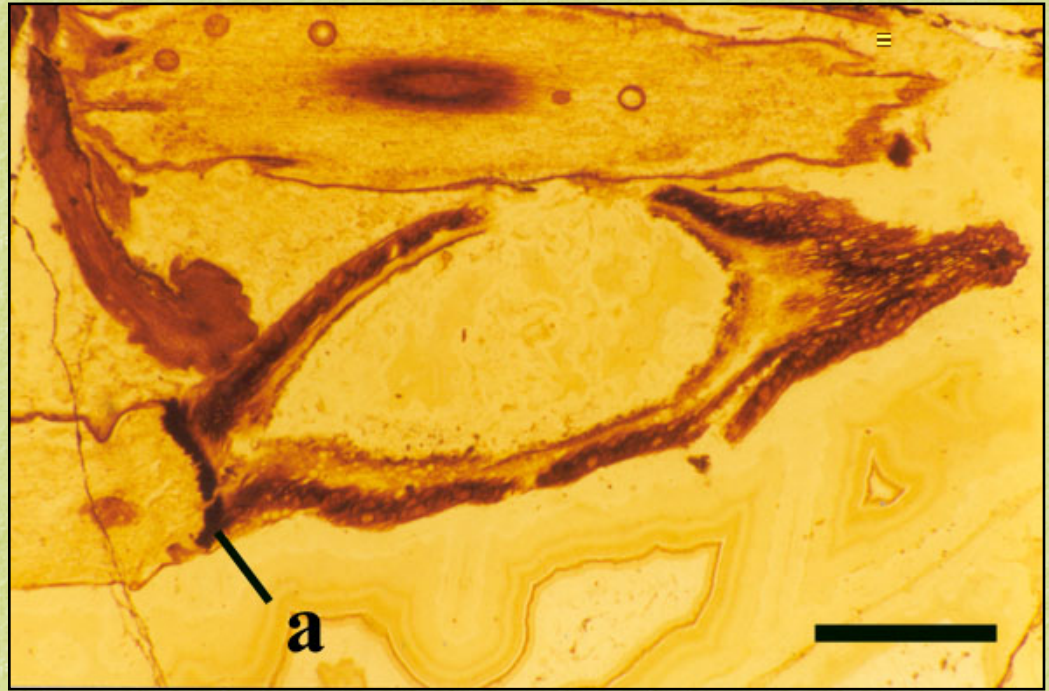
Like *Aglaophyton*, *Rhynia* laid directly on the ground surface. *Rhynia* possesses a creeping rhizome displaying repeated dichotomous and adventitious branching, locally turning upright, passing upwards into the 'aerial' axes. The rhizomal axes are cylindrical and naked and generally exhibit a similar morphology and internal anatomy to the aerial axes though they lack stomata. The other main difference is exhibited by the hemispherical projections, which commonly support tufts of unicellular rhizoids (see inset right). However, occasionally hemispherical projections on the upright 'aerial' axes may also bear rhizoids.



Above: A hemispherical projection on a *Rhynia* axis bearing tufts of rhizoids (scale bar = 250 μ m).

Sporangium

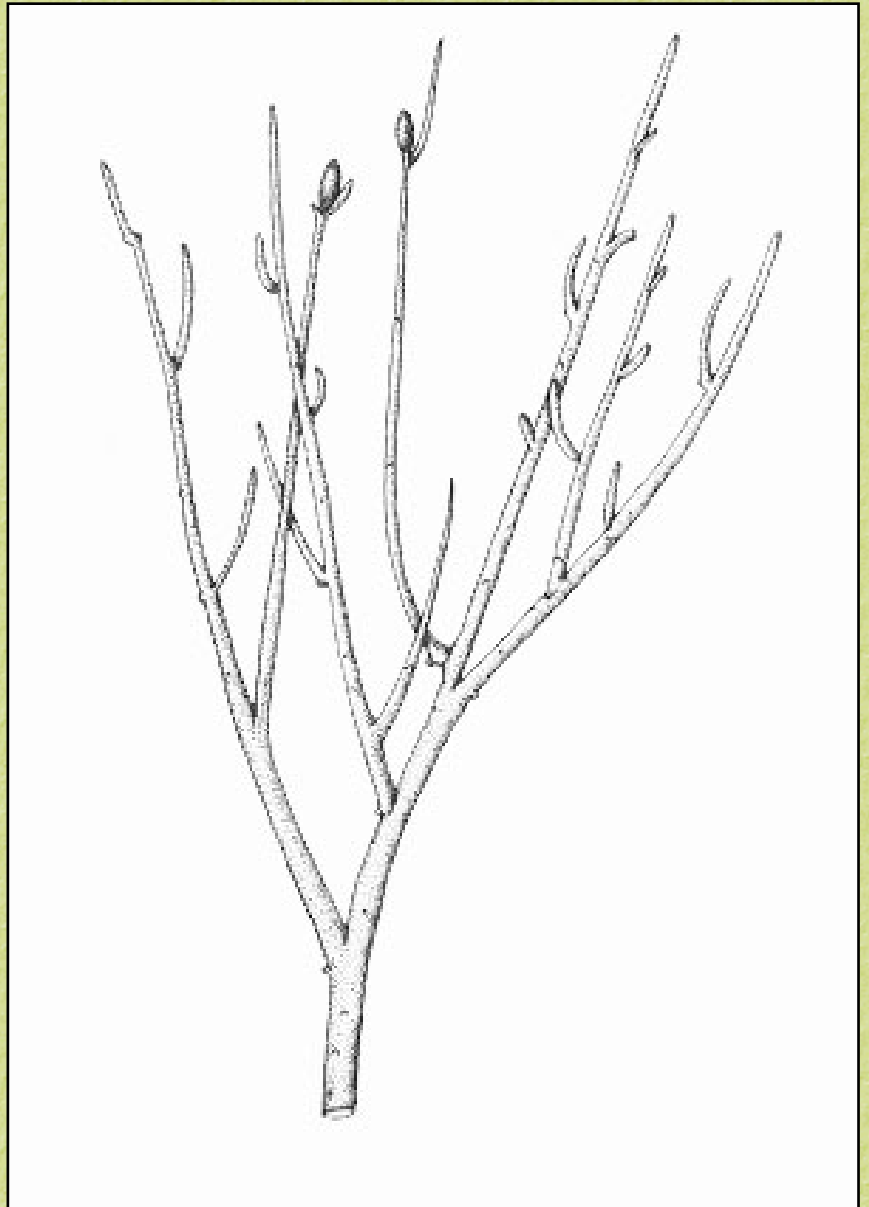
The **sporangia** of *Rhynia* are not particularly common. They are fusiform, displaying a maximum size of 3.6mm by 2.4mm. The disposition of the sporangia is terminal, being located on the adventitious branches of fertile aerial axes. No dehiscence mechanism has been observed though a dark cellular layer or 'sterile pad' at the base of the sporangium has been interpreted as a site of **abscission** by **D. S. Edwards (1980)** (see inset right). The sporangial wall comprises three layers: an outer epidermis, a poorly preserved **parenchymatous layer** and an inner **tapetal layer**.



Above: A split, empty sporangium of *Rhynia* still attached to a prostrate, partially decayed axis showing the dark 'sterile pad' (**a**) (scale bar = 1mm) (Copyright owned by The Natural History Museum).

Reconstruction

Right: Diagrammatic reconstruction of the sporophyte *Rhynia gwynne-vaughanii* showing two fertile adventitious branches with terminal fusiform sporangia (rhizomal axes not shown) (after [D. S. Edwards 1980](#)).



Relationships

Rhynia gwynne-vaughanii being a naked, simply branched sporophyte has been assigned to a primitive group of vascular plants known only from fossils, and called the **rhyniophytes**.

The presence of hemispherical projections on the axes remains a point of speculation and their like is not seen in any of the other Rhynie plants. Various interpretations have been proposed:

- Damage from arthropods sucking sap ([Kevan et al. 1975](#)).

- Wounding by nematodes, mites, parasites or fungi ([Edwards and Selden 1993](#)).
- Damage from splashes of hot water from geysers, or from volcanic ash ([Kidston and Lang 1921a](#)); an unlikely explanation considering the small size and disposition of the projections on the plant axes, and also since they have not been observed on any of the other Rhynie plants.
- [Pant \(1962\)](#) and [Lemoigne \(1968a, b\)](#) interpreted the hemispherical projections as sites of **archegonia**, though this interpretation has never been generally accepted.

Palaeoecology

Rhynia was the most common vascular plant in the Early Devonian ecosystem at Rhynie, at least in the areas of sinter deposition, both numerically and in terms of ground cover ([Powell et al. 2000b](#)). The plant appears to have been entirely subaerial with its naked, branching 'rhizomes' creeping across the ground surface with the upright portions of the plant growing to give a **thicket-like appearance**. Although the hemispherical projections on the 'rhizomes' bear the rhizoids for taking up water from the ground surface, the fact that those on the upright stems occasionally exhibit rhizoid tufts suggest *Rhynia* was also capable of taking up atmospheric water.

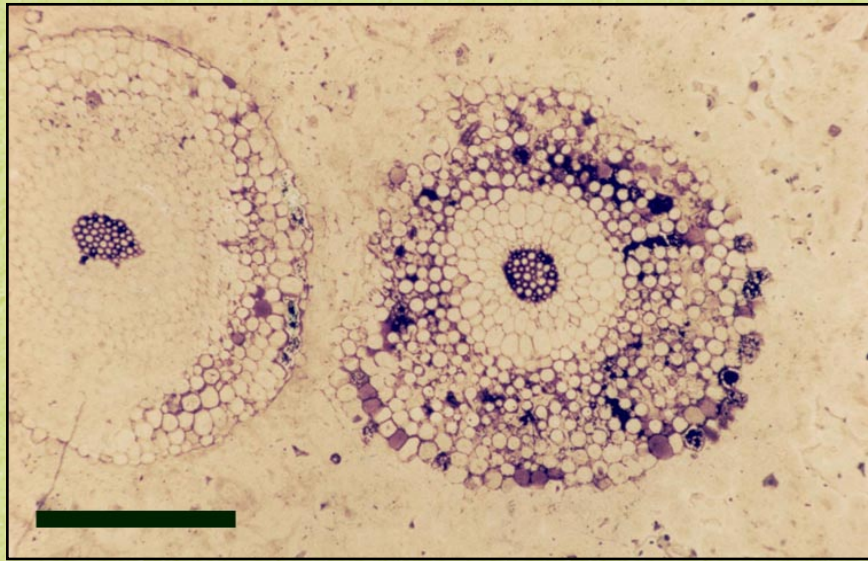
Where found in growth position in the chert beds it is typically, though not exclusively the only *in situ* vascular plant present, and is commonly found above sandy chert layers and allochthonous litter horizons. This suggests *Rhynia* commonly grew as monotypic stands, **an early colonizer of well-drained sinter and sandy substrates**.

However, the plant is also found associated with all other Rhynie plants, though only very rarely with *Horneophyton*. This suggests *Rhynia* was tolerant of a wide range of habitats and could also withstand interspecies competition within the Early Devonian ecosystem at Rhynie ([Powell et al. 2000b](#)).

CONTENTS PAGE



Trichopherophyton



Above: Transverse sections through rhizomal axes of *Trichopherophyton teuchansii* (scale bar = 1mm).

[Introduction](#)

[Morphology](#)

[Palaeoecology](#)

Introduction

Trichopherophyton is one of the more recent additions to the Rhynie chert list of vascular plants. It was formally described by [Lyon & Edwards \(1991\)](#) and assigned the species name *Trichopherophyton teuchansii*, and was the first true [zosterophyll](#) recorded from the cherts. This is the scarcest of the Rhynie plants having only been found in a few beds of chert.

A reconstruction of the whole plant has not yet been attempted and the gametophyte stage of the plant remains unknown. The overall morphology and palaeoecology of *Trichopherophyton* is outlined below.

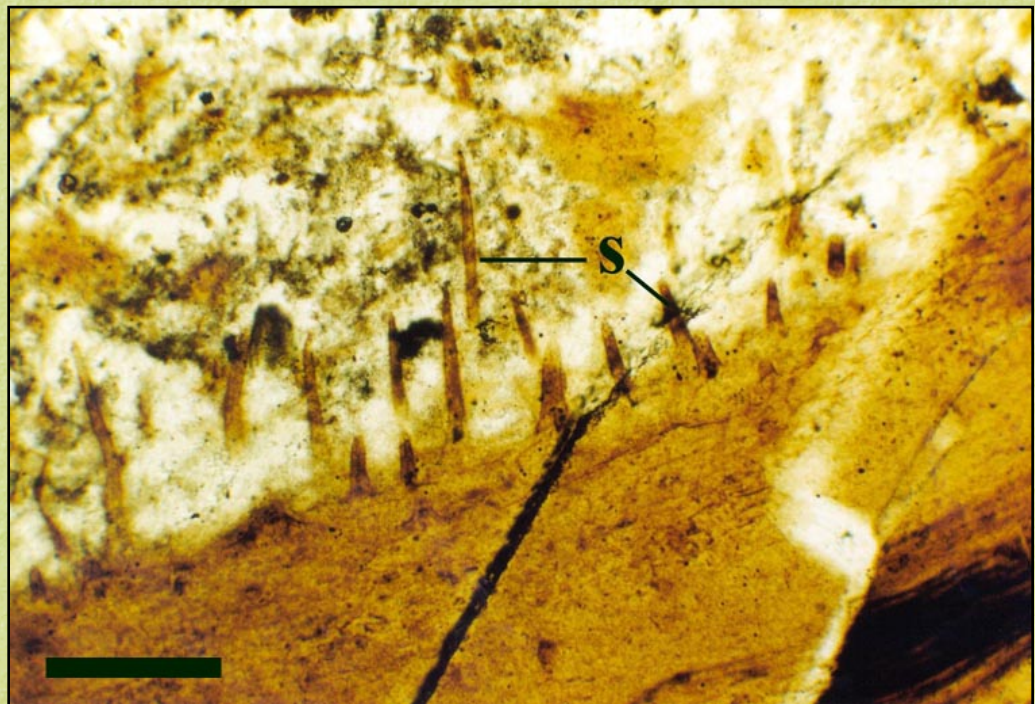
Morphology

Aerial Axes

The aerial axes of the plant exhibit a maximum diameter of 2.5mm. The branching of *Trichopherophyton* is both **dichotomous** and **pseudomonopodial** and it is the only plant known in the Rhynie flora to display **circinate vernation**.

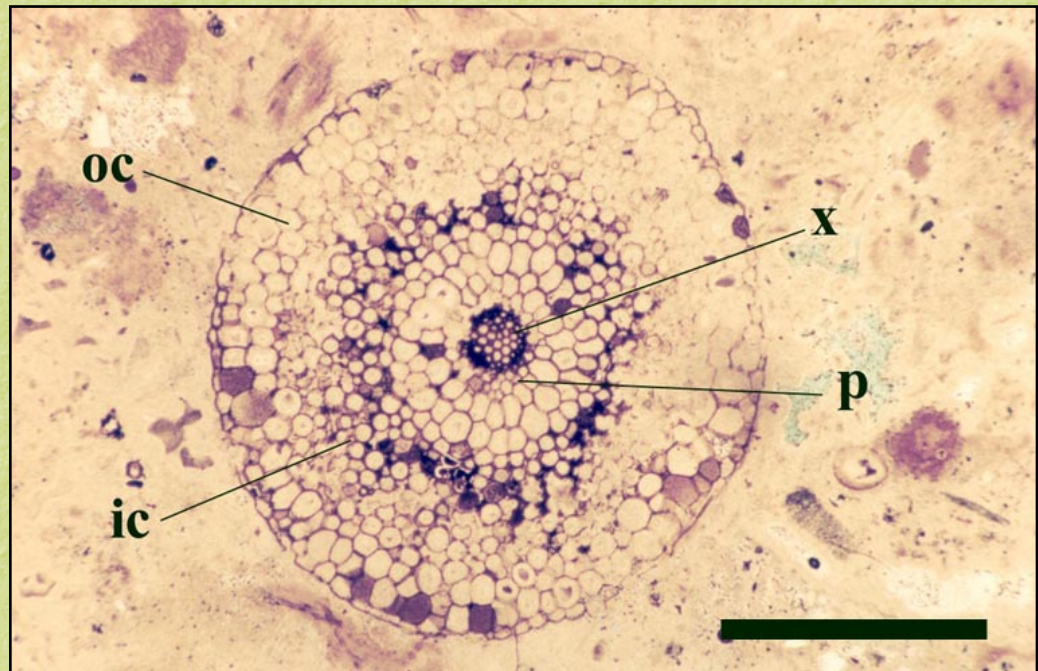
Generally the **cuticle** of *Trichopherophyton* is poorly preserved and as a result **stomata** have not been observed, the rest of the **epidermis**, however, is usually well preserved and very often exhibits unicellular **spinose projections** emerging at 90° to the axis of the plant (see inset right). These spiny outgrowths are one of the most characteristic features of *Trichopherophyton*.

Right: Longitudinal section of an aerial axis showing epidermis with conspicuous unicellular spinose projections (s) (scale bar = 500µm).



The **cortex** can be divided into a distinct outer cortex comprising closely packed cells and an inner cortex or more loosely packed cells with an inter-cellular air-space network. Many cells of the inner cortex contain dark coloured residues (see inset right).

Right: Transverse section through an axis of *Trichopherophyton teuchansii* showing xylem (**x**), phloem (**p**), inner cortex (**ic**) and outer cortex (**oc**) (scale bar = 1mm).



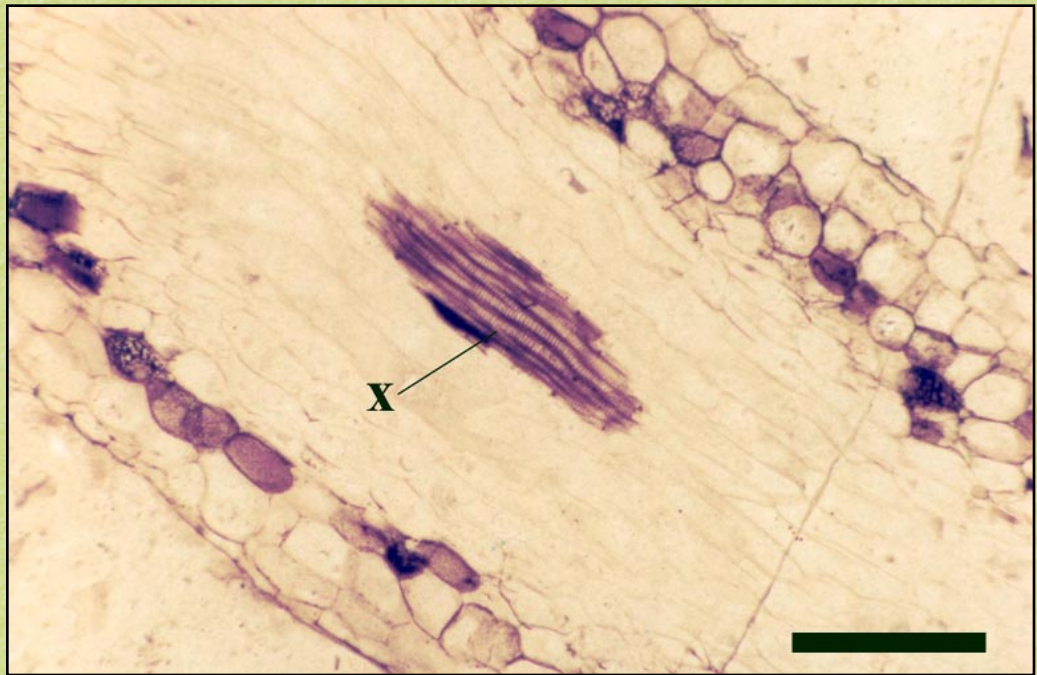
The **vascular tissue** comprises a very distinct **xylem** strand (see inset above right). It is **sub-terete**, **exarch** and displays both annular and spiral thickening. A narrow zone, uniform in thickness, of thin-walled cells surrounds the xylem strand and probably represents **phloem** (see inset above right).

Rhizomal Axes

Observed within many of the chert specimens containing the spinose aerial axes of *Trichopherophyton* are other generally more common axes of a slightly differing but distinctive morphology that are believed to represent the rhizomes of the plant although there remains no unequivocal evidence for organic continuity between the two.

These axes are generally slightly smaller than the aerial axes, having a maximum diameter of 2.3mm.

They exhibit a generally smooth epidermis, lacking the spinose outgrowths though epidermal cells may be papillate and occasionally may bear blunt-tipped emergences that may represent rhizoids. The cortex is quite narrow and less distinctly divided compared with the aerial axes, though again cells of the inner cortex commonly show dark coloured residues (see inset right). A zone of thin-walled cells surrounding the xylem strand may represent phloem. As with the aerial axes the sub-terete xylem strand is very distinctive being exarch and showing narrow annular and spiral thickenings (see inset right).



Above: Slightly oblique section of a rhizomal axis clearly showing the sub-terete xylem strand (x) (scale bar = 500 μ m).

Sporangium

The sporangia or fertile elements of *Trichopherophyton* have been observed in a few specimens but have not as yet been fully described. However, sporangia do appear to be reniform (kidney-shaped) with dimensions up to a maximum 3.7mm by 2.5mm. They are attached laterally to the aerial axes with a vascularised sporangial stalk though their spatial distribution is uncertain. The sporangia appear to be bi-valved with a marginal dehiscence mechanism. Characteristically the sporangia display the same unicellular spinose projections emerging from the epidermis as seen in the aerial axes.

The *in situ* [spores](#) of *Trichopherophyton* appear to vary between 55 and 80 μ m in size, are [retusoid](#) and smooth walled and display a triangular thickening associated with the trilete mark. These spores are comparable to species of the spore genus *Retusotriletes*.

Relationships

Trichopherophyton teuchansii is undoubtedly a **zosterophyll**, fitting into the classification of [Banks](#)

(1975), showing lateral, reniform sporangia with a well-developed marginal dehiscence mechanism as well as an exarch xylem strand with thickenings. However, there remain other features, although characteristic of this plant, that are rarely encountered in true zosterophylls; namely a sub-terete xylem strand and the presence of unicellular spiny epidermal projections on the aerial axes and sporangia.

The circinate vernation seen exclusively in *Trichopherophyton* is a feature that is also observed in most extant ferns. This suggests that the plant has a more advanced anatomy than that of the other Rhynie plants.

Palaeoecology

Generally *Trichopherophyton* appears to be relatively rare in comparison with the other vascular plants and has been found to occur in only a few beds of chert. This may partially reflect the scarcity of the plant within the original ecosystem or may simply reflect sampling bias. However, within the few beds within which it occurs, it is preserved both in autochthonous growth position and as litter, but **always as part of a diverse flora** including *Nothia*, *Horneophyton* and locally *Rhynia*. It seems likely therefore that *Trichopherophyton* was a **late coloniser of humus-rich substrates** ([Powell et al. 2000b](#)).

[CONTENTS PAGE](#)



Ventarura



Above: Polished slab of Windyfield chert showing aerial and rhizomal axes of *Ventarura lyonii*. Many of these axes are inverted and therefore not in growth position.

[Introduction](#)

[Morphology](#)

[Relationships](#)

[Palaeoecology](#)

Introduction

Ventarura is the most recently identified element of the Rhynie flora. The plant was formally described by [Powell *et al.* \(2000a\)](#) and assigned the name *Ventarura lyonii*. The float blocks from which the plant were described all originated from the Windyfield chert of the Rhynie hot spring complex. Many thin sections made of this material

have revealed details of the subaerial and probable rhizomal axes, the pattern of branching, and the morphology of the sporangia of the plant.

A preliminary reconstruction of the sporophyte stage of the plant has recently been attempted (see below), though the gametophyte stage of the plant remains unknown. The overall morphology and palaeoecology of *Ventarura* is outlined below.

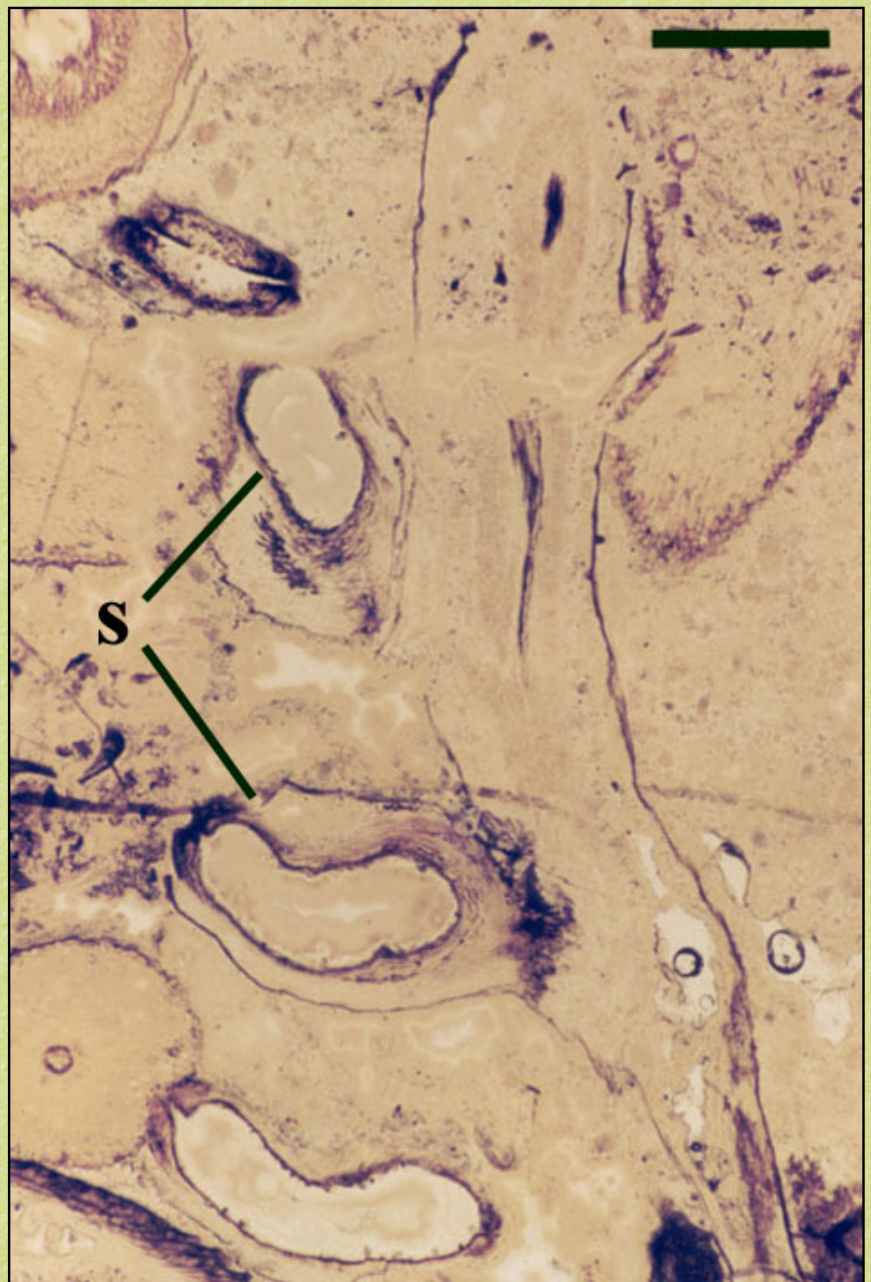
Morphology

Aerial Axes

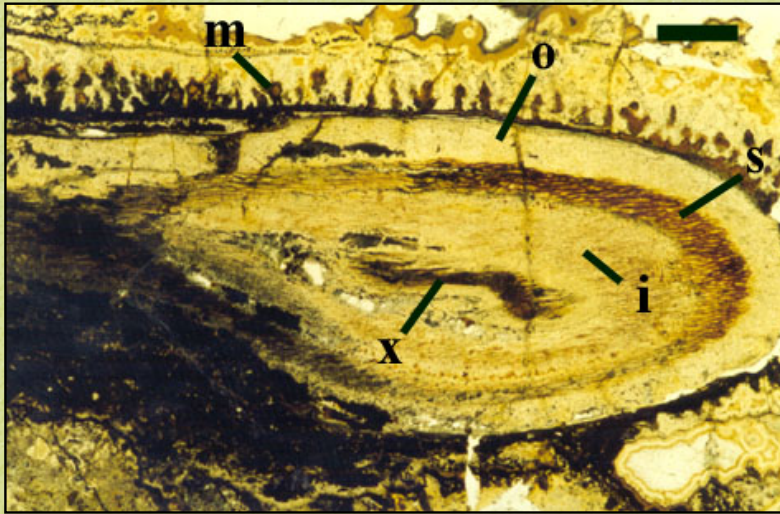
The aerial axes of *Ventarura* (see inset right) have a maximum diameter of 7.2mm and exhibit primarily **dichotomous** branching. The angle of dichotomy usually being at 25°. It is not known what height the plant attained, but it was in excess of 12cm. The axes are smooth though the **epidermis** exhibits unicellular peg-like projections. The details of the **cuticle** are not fully known and the morphology of the **stomata** has not been resolved. Occasionally, enigmatic elliptical features are seen on the surface of the cuticle. It is not known exactly what these are, but they may represent the sites of projections that have been lost.

The **cortex** of the aerial axes of *Ventarura* is quite distinctive. An inner and outer cortical layer is separated by a dark middle cortex zone of **sclerenchymatous** cells (see inset below left). The outer cortex comprises closely packed thin-walled cells. The inner cortex again comprises thin-walled cells but with a well-developed inter-cellular air space network.

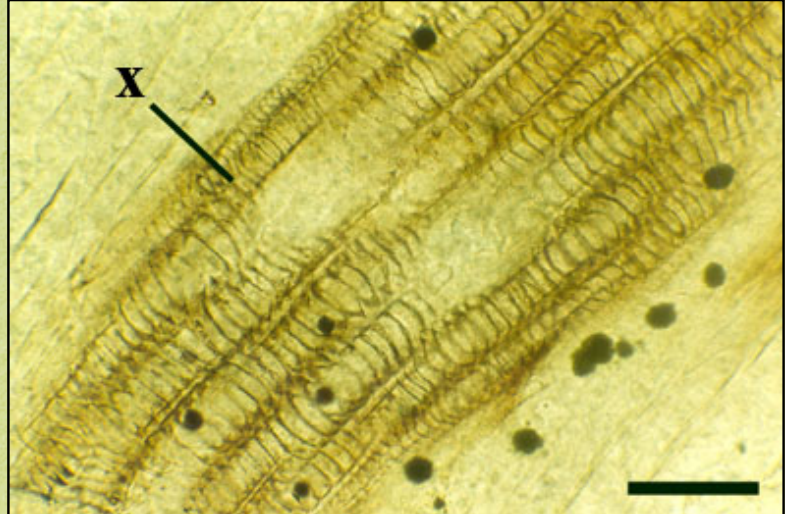
Right: Longitudinal section of a fertile aerial axis with laterally attached sporangia (s) (see below) (scale bar = 2mm).



The **vascular strand** of *Ventarura* comprises a generally poorly preserved outer zone of uniform width, tentatively interpreted as **phloem** tissue. The **xylem** strand is **terete** and **exarch** with annular and spiral thickenings (see inset below right).



Above: Slightly oblique section through an aerial axis of *Ventarura* showing outer cortex (o), middle cortex (s), inner cortex (i) and xylem strand (x). The cuticle of the axis is coated by a brown coloured microbial mucilage (m) (scale bar = 2mm).



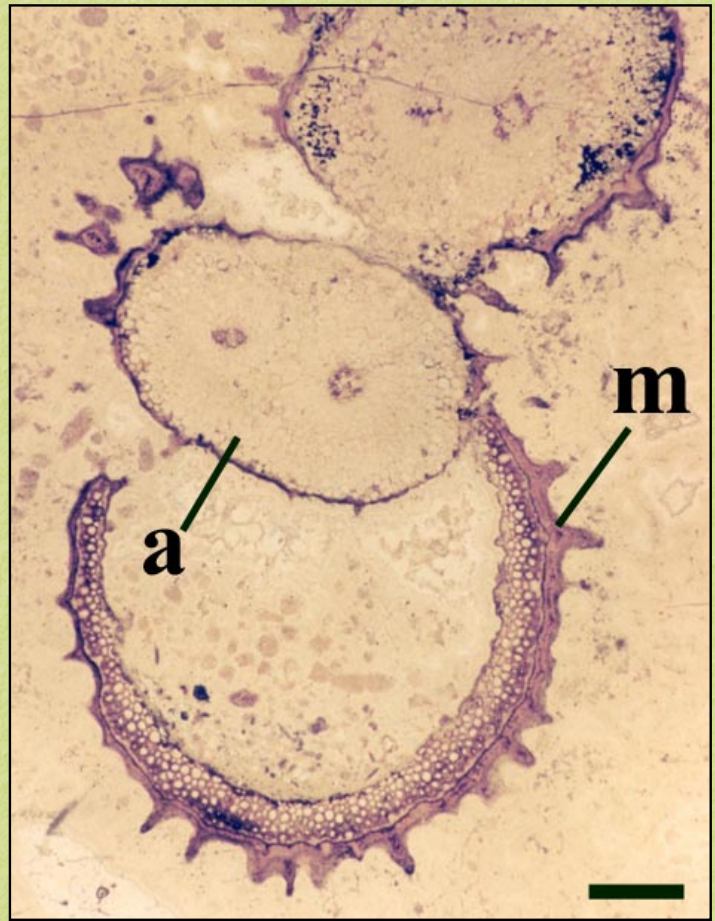
Above: Close-up of xylem strand (x) of *Ventarura*. The dark patches are framboids of pyrite (scale bar = 100µm).

Rhizomal Axes

Observed within many of the chert blocks containing the aerial axes of *Ventarura* are other smaller axes of a slightly differing but distinctive morphology that are believed to represent the rhizomes of the plant although there remains no unequivocal evidence for organic continuity between the two.

These axes branch repeatedly and tend to exhibit unicellular peg-like outgrowths from the epidermis (interpreted as representing rhizoids) and characteristically lack the sclerenchymatous middle cortex seen in the aerial axes.

Right: Straw of a *Ventarura* axis with microbial mucilage (**m**) cut by a later branching rhizomal axis (**a**) (scale bar = 1mm).



Sporangium

The [sporangia](#) of *Ventarura* are reniform (kidney-shaped) to pear shaped with dimensions up to a maximum 5.2mm by 2mm. They are attached laterally to the aerial axes with a vascularised sporangial stalk. Their spatial distribution is not fully known but at least appear to form in a vertical sequence along the fertile axes (see inset top right in section on 'aerial axes'). The sporangia are bi-valved with a well-developed marginal dehiscence mechanism (see inset right).

Right: Section through an empty sporangium of

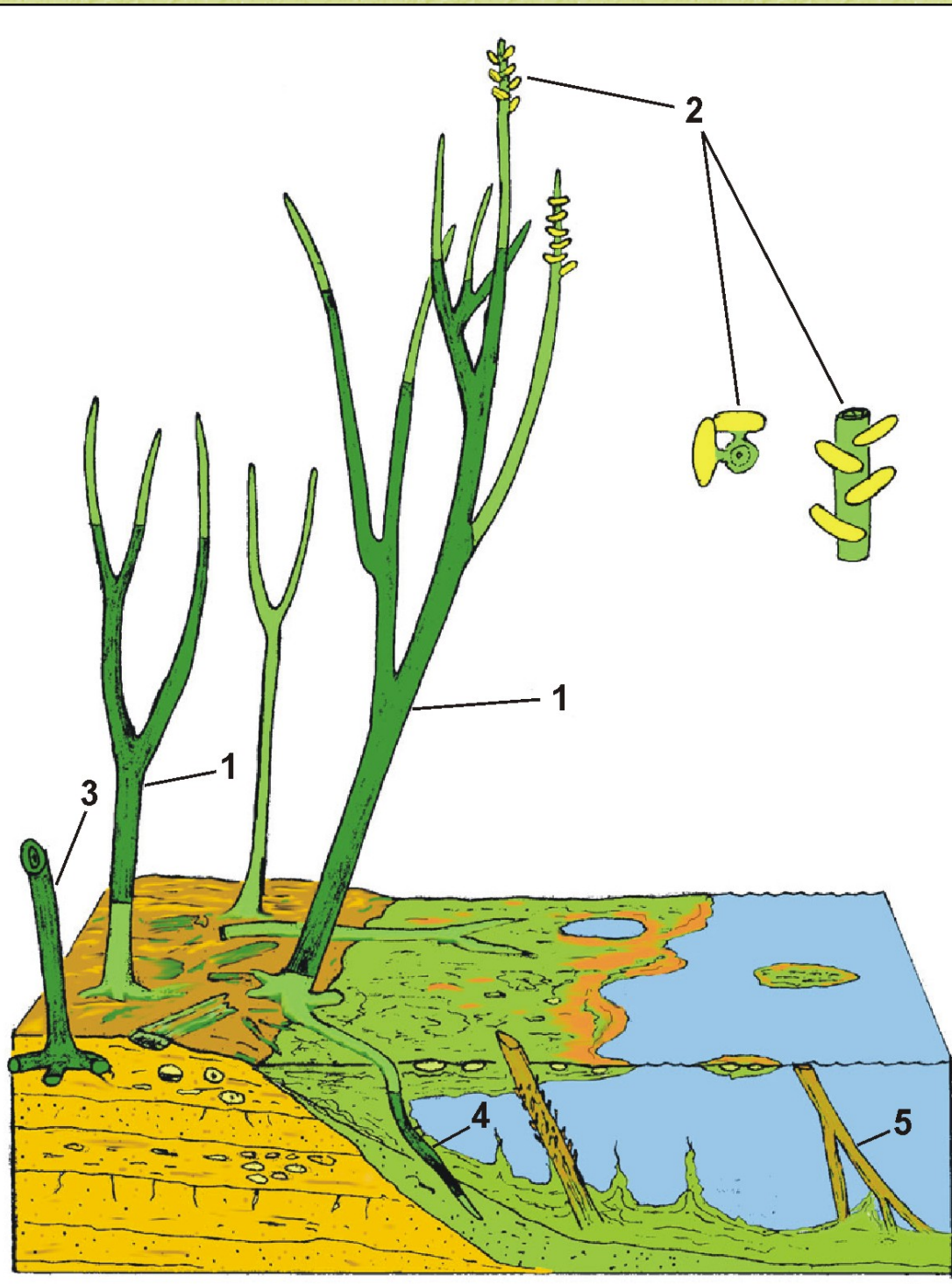
Ventarura showing the well-developed marginal dehiscence mechanism (**d**) (scale bar = 1mm).



Preliminary reconstruction

Serial sections of a block of Windyfield chert have revealed more of the general anatomy of *Ventarura* than could be described by [Powell *et al.* \(2000a\)](#). This reconstruction (see inset left) was displayed at the conference on the Rhynie chert held in Aberdeen in September 2003.

In the sketch the individual sections of the plant that could be traced in the block are darkly shaded, and reveal a variety of branching styles are



present.

Numbered features on the reconstruction are:

1. Branched sections of aerial axes traced within a chert block.
2. Sporangia in regular en echelon rows on axes of 2-3 mm diameter. Sporangia up to 4 mm wide.
3. Branched horizontal rhizomes attached to aerial axis.
4. Rhizomes penetrating bacterial meshworks and decayed aerial axes in water. Growth of the plant probably extended into floating bacterial mats, resulting in vertical penetration of rhizomes into water underneath the mat.
5. Portions of aerial axes were preserved in an inverted position after floating in pools adjacent to growing areas (see heading photograph).

We are still seeking the connections between the fertile axes seen in thin sections and the main aerial axes, also further information on rhizome branching, sporangial arrangement, and the terminations of aerial axes and rhizomes. The search continues prior to

Relationships

Ventarura exhibits a number of features that assist in classification; particularly the morphology of the xylem tissue, and the morphology and disposition of the sporangia. The xylem strand is characteristically exarch with thickenings. The sporangia are reniform to pear-shaped with a well-developed dehiscence mechanism, and have a lateral disposition on the aerial axes to which they are attached by a vascularised sporangial stalk. These features indicate *Ventarura* is undoubtedly a tracheophyte allied with the [zosterophylls](#) and as such is the second zosterophyll known from the Rhynie chert (see also [Trichopherophyton](#)).

Palaeoecology

To date *Ventarura* has only been found in a number of chert float blocks from pods of the Windyfield chert. Although locally very well preserved, much of the vegetative and fertile material appears to be at least partially transported, and deposited in freshwater pools evidenced by many of the branched aerial axes being inverted (see heading photograph). The chert texture is typical of silicified subaqueous deposits, containing the crustacean *Lepidocaris*, microcoprolites and bacterial coatings on plant debris.

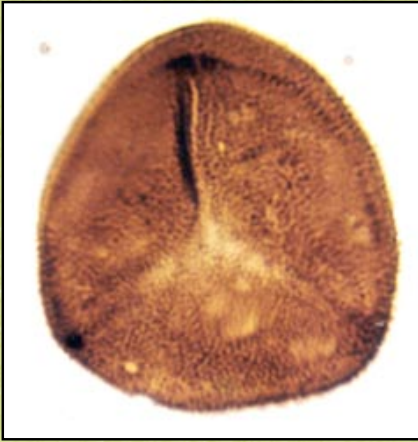
As such it remains difficult to sufficiently interpret the palaeoecology of this new plant but with the presence of apparently *in situ* rhizomatic axes in the chert blocks it seems likely that the plant probably grew at the edges of or at least within the vicinity of these pools and may have preferred sandy and organic-rich substrates.

CONTENTS PAGE



Rhynie Spores

Fossilised spores from vascular plants are quite common in beds of the Rhynie chert and also within the finer grained interbedded sediments such as shales and mudstones. They are usually extracted from the sedimentary rocks by macerating rock samples in solutions of Hydrofluoric acid which dissolves the silica minerals in the sediment and leaves the resistant spores and other acid-insoluble organic remains for analysis ([Wellman & Axe 1999](#)). Interestingly, upon extraction the spores often appear better preserved within the mudrocks than in the cherts, though this may be a reflection of the effects of silicification and replacement of the original organic material.



Above: *Apiculiretusispora* sp., spore diameter approximately 40µm (Copyright owned by University of Sheffield).



Above: *Emphanisporites* sp., spore diameter approximately 60µm (Copyright owned by University of Sheffield).



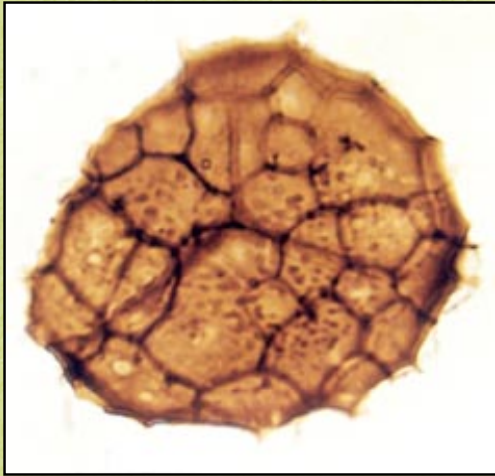
Above: *Brochotriletes* sp., spore

Many genera and species have been recognised and described, though there still remains a degree of uncertainty as to which of the known vascular plants of the Rhynie chert they can be assigned to. *In situ* spores have been described in the past for *Horneophyton* and *Rhynia* by [Bhutta \(1973a, b\)](#).

There may well be spores present that are representative of other plants that have not been so far discovered in the cherts. The abundance and variety of spores present in the sequence of Rhynie sediments has been useful in terms of [biostratigraphy](#) in determining the [age of the rocks](#) ([Wellman 2004](#)).



diameter approximately 50µm
(Copyright owned by University of Sheffield).



Above: *Dictyotriletes sp.*, spore diameter approximately 50µm
(Copyright owned by University of Sheffield).

The images to the left and right display a few of the spore types or **palynomorphs** that have been found.

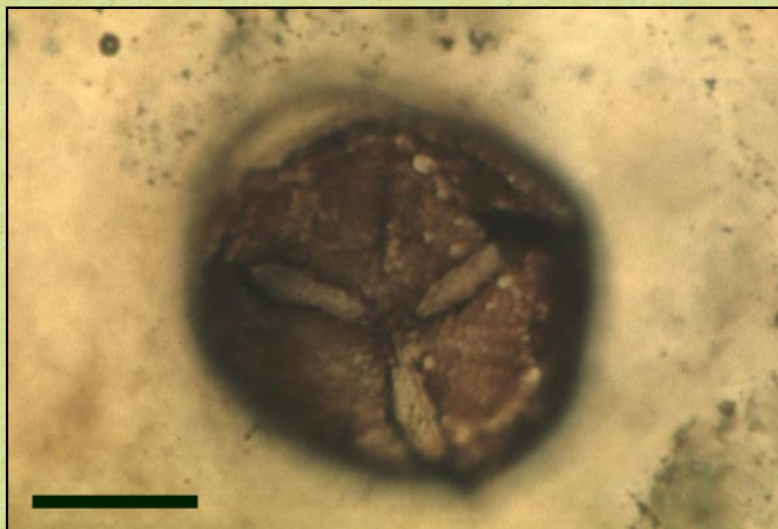
The study of the fossil spores or palynology of the Rhynie chert and sediments is ongoing at the [University of Sheffield](http://www.sheffield.ac.uk).

Above: *Retusotriletes sp.*, spore diameter approximately 40µm
(Copyright owned by University of Sheffield).

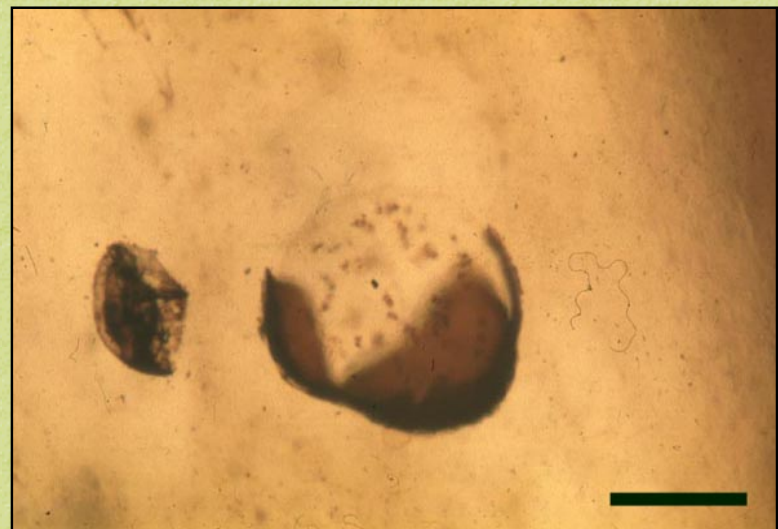


Above: A zonate spore, diameter approximately 50µm (Copyright owned by University of Sheffield).

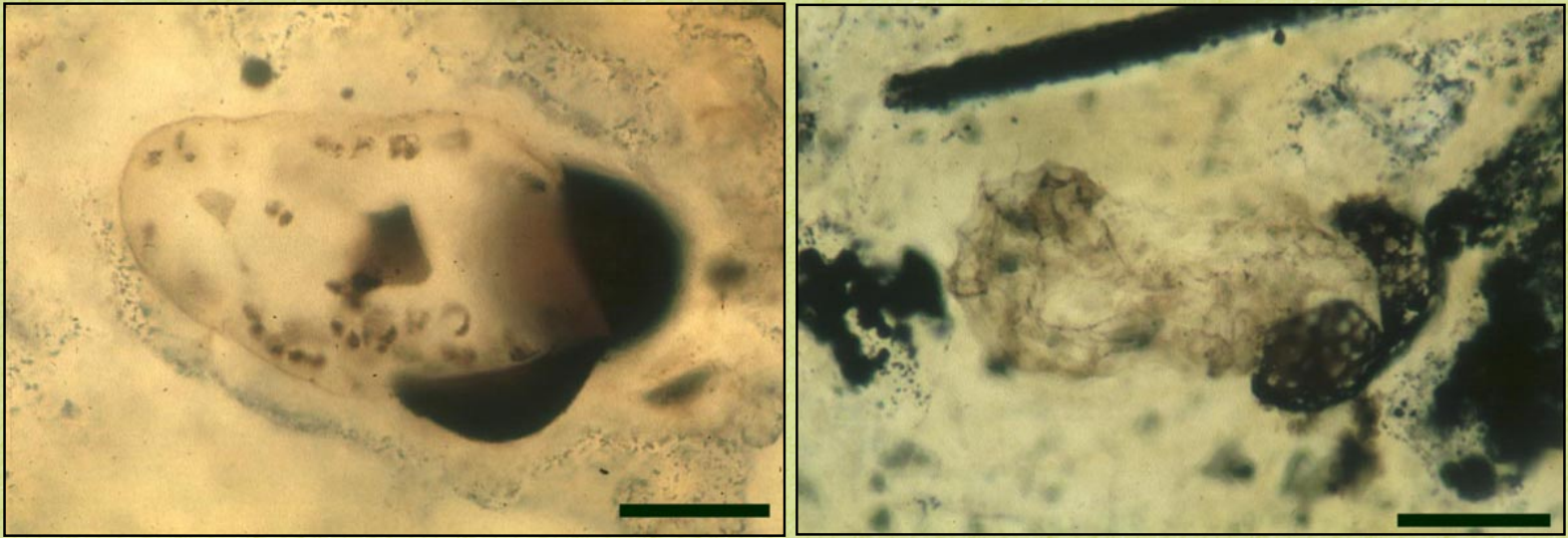
In the Rhynie chert many spores have also been found preserved during various stages of germination. This feature was first described by [Lyon \(1957\)](#). The following four images are some examples of stages in germination of *Retusotriletes* (see also insets above right), these are spores of *Aglaophyton major*.



Above: Spore preserved at the initial stage of germination where the trilete mark is beginning to split (scale bar = 25µm) (Copyright owned by University Münster).



Above: Spore preserved after the trilete mark has split with the embryo beginning to emerge (scale bar = 50µm) (Copyright owned by University Münster).



Above left and right: Preservation at further stages of embryo development (scale bar = 50 μ m)
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CONTENTS PAGE



Rhynie Chert Flora:

Basic Information on the Remaining Plant Groups in the Rhynie Chert

Introduction

A number of other flora have been described from the Rhynie chert, including the enigmatic [nematophytes](#), [cyanobacteria](#), various types of algae (including simple filamentous and unicellular [chlorophytes](#), and stoneworts or [charophytes](#)). Various types of [fungi](#) are also present, including terrestrial and aquatic types; the earliest recorded [lichen](#) has also been described.

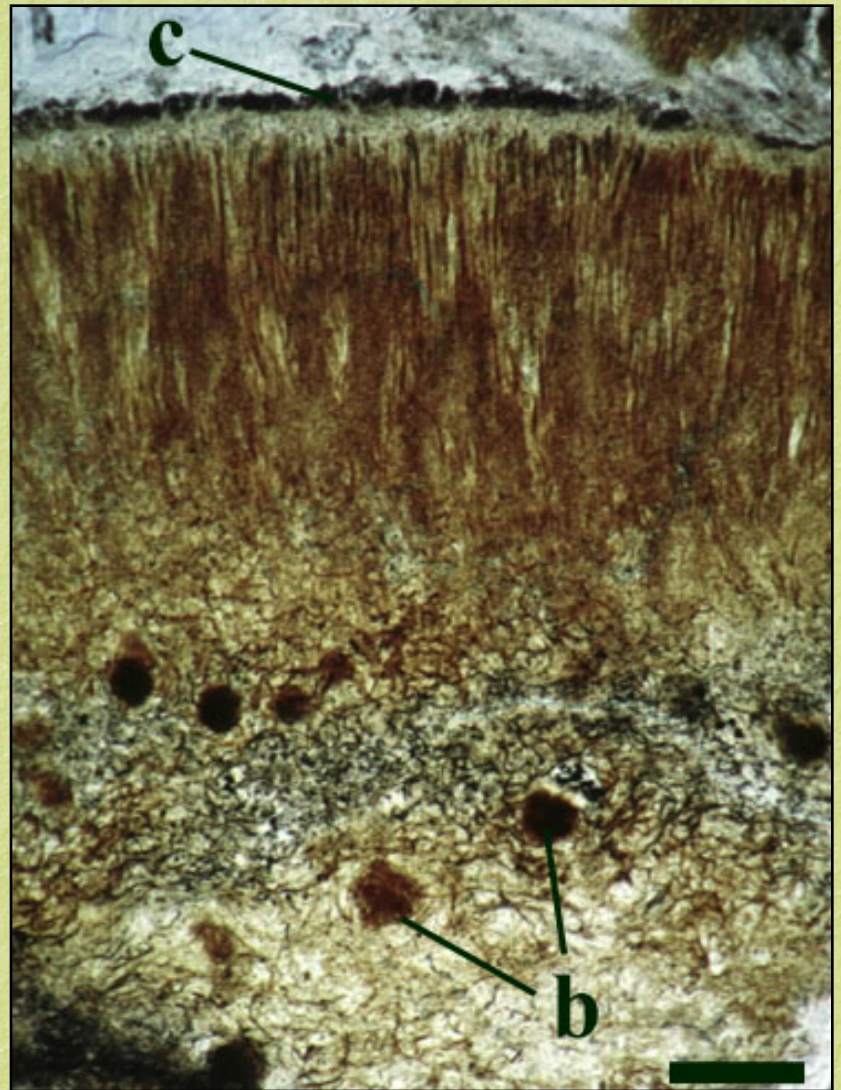
Nematophytes

An extinct, enigmatic group of plants comprising primarily an inner loose mesh-like plexus of spirally coiled tubes. The tubes may be smooth-walled or show spiral-thickenings; branching of these takes place in small knots. The tubes become closely packed, and may be orientated perpendicular towards the edge of the plexus where they meet an outer cuticular envelope.

Two nematophytes are known from the Rhynie chert: *Nematophyton taiti* ([Kidston & Lang 1921b](#)) (see inset right) and *Nematoplexus rhyniensis* ([Lyon 1962](#)). Both are generally fragmentary and poorly preserved.

The gross morphology of nematophytes is not fully known, though some Carboniferous types are believed to have resembled prostrate logs, perhaps with fronds. Their internal structure show similarities with certain algae, and the spirally thickened tubes resemble the tracheids in vascular plants.

The habitat of nematophytes is also not fully known, but they may have been semi-aquatic plants with emergent fronds.



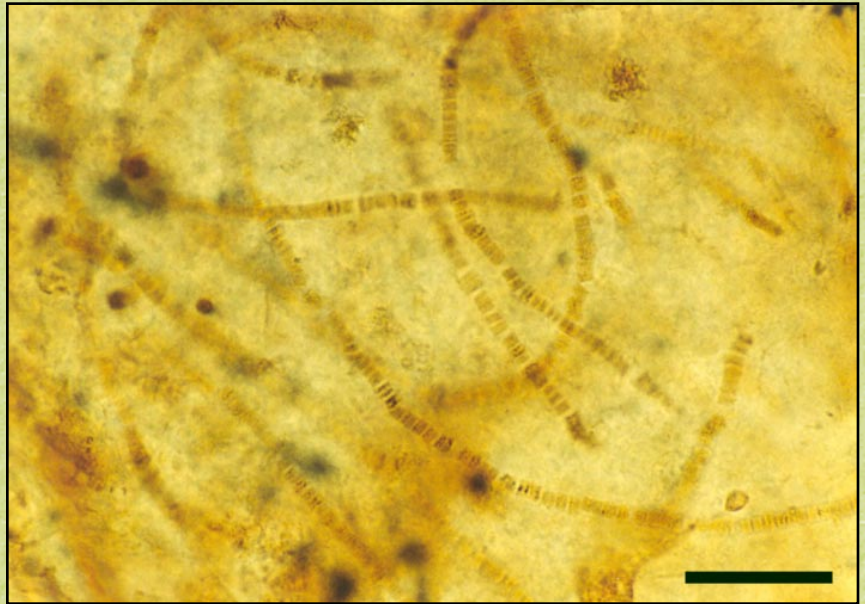
Above: *Nematophyton taiti*, showing loose plexus of coiled tubes (centre and bottom) with branch knots (**b**), passing upward into more tightly packed orientated tubes (top) with a probable external cuticle layer (**c**) (scale bar = 1mm).

Cyanophytes

These are simple photosynthetic bacteria, commonly termed **cyanobacteria**. These may be unicellular organisms or comprise filamentous chains of cells. Being prokaryotic organisms, the cells do not contain nuclei.

A number of probable cyanobacteria are found in the Rhynie chert, some contributing to distinct stromatolitic laminae in the laminated cherts, possibly having originally grown as cyanobacterial mats on sinter surfaces. Other types are found within 'clotted' chert textures, being deposited in more aquatic settings, and still others within decaying plants (see inset right).

Some of the Rhynie cyanobacteria, such as *Archaeothrix* (inset right), possessed **heterocysts** and therefore probably played a significant roll in fixing atmospheric nitrogen into the soil.



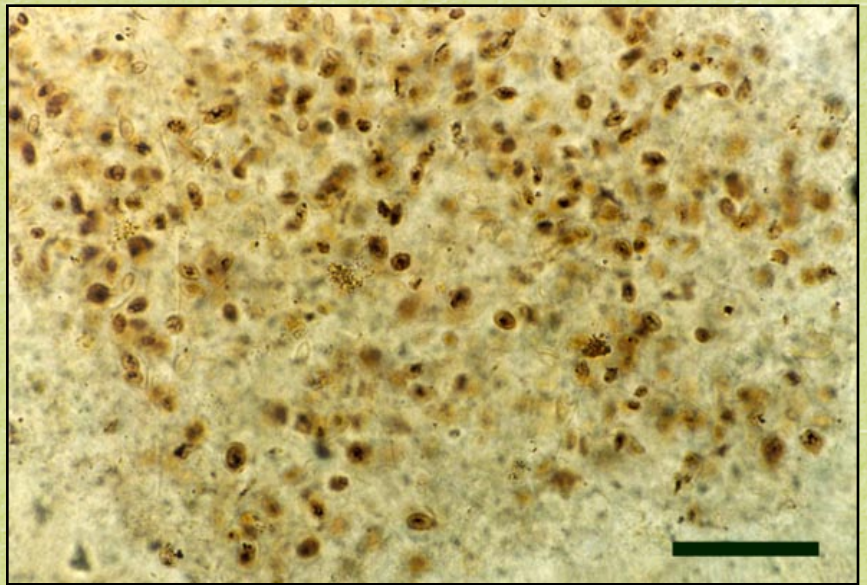
Above: Filaments of the cyanobacterium *Archaeothrix oscillatoriformis* within a stem of *Rhynia gwynne-vaughanii* (scale bar = 50µm).

Chlorophytes

Chlorophytes or green algae are photosynthetic eukaryotic organisms. Being eukaryotes their cells contain nuclei. They may be unicellular or form filamentous chains of cells, or may form more complex structures such as stoneworts or charophytes (see below). Most are found in freshwater settings.

A number of filamentous and unicellular chlorophytes are known from the Rhynie

chert, particularly in chert beds deposited in aquatic environments, though very often the poor preservation of cell contents makes their identification very difficult (see inset right).



Above: A number of unicells in Rhynie chert. Some of these displaying cell contents may represent unicellular eukaryotic algae (scale bar = 50µm).

Charophytes

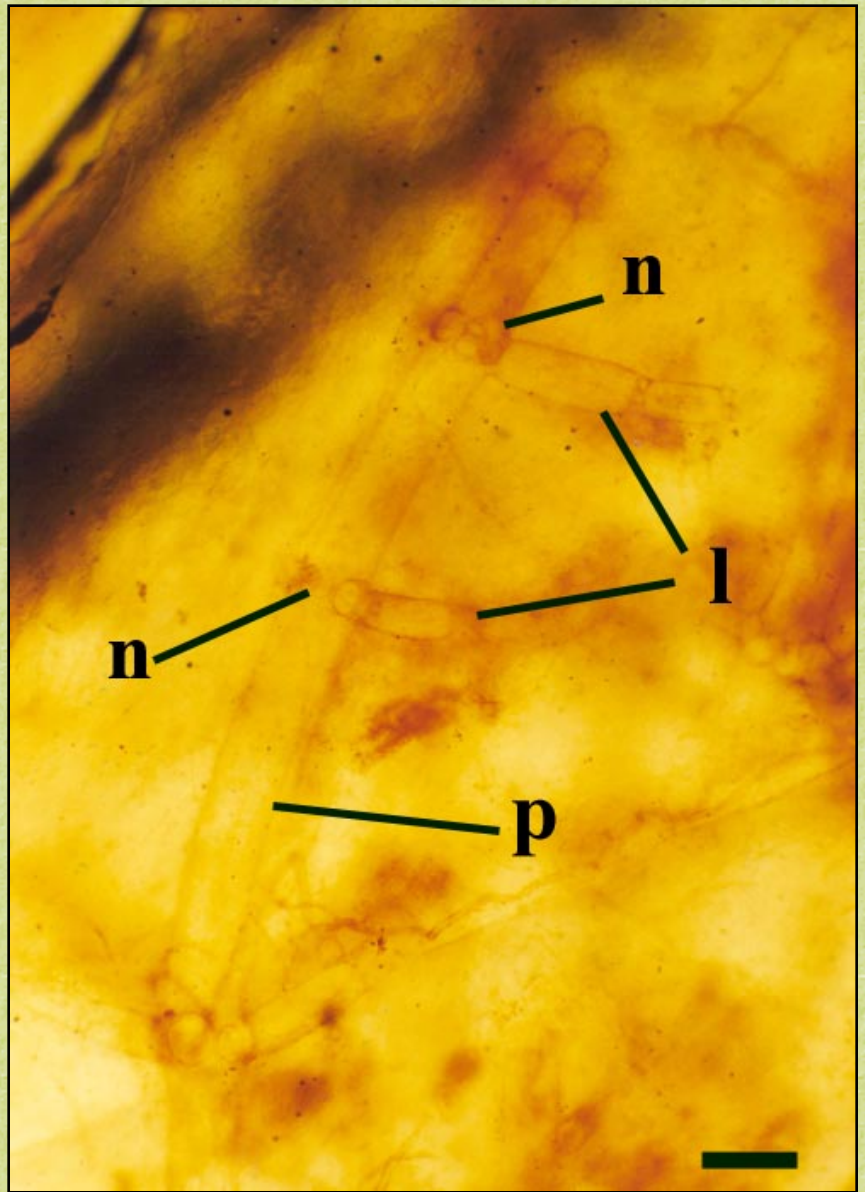
Charophytes are large structurally complex green algae. These plants comprise a series of multi-cellular **nodes** and long single cells or **internodes**. Branching occurs at the nodal cells and may be repeated. Charophytes also exhibit structurally complex **gametangia**. These organisms are aquatic, living in fresh to brackish water.

One probable charophyte has been described from the Rhynie chert, *Palaeonitella cranii* ([Kidston & Lang 1921b](#)). The reproductive structures of *Palaeonitella* have not been discovered and therefore its status has not been fully resolved.

Palaeonitella was an aquatic plant, being commonly found within 'clotted' chert textures, along with the crustacean

Lepidocaris.

Right: *Palaeonitella cranii* showing clusters of nodal cells (**n**) interspersed with long internodal cells (**p**). Lateral branches (**l**) are emerging from the nodes (scale bar = 150µm).



Fungi

Fungi are multi-cellular, non-photosynthetic eukaryotic organisms, generally being saprophytic (feeding on dead organic matter) or parasitic in their lifestyle; though some types form symbioses with plants (**endotrophic mycorrhizae**), or with an alga or cyanobacterium to form lichens.

Numerous fungi are recorded from the Rhynie chert ([Taylor *et al.* in press](#)), including the earliest best preserved examples of endotrophic mycorrhizae in plant tissue ([Taylor *et al.* 1995b](#)) (see

inset right). The earliest **ascomycetes** (true fungi that produce their spores within a sack-like structure called the ascus) are also present ([Taylor et al. 1999, in press](#)); together with various tiny aquatic or soil living **chytridiomycetes** or chytrids. A number of the latter have shown evidence of parasitism on other Rhynie plants and even on other fungi (an interaction called **mycoparasitism**).

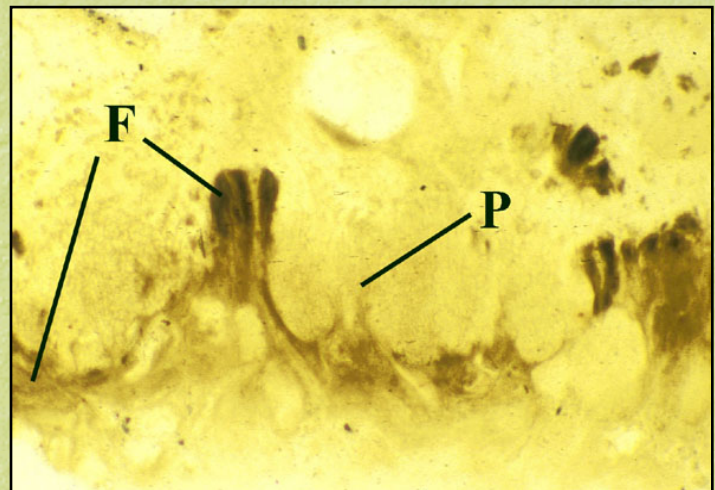


Above: Endotrophic mycorrhizae (**f**) occupying intercellular spaces within the cortex of *Aglaophyton major* (scale bar = 30 μ m) (Copyright owned by University Münster).

Lichens

Lichens are non-vascular plants formed by the symbiotic relationship between a **fungus** and an **alga** or a **cyanobacterium**. The lichen thallus comprises distinct layers of fungal hyphae (the **mycobiont**) and the alga/cyanobacterium (the **photobiont**).

The earliest lichen is recorded from the Rhynie chert, *Winfrenatia reticulata* ([Taylor et al. 1995, 1997](#)) (see inset right). *Winfrenatia* most likely colonised hard substrates. Degrading sinter surfaces could have provided a suitable substrate. It may have been able to weather the rock surfaces it was colonising, thus contributing to soil formation.

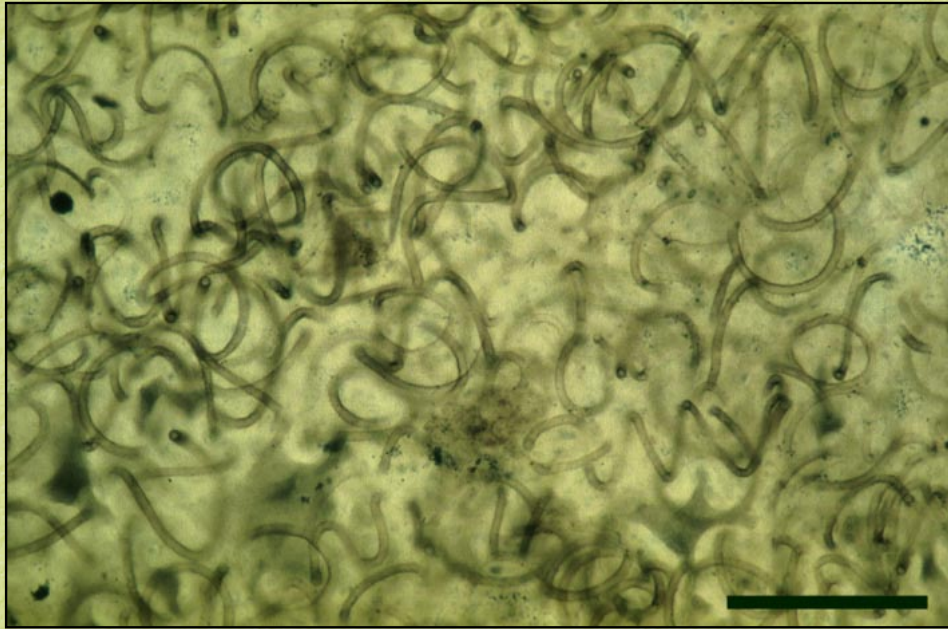


Above: Longitudinal view of the thallus of *Winfrenatia reticulata*. Tightly aggregated fungal hyphae (**F**) can be seen (the mycobiont). The surface of the thallus showing a series of pockets (**P**) with nets of fine hyphae containing the cyanobacterium (the photobiont) (Copyright owned by University Münster).

CONTENTS PAGE



Nematophytes



Above: *Nematoplexus rhyniensis* showing typical open meshwork of spirally coiled tubular cells (scale bar = 200 μ m) (Copyright owned by University Münster).

[Introduction](#)

[Morphology](#)

[Palaeoecology](#)

Introduction

Nematophytes or the **Nematophytalea** are an extinct group of enigmatic plants known only from Devonian and Carboniferous sedimentary rocks. Their systematic position is unresolved, showing certain affinities with fungi, algae and also, tentatively, with vascular plants. Their gross morphology and habitat (particularly as to whether they were aquatic, semi-aquatic or fully terrestrial plants) are also not fully known, but some appear to have been

cylindrical organisms up to 1 metre in length (see [Stewart 1999](#)). Nematophytes appear to generally comprise networks of intertwined spirally coiled tubular cells showing both smooth and spirally-thickened walls (the latter similar in appearance to [tracheids](#) in vascular plants), with branching localised in distinct 'knots'. The plants appear to have had a variably preserved cuticle-like layer on their outer surface. Certain Carboniferous nematophytes appear to have attained quite a large size, in life probably looking like prostrate logs.

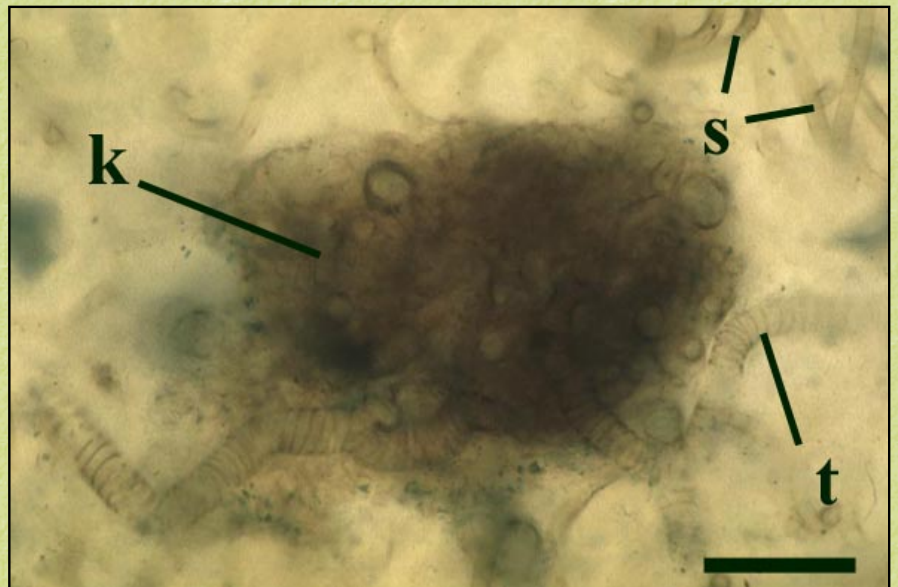
At Rhynie, sandstone casts of probable nematophytes have been found in the past in the [Quarry Hill Sandstone](#). Two incomplete nematophytes have been described from the Early Devonian Rhynie chert: *Nematophyton taiti* ([Kidston & Lang 1921b](#)) and *Nematoplexus rhyniensis* ([Lyon 1962](#)). Fragmentary nematophyte remains also occur in the Windyfield chert ([Fayers & Trewin in press](#)). For the purposes of this resource, the morphology of one of the Rhynie nematophytes, *Nematoplexus rhyniensis* is outlined below:

Morphology

Nematoplexus rhyniensis

Nematoplexus rhyniensis was first described by [Lyon \(1962\)](#), and is only known from incomplete, partially decayed, and generally fragmentary remains. As such, like other nematophytes, the gross morphology of the organism and its overall size is unknown. Conforming to the general internal nematophyte structure, *Nematoplexus* comprises an open meshwork or plexus of intertwined, spirally coiled tubular cells (see heading photograph). The tubes show no preferred orientation, but in the sample described by [Lyon \(1962\)](#) they appear more compacted towards the outer surface of the plexus where they abut onto a structureless clear zone which may represent a partially decayed natural surface layer or membrane.

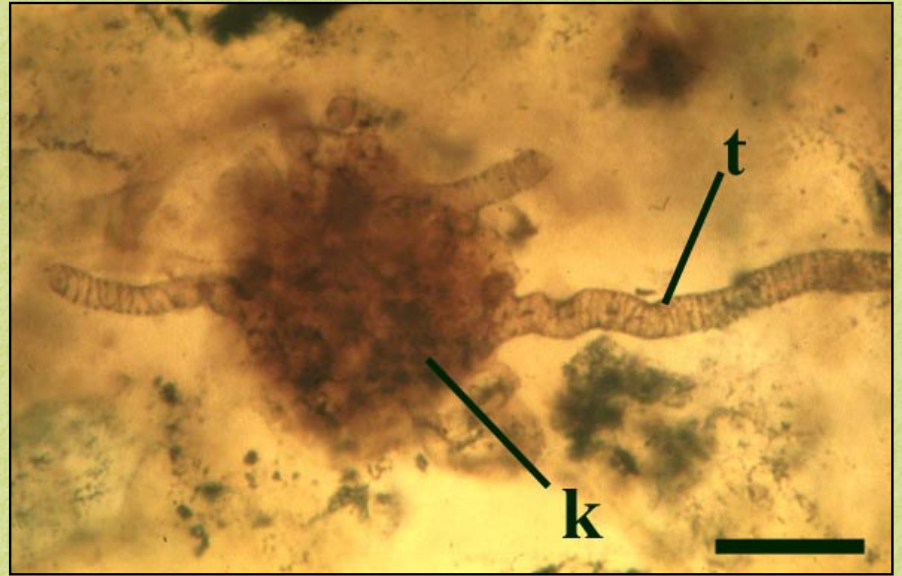
Branching of the tubes occurs in what appear to be dark, amorphous spots, but in better preserved samples these, in fact, comprise very tightly coiled knots of tubes showing repeated and closely spaced branching (see insets right and below right). These branch-knots occur in two discrete sizes, the smaller ranging from 45µm to 76µm in size and the larger knots between 99µm and 270µm.



Above: Taken from the holotype of *Nematoplexus rhyniensis*, this image shows a typical branch knot (**k**) with tubes with thickenings (**t**). Smooth tubes (**s**) are also shown (scale bar = 100µm) (Copyright owned by University Münster).

The tubes show two distinct morphologies. The most abundant form are smooth-walled, non-septate tubes ranging from 7 μ m to 10 μ m in diameter, typically appearing as lax intertwined coils (see inset below left). Branching of the smooth-walled tubes occurs within the smaller branch-knots.

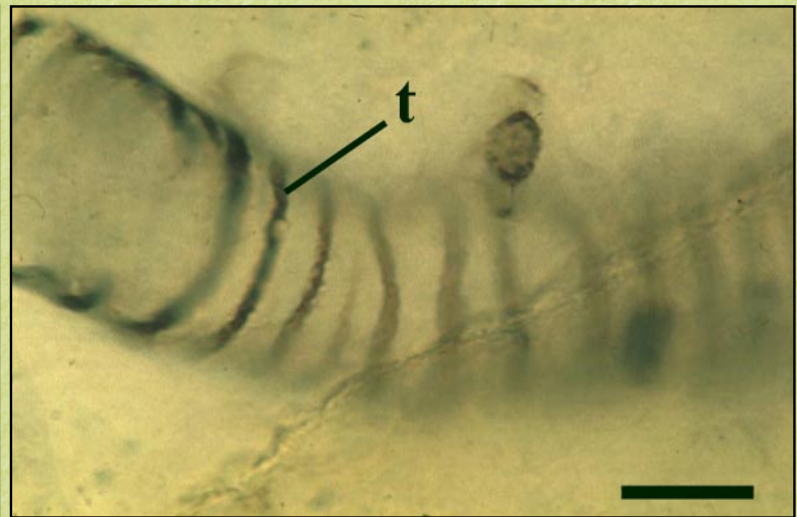
The second type are thin-walled tubes displaying conspicuous spiral thickenings within the wall layer. These range from 2 μ m up to 28 μ m in diameter and are again non-septate (see inset below right). The spirally thickened tubes are generally found as short isolated fragments or as irregular clusters within the smooth-walled tube plexus. Branching of these tubes occurs within the larger branch-knots. Occasionally tubes of both types may originate from a single, large branch-knot, though no organic connectivity between the two types have been observed.



Above: Another branch knot (**k**) of *Nematoplexus* with emerging tubes with spiral thickenings (**t**) (scale bar = 100 μ m) (Copyright owned by University Münster).



Above: A spirally coiled smooth-walled tube of *Nematoplexus* (scale bar = 50 μ m) (Copyright owned by University Münster).



Above: A thin-walled tube of *Nematoplexus* with spiral thickenings (**t**) (scale bar = 10 μ m) (Copyright owned by University Münster).

Palaeoecology

As stated in the introduction, the habitat of *Nematoplexus* and nematophytes in general remains unresolved.

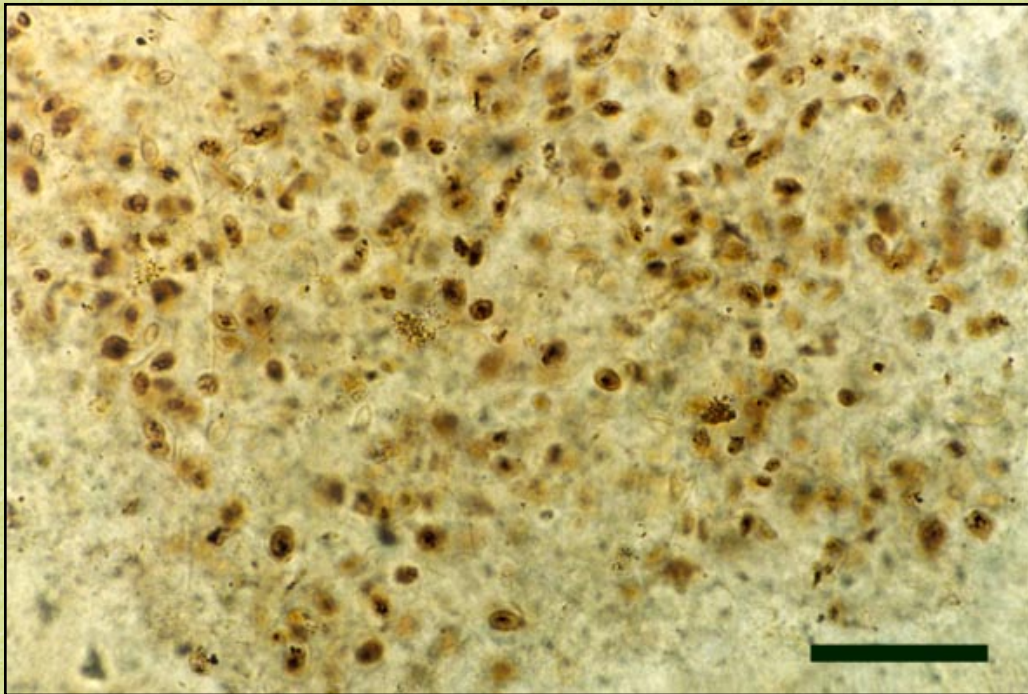
A number of authorities believe that nematophytes were aquatic plants. In the Rhynie chert the two nematophytes *Nematoplexus* and *Nematophyton* are typically found in association with filamentous green algae (chlorophytes), charophytes, cyanobacteria, occasionally with the crustacean *Lepidocaris* and with coprolites in a 'clotted' chert matrix; indicative of silicification in a freshwater, aquatic environment. However, in these instances, it may be that the nematophyte remains had been transported, after death, into such aquatic settings or alternatively had been drowned *in situ* after a flooding event.

They may, however, have been terrestrial or at least semi-aquatic organisms, suggested by the resemblance of the spirally-thickened tubes seen in the Rhynie chert nematophytes to the thickened tracheids in the xylem of vascular plants. It may be that these organisms grew in shallow water with the spirally-thickened tubes differentiated in emergent fronds or 'leaves'. However, to date, no unequivocal evidence of such differentiation has been found in any fossil nematophytes.

CONTENTS PAGE



Chlorophytes



Above: A number of unicells in Rhynie chert. Some of these displaying cell contents may represent unicellular eukaryotic algae (scale bar = 50 μ m).

[Introduction](#)

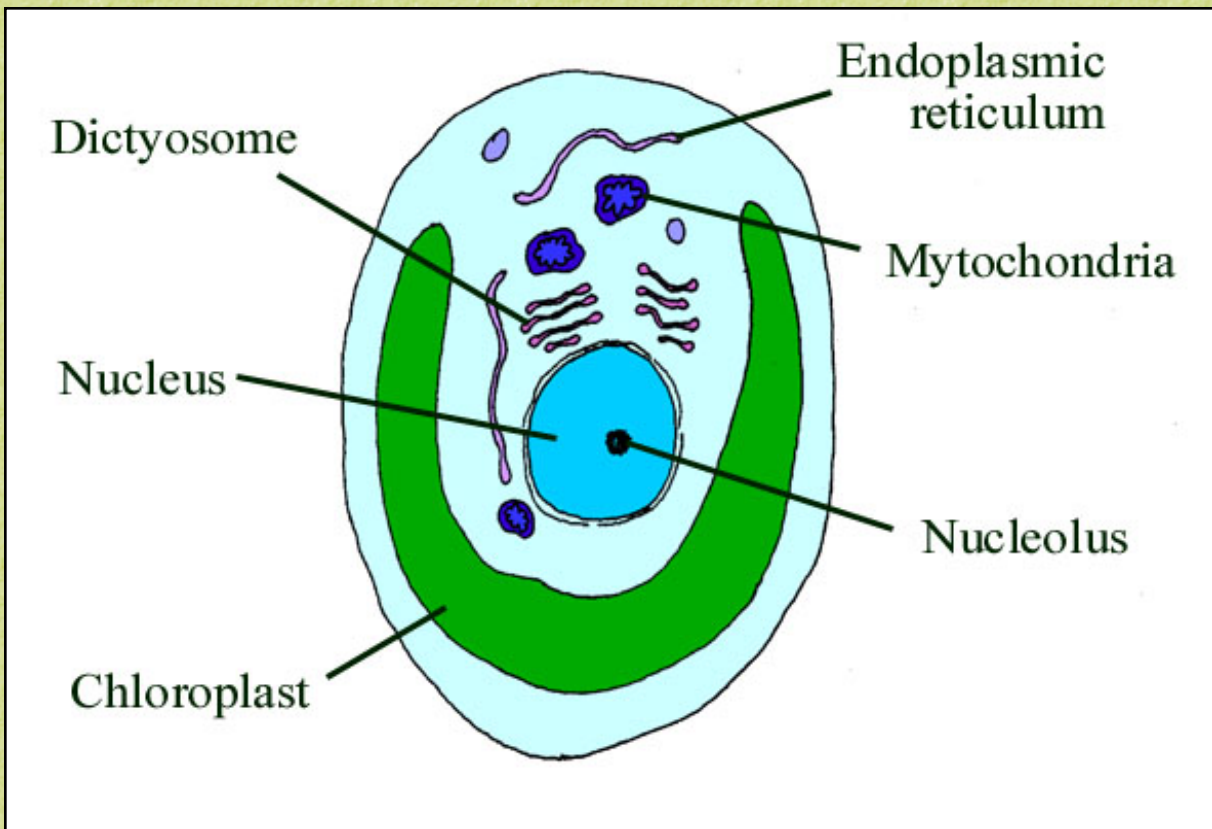
[Fossil Record](#)

[Morphology](#)

Introduction

Chlorophytes are a particular division of [eukaryotic](#) algae comprising the green algae. They are

characterised by containing two types of chlorophyll, *a* and *b* and starch is formed in **chloroplasts** (see inset below). Green algae may be unicellular but can also form complex multicellular structures such as that seen in the stoneworts or **charophytes** (see section on **charophytes**). These non-vascular plants are typically found in freshwater environments.



Above: Diagrammatic section through a single eukaryotic cell.

Fossil Record

Chlorophytic algae are among the oldest known fossils, being recorded from Precambrian rocks primarily from the Ediacara fauna. These Ediacaran fossils are **acritarchs** and were probably formed by unicellular algae. In fact the discovery of undoubted chlorophytes in the 850 million year old Late Proterozoic Bitter Springs Chert in Australia was the first ever evidence of early eukaryotes. Multicellular chlorophytes are first seen in Cambrian strata where they helped to build algal reefs. Very well preserved chlorophytes are also known from the famous Middle Cambrian Burgess Shale in British Columbia, Canada.

Apart from 'charophytes', a number of other chlorophytes have been found in the Rhynie chert including unicellular and filamentous types. Of these, to date, two filamentous types have been formally described by [D.S. Edwards and Lyon \(1983\)](#); *Mackiella rotunda* and *Rhynchertia punctata*. The morphology of

these simple green algae is outlined below.

Note: It must be remembered that the affinities of many fossil algae, including those found in the Rhynie chert remain uncertain. This is primarily because modern classifications of algae are based on biochemical and ultrastructural features which are rarely or indeed never preserved in the fossil record ([D.S. Edwards & Lyon 1983](#)). Also, positive identification may be compounded by the variable preservation of cell contents.

Morphology

Mackiella rotunda

This alga comprises unbranched filaments up to 850µm in length forming an unattached thallus with no rhizoids. The filaments consist of up to 25 cylindrical cells, each cell typically being more-or-less equal in length and in width (23µm to 41µm and 28µm to 40µm respectively). The terminal cells of the thallus are rounded and slightly longer than the other cells (29µm to 49µm in length). The cell walls are thin and do not show a mucilaginous sheath. The cell contents comprise fine granular material and a dark spherical body, 3.5µm in diameter, interpreted by [D.S. Edwards and Lyon \(1983\)](#) as a **pyrenoid** or the chloroplast.

Mackiella was a eukaryotic alga. Because the alga shows unattached filaments that may fragment into short filaments and the cells possess a single pyrenoid, D.S. Edwards and Lyon ([1983](#)) tentatively assigned *Mackiella* to the extant order **Ulotrichales**.

Rhynchertia punctata

This alga consists of an unbranched, unattached thallus comprising multicellular filaments of cells 8µm to 17µm in width and commonly twice that in length. The terminal cells of the thallus are rounded and slightly shorter than the other cells. The cells are thin walled and do not show a mucilaginous sheath. The cell contents may be uniform, or with a single dark body (possibly a chloroplast) or may contain many small ovoid bodies. The latter have been interpreted to be reproductive elements, possible zoospores or gametes ([D.S. Edwards & Lyon 1983](#)).

Rhynchertia filaments have been found in association with the nematophyte *Nematoplexus*, primarily within 'gelatinous' areas where the latter appears to have degraded ([Lyon 1962](#)). Based on gross morphology, this alga has also been tentatively assigned to the **Ulotrichales** by D.S. Edwards and Lyon

(1983).

CONTENTS PAGE



Fungi



Above: Fungal hyphae and spore cysts in a stem of *Asteroxylon mackiei*. Two species of fungi appear to be present, the smaller cysts (bottom left) are probably *Palaeomyces asteroxyli*, the larger thick-walled cysts probably belong to *Palaeomyces gordonii* (scale bar = 200 μ m).

[Introduction](#)

[Fossil Record](#)

[Morphology](#)

Introduction

Fungi are an important group of multicellular **eukaryotic** organisms comprising a meshwork of thread-like filamentous cells joined end-to-end. The whole body of a fungus is called the **mycellium**. Fungi are usually classified into four main divisions; the **chytridiomycetes** or chytrids (tiny, predominantly aquatic fungi), the **zygomycetes** (bread molds and mycorrhizae), the **ascomycetes** (terrestrial, mostly saprophytic fungi, including cup fungi and yeasts), and the **basidiomycetes** (club fungi, including toadstools and mushrooms; entirely terrestrial); the differences made primarily on the process of reproduction and the morphology of the **sporangia** since the reproductive structures are generally more diverse than the mycellium.

- Chytrids have motile sexual and asexual spores with posterior **flagella**.
- Zygomycetes have thick-walled resting sexual spores called **zygospores**, their asexual spores are produced in a sporangium and called **sporangiospores**.
- Ascomycetes produce sexual spores (**ascospores**) in a sack-like body called an **ascus**, their asexual spores are produced externally, borne on a **conidiophore**.
- Basidiomycetes produce their spores externally from a club-like structure called a **basidium**, these generally have no asexual spores.

Fungi may reproduce sexually or asexually and like plants show alternations in their life cycle.

Fungi are unable to build structural materials by photosynthesis (they are **heterotrophic** organisms). They live on organic material from other living things, alive or dead and are therefore generally parasitic or saprophytic. Some types of fungi, however, form symbioses with plants. Certain fungi are **mutualists** forming symbioses with a green alga (chlorophyte) or a cyanobacterium to create **lichens**. Some types of symbiotic zygomycetes live within plants and are called **endotrophic mycorrhizae** (literally "fungus-root"). The latter are fungal hyphae that grow into the cells of plants, branching within them to form **arbuscles** where the exchange of nutrients takes place. The hyphae also occasionally grow to form thick swellings or **vesicles** and are thus often termed **vesicular-arbuscular mycorrhizae**. In both cases of symbiosis the fungus supplies the plant 'partner' with water and mineral nutrients, especially if these are in short supply in the soil; whereas the plant supplies the fungus with carbohydrates from photosynthesis.

Fossil Record

Fossil fungi tend to be microscopic and not always found with their reproductive structures attached, therefore positive identification is often extremely difficult. They are not especially rare as fossils, though the best preserved examples are generally found in amber, for example the Oligocene Baltic ambers and Cretaceous ambers from northern France.

The earliest record of fungi in the fossil record are of probable chytridiomycetes or chytrids from Vendian strata (Late Precambrian, 650 to 544 million years ago) of northern Russia. The Early Devonian Rhynie

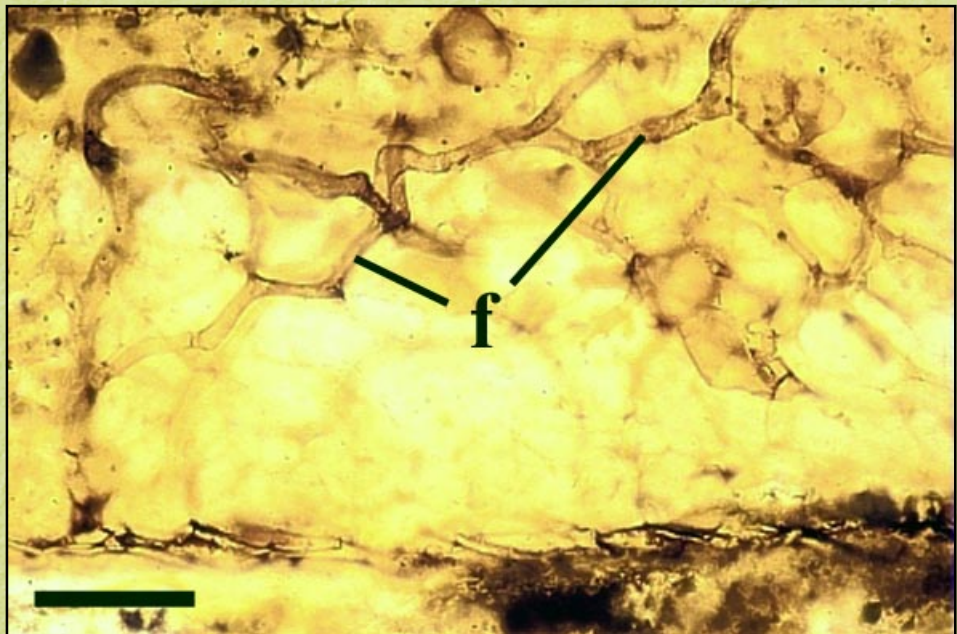
chert is host to a plethora of fossil fungi including various endotrophic mycorrhizae, the earliest ascomycetes, several chytridiomycetes and various other undescribed fungi (see [Kidston & Lang 1921b](#); [Hass & Remy 1992](#); [Taylor et al. 1992a](#) & [b](#); [Hass et al. 1994](#); [Remy et al. 1994a](#) & [b](#); [Taylor et al. 1994](#), [1995](#), [1999](#), [in press](#)).

For the purposes of this resource, the morphology and palaeoecology a small selection of different types of fungi from the chert are outlined below:

Morphology

Endotrophic Mycorrhizae

As we have seen above, endotrophic mycorrhizae are fungal hyphae that grow within cortical cells of many plants (see inset right) with which they share a symbiotic relationship (see also the section on [Evidence for plant/animal interactions](#)). These have been found within many of the well preserved Rhynie plants, though to date the only vesicular-arbuscular mycorrhizae formally described have been those found in the outer cortex of stems of *Aglaophyton major* and named *Glomites rhyniensis* ([Taylor et al. 1995b](#)) (see insets right and below right).

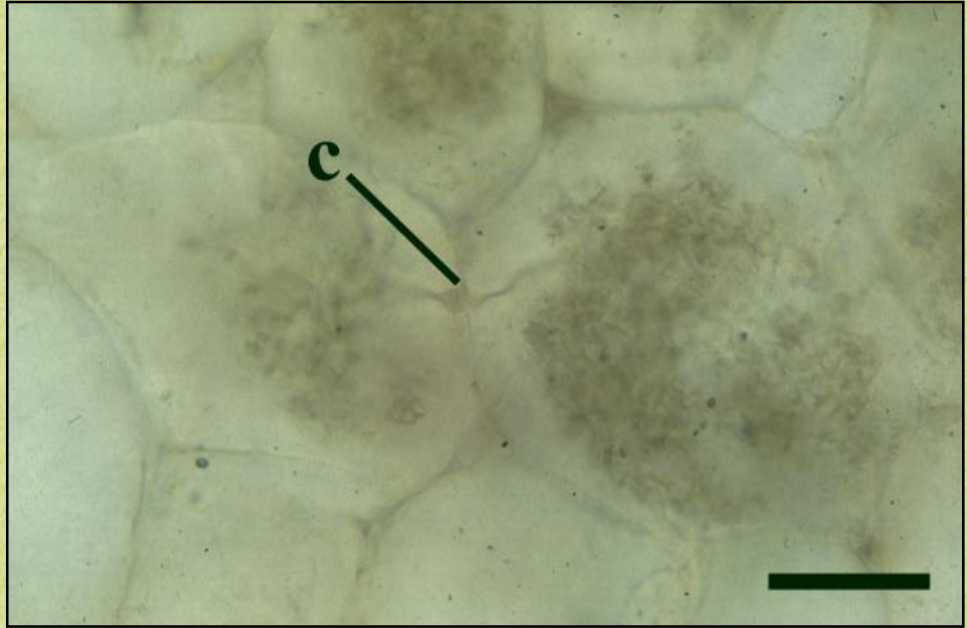


Above: Fungal hyphae (f) penetrating the outer cortex of an *Aglaophyton major* stem (scale bar = 100µm)
(Copyright owned by University Münster).

Fungal hyphae of these mycorrhizae are often found to crowd the intracellular spaces in the cortex of the plant. Many thin sections show where the fungus has penetrated and entered the cells, in which they have formed the tree-shaped arbuscles (see inset right).

These fungi were terrestrial symbionts, though in part may also have been saprophytic after the death of the plant partner.

Right: Cortical cells of *Aglaophyton major* with well developed arbuscles. The places where the fungus penetrated the cell wall are shown (c) (scale bar = 20 μ m)
(Copyright owned by University Münster).



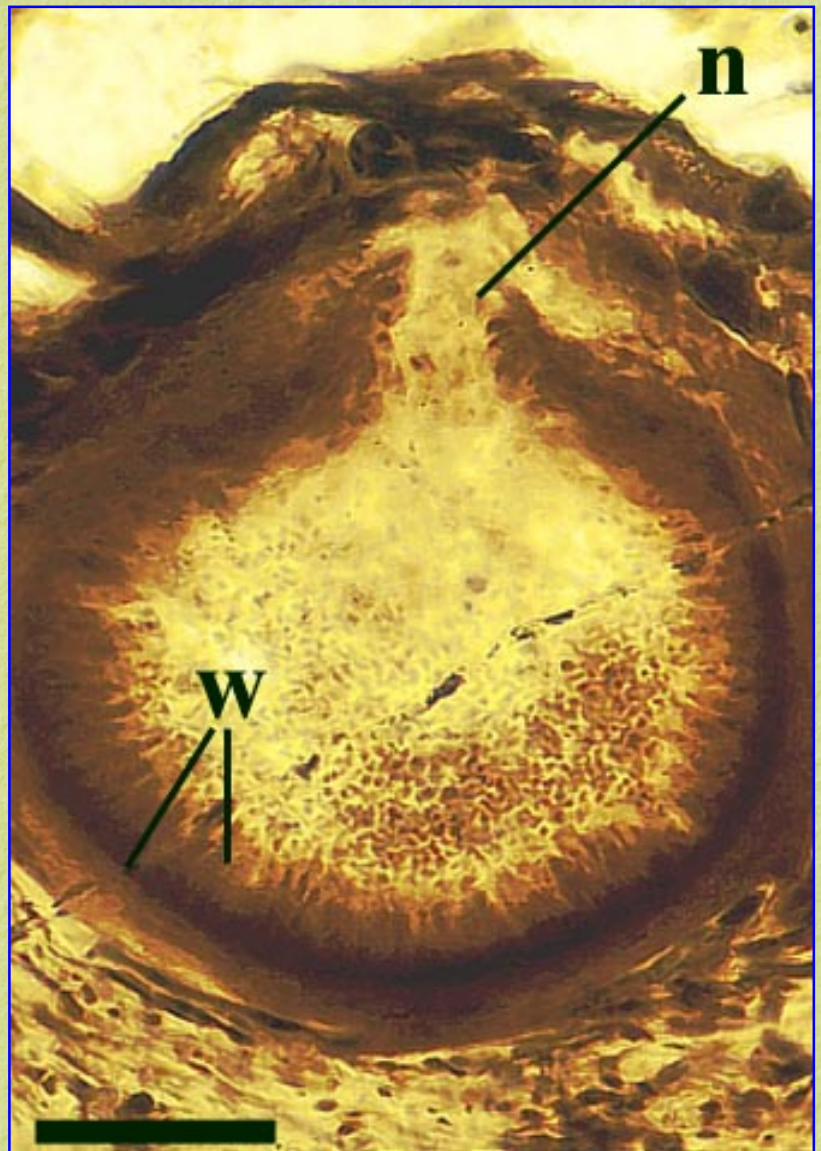
Ascomycetes

The earliest unequivocal ascomycetes have been described from the Rhynie chert by [Taylor *et al.* \(1999\)](#). The flask-shaped **ascocarps** or **peritheca** (fruiting bodies) of these fungi have been found just below the epidermis of partially decayed stems, rhizomes and microphylls of the lycophyte *Asteroxylon mackiei*. The peritheca are on average 400 μ m in size and often appear to have developed in the stomatal chambers of the plant (see inset right). The walls of each perithecium comprise two layers of hyphae forming a thickened wall. In mature samples the **asci**, approximately 50 μ m in length, appear to arise from the inner wall of hyphae. Each ascus contains between sixteen and thirty two ascospores, these are approximately 5 μ m in length.

These ascomycetes were terrestrial and

probably saprophytic.

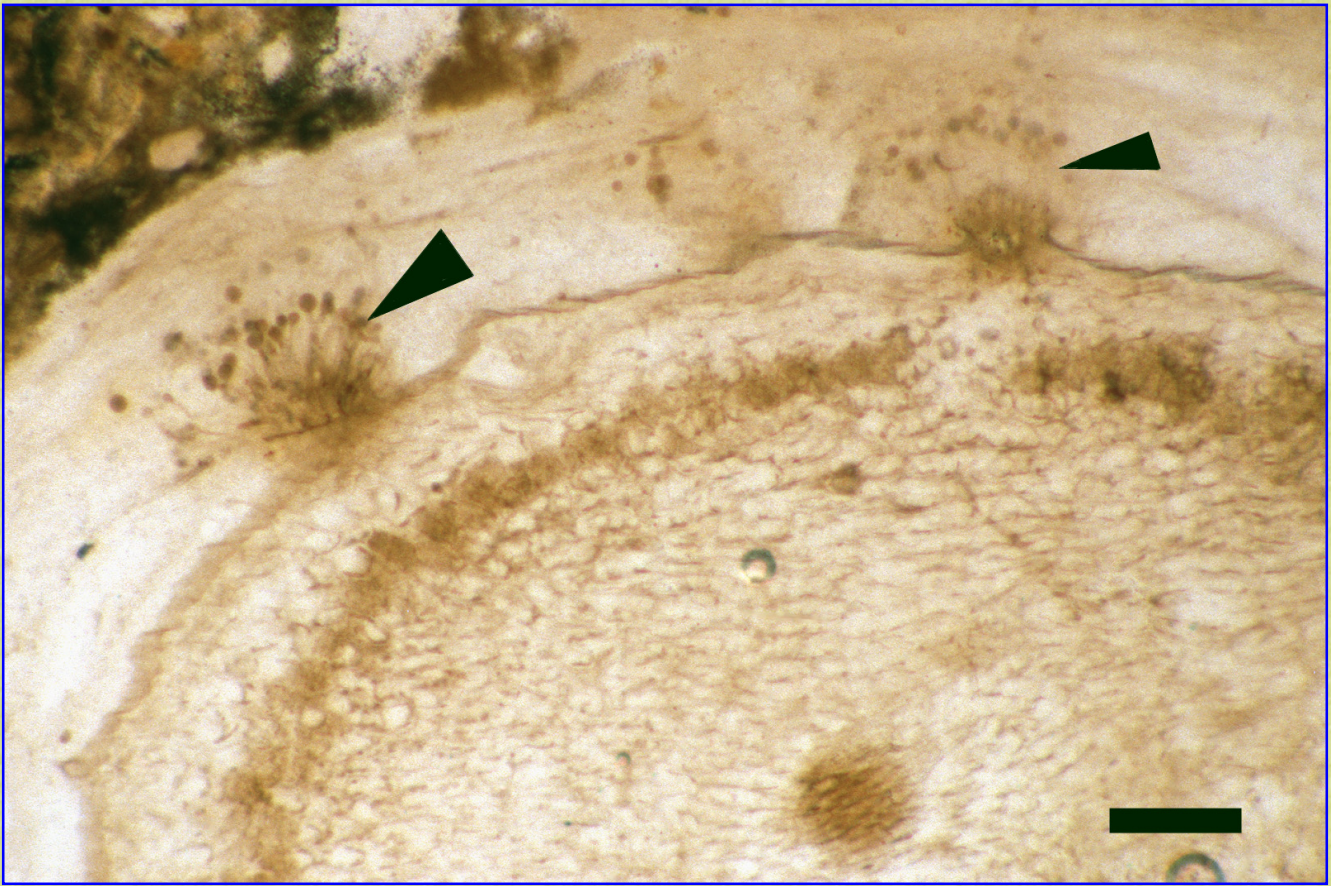
Right: Mature perithecium in a stomatal chamber of *Asteroxylon*. This shows the two layers of the wall (w) and the opening through which the ascospores are released (n). Click on the image for a close up! (scale bar = 100µm) (Copyright owned by University Münster).



Read more about the Rhynie chert ascomycetes on the web site of the Palaeobotanical Research Group, University of Münster [here](#). The formal description and diagnosis for the fossil ascomycete is currently awaiting publication ([Taylor *et al.* in press](#)).

Chytridiomycetes

The tiny, predominantly aquatic chytrids are the most common forms of fungi found in the Rhynie chert. Most resemble fungi from either of two extant orders, the **Blastocladales** and the **Spizellomycetales**. Both orders include saprophytic and parasitic fungi, though living spizellomycetales are mostly found in damp and water-logged soil.

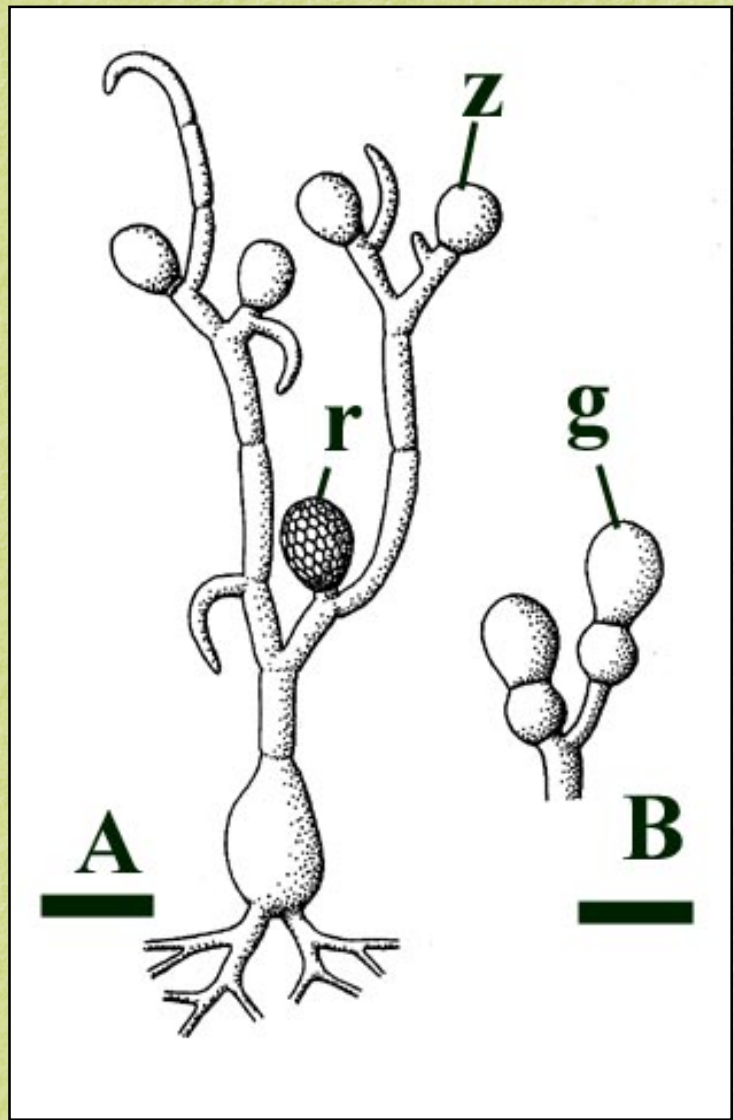


Above: Transverse section of an *Aglaophyton* stem with fungal tufts of *Palaeoblastocladia milleri* (arrowed) on the epidermis. Click on image for a close up! (scale bar = 200µm) (Copyright owned by University Münster).

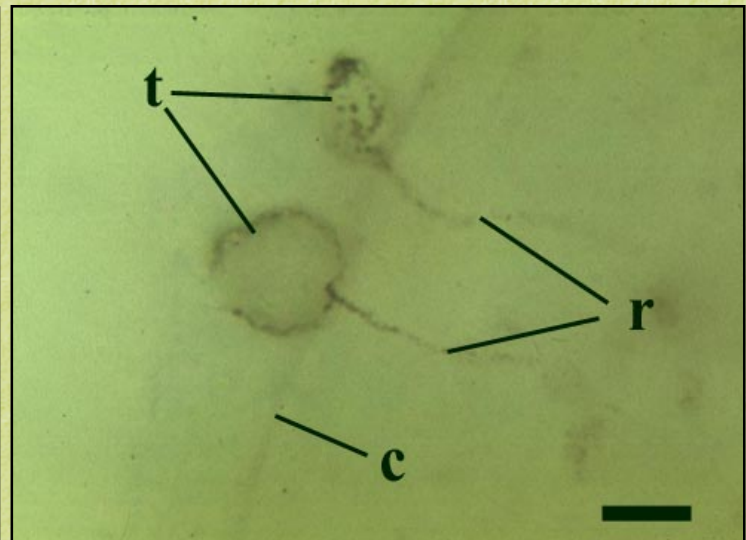
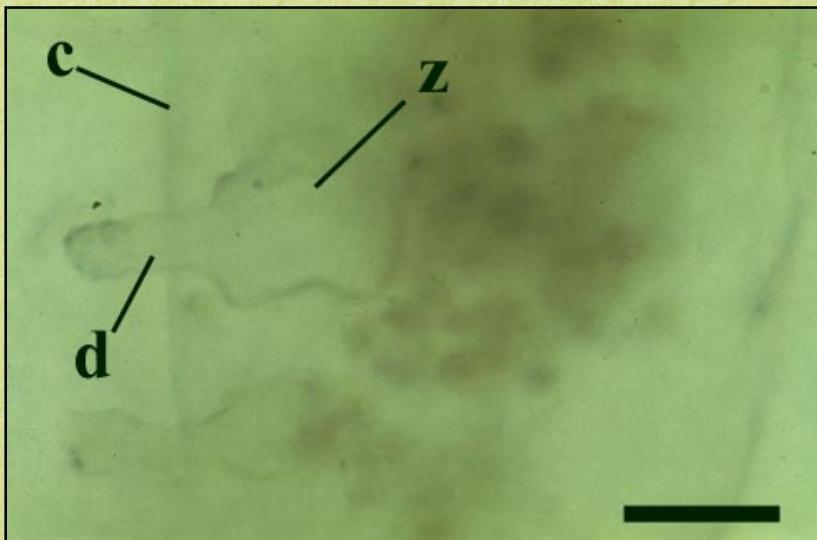
One of the Rhynie chytrids, *Palaeoblastocladia milleri*, ([Remy, et al. 1994](#)) is a blastocladalean. It occurs as tufts that arise from the stomata or from between the cuticle and epidermis of *Aglaophyton major* stems (see inset above). The non-septate hyphae of the fungus form two types of mature thalli. The **sporothalli** (the **sporophyte** generation of the fungus) show repeated **dichotomous** branching and bear terminal globose zoosporangia and pitted, thick-walled resting sporangia (see inset right). The **gametothalli** (the **gametophyte** generation of the fungus) also show dichotomous branching and bear terminal chains of two or three globose **gametangia** (see inset right).

This chytrid was aquatic and a saprophyte.

Right: Idealised reconstruction of *Palaeoblastocladea milleri*. **A**: Sporothallus showing terminal zoosporangia (**z**) and resting sporangia (**r**) (scale bar = 40µm). **B**: Part of a gametothallus showing terminal gametangia (**g**) (scale bar = 20µm) (after [Remy et al. 1994](#)).



Other Rhynie chert chytrids were clearly aquatic parasites, three types have been described as parasites on the probable charophyte *Palaeonitella cranii* by [Taylor et al \(1992\)](#). Below are images of two of these, *Milleromyces rhyniensis* (inset below left) and *Lyonomyces pyriformis* (inset below right).



Above: The zoosporangium of *Milleromyces rhyniensis* within a *Palaeonitella* cell. The cell wall of the alga (**c**) is penetrated by a cylindrical discharge tube (**d**). The globose zoosporangium inside the cell (**z**) is empty and partially collapsed (scale bar = 20µm) (Copyright owned by University Münster).

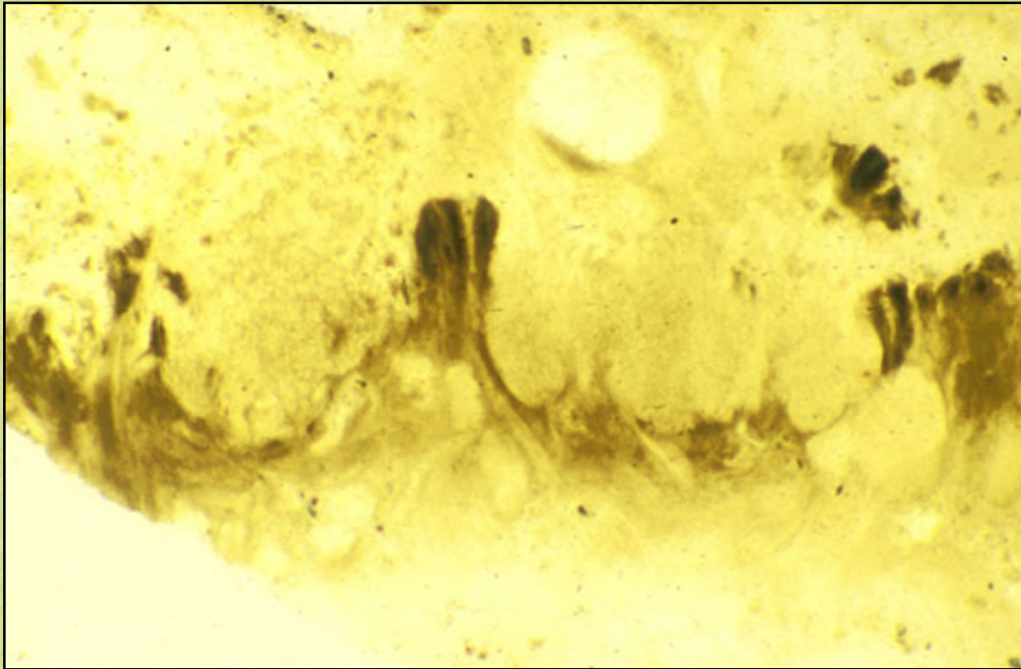
Above: Two spherical thalli of *Lyonomyces pyriformis* (**t**) attached to the outside of a *Palaeonitella* cell. The cell wall (**c**) is penetrated by two collapsed rhizoids (**r**) (scale bar = 10µm) (Copyright owned by University Münster).

A review of the Rhynie chert fungi is currently awaiting publication ([Taylor et al. in press](#)).

CONTENTS PAGE



Lichens



Above: The thallus of the cyanolichen *Winfrenatia reticulata* (Copyright owned by University Münster).

[Introduction](#)

[Fossil Record](#)

[Morphology](#)

[Palaeoecology](#)

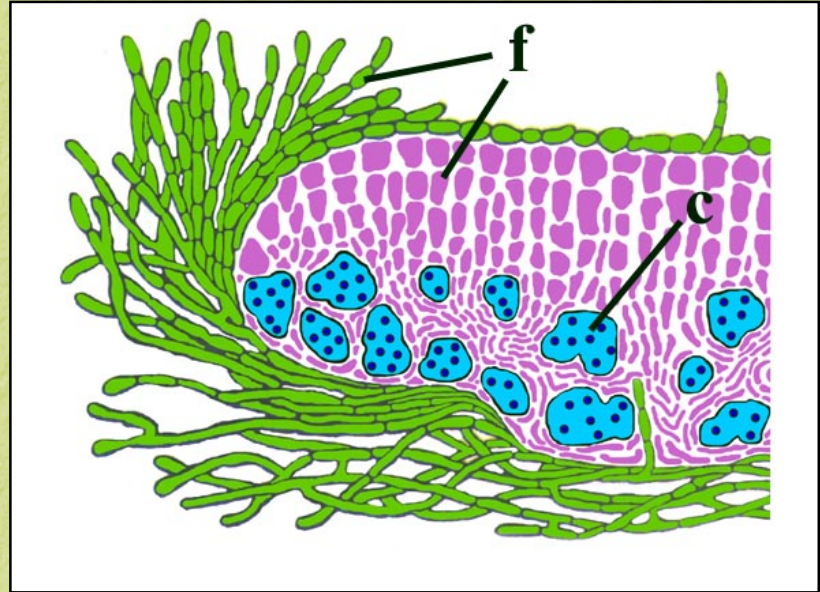
Introduction

The earliest known fossil lichen, *Winfrenatia reticulata* ([Taylor et al. 1995](#), [1997](#)) has been described from the Rhynie chert.

Lichens are a group of non-vascular plants that are formed by a symbiotic association between a **fungus** (termed a **mycobiont**) and **green alga** or a **cyanobacterium** (termed a **photobiont**). The relationship is mutually beneficial since the photobiont can obtain water and nutrients as well as some degree of protection from the fungus whereas the mycobiont gains a source of carbon. Today lichens are relatively diverse and have adapted to a number of different habitats, for example, being found in mountain, desert and tundra regions.



Above: Modern lichens encrusting a rock surface near a hydrothermal area, Iceland.



Above: Diagrammatic section through a lichen showing the layered fungal hyphae (f) and alga or cyanobacterium (c).

Fossil Record

Lichens are not common in the fossil record. This partly reflects the fact that the habitats in which they are often found, are rarely conducive to fossil preservation. A few fossil lichens have been described from Mesozoic and Cenozoic rocks, most notably from Oligocene Baltic amber ([Larson 1978](#); [Garty et al. 1982](#)). It has been suggested that a number of the Precambrian Ediacara fossils may represent lichens ([Retallack 1994](#)) though this remains rather suspect. It is evident that complex microbial communities were present even 3,500 million years ago, however, whether any of these comprised physiological symbioses is uncertain. Thus *Winfrenatia reticulata*, from the Rhynie chert is considered the oldest known lichen. The morphology of *Winfrenatia* is outlined below.

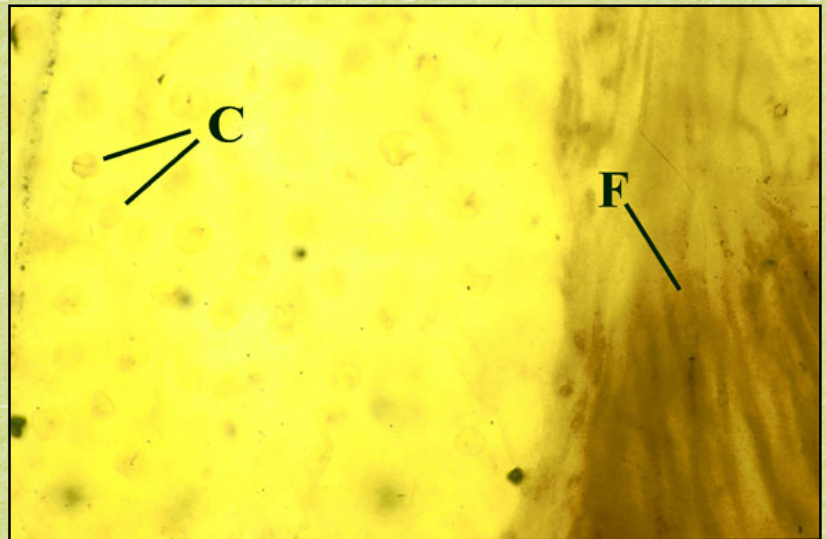
Morphology

The overall morphology of the fossil thallus of *Winfrenatia* is relatively simple. It comprises thin layers between 1 and 2mm thick that contain tightly packed aggregates of fungal hyphae (the mycobiont) (see inset right).



Above: Thin section showing a longitudinal view of the thallus of *Winfrenatia reticulata*. Tightly aggregated fungal hyphae (F) can be seen (the mycobiont). The surface of the thallus showing a series of pockets (P) (Copyright owned by University Münster).

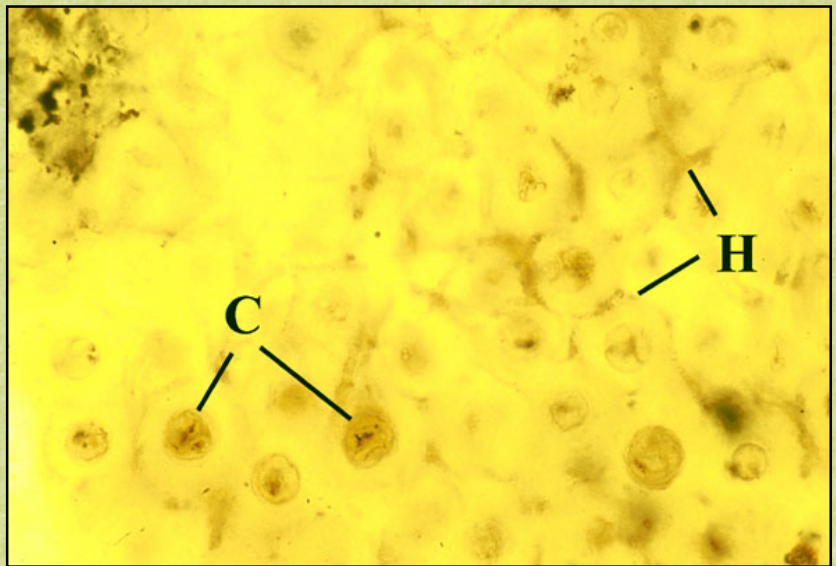
The surface of the lichen exhibits a series of small pockets that contain an open meshwork or 'net' of 1-4µm diameter fungal hyphae (see insets above right and right). Each 'net' is about 25µm in diameter and contains a single cell or cluster of daughter cells that represent the photobiont (see inset below right). The size of cells and number of daughter cells in the hyphal nets generally increases towards the top of the thallus. Each cell is coated with a relatively thick mucilaginous envelope.



Above: Close-up of thallus showing tightly aggregated hyphae (F) and one of the surface 'pockets' containing a fine net of hyphae enclosing cells of the photobiont (C) (Copyright owned by University Münster).

Right: Close-up of 'net'

showing fungal hyphae
(**H**) enclosing cells of
the photobiont (**C**)
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Palaeoecology

As with modern cyanolichen equivalents, during the early Devonian at Rhynie *Winfrenatia* was most likely an early coloniser of hard substrates. Degrading sinter surfaces could have provided a suitable substrate. Similarly it may have been able to weather the rock surfaces it was colonising and thus contributing to soil formation.

The presence of a cyanolichen in the early Devonian is thus important in understanding the ecology of early terrestrial communities as well as the evolution of land plants.

CONTENTS PAGE



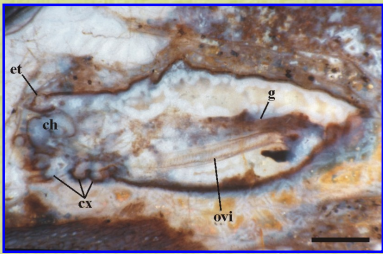
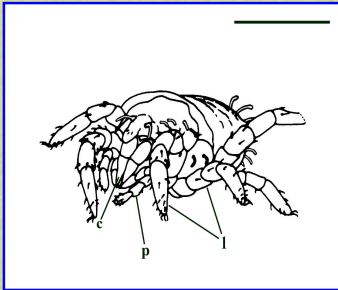
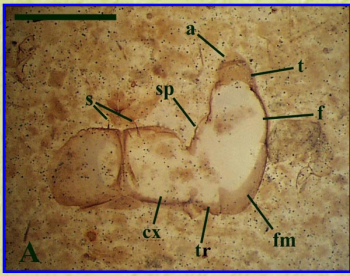
The Rhynie Chert Fauna:

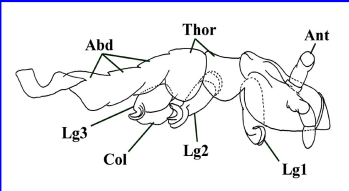
A general list of the fauna together with illustrations

The following is a list of the Rhynie chert arthropod fauna that have been described to date. A controversial arthropod known from the remains of a single specimen, *Rhyniognatha hirsti* ([Tillyard 1928](#)), is now believed to be closely related to the pterygote insects based on the structure of its mandibles ([Engel & Grimaldi 2004](#)). Also included for completeness is an arthropod of uncertain affinities; *Rhynimonstrum dunlopi* ([Anderson & Trewin 2003](#)). Discoveries of new elements of the Rhynie fauna have recently been made, and once described and published will be added to this list in due course.

Click on the image thumbnails for a close up:

Arthropod Group	Species Described from the Rhynie chert	Useful Texts	General Features	Palaeoecology	Image
Trigonotarbids	<i>Palaeocharinus rhyniensis</i>	Hirst 1923 ; Dunlop 1994, 1996b , Shear et al. 1987 ; Selden et al. 1991 ; Fayers et al. 2004	Extinct arachnids similar in appearance to spiders but lacking spinnerets and possessing a segmented abdomen.	Predator, living in terrestrial habitats. Often found in plant-rich beds, occasionally within empty sporangia and hollow plant stems.	
	<i>Palaeocharinus hornei</i>				
	<i>Palaeocharinus tuberculatus</i>				
	* <i>Palaeoecteniza crassipes</i>				

<p>Harvestmen</p>	<p><i>Eophalangium sheari</i></p>	<p>Dunlop et al. 2003, 2004</p>	<p>Arachnids lacking a distinct division between the head and body, with a segmented abdomen. Typically possess a small ovoid body with long slender legs.</p>	<p>Predator / saprovores / detritivores, living in damp terrestrial habitats, mostly in plant litter.</p>	
<p>Mites</p>	<p><i>Protacarus crani</i> <i>Protospeleorchestes pseudoprotacarus</i> <i>Pseudoprotacarus scoticus</i> <i>Palaeotydeus devonicus</i> <i>Paraprotocarus hirsti</i></p>	<p>Hirst 1923; Dubinin 1962; Bernini 1986</p>	<p>Very small arachnids that lack a distinct division between the head and the body and have a smooth abdomen.</p>	<p>Micro-herbivores / saprovores, living in damp terrestrial habitats, primarily in plant litter and soil. Some probably also fed on sap from living plants. Occasionally found within empty sporangia.</p>	
<p>Myriapods</p>	<p><i>Crussolum</i> sp.</p>	<p>Shear et al. 1998; Anderson & Trewin 2003</p>	<p>A centipede similar to the modern house centipede, possessing strong poison jaws or 'forcipules', long antennae and 15 pairs of long multi-segmented walking legs.</p>	<p>Active predator, living in damp terrestrial habitats, such as in soils, plant litter and under stones.</p>	

<p><i>Leverhulmia mariae</i></p>	<p>Anderson & Trewin 2003</p>	<p>A small myriapodous arthropod with at least 5 pairs of walking legs, each with densely crowded hairs or setae on the posterior of the last (tarsal) segment.</p>	<p>Saprovore / detritivore, living in damp terrestrial habitats, most probably in plant litter.</p>	
<p><i>Rhyniella praecursor</i></p>	<p>Hirst & Maulik 1926; Tillyard 1928; Scourfield 1940a,b; Whalley & Jarzembowski 1981</p>	<p>A springtail (Collembola), with 3 pairs of legs, an abdomen of 6 segments, possessing a furcula or jumping organ on the 4th abdominal segment and a curious ventral tube on the 1st abdominal segment.</p>	<p>Saprovore, living in damp terrestrial habitats, particularly in plant litter and soil.</p>	

Hexapods

Rhyniognatha hirsti

[Hirst & Maulik 1926](#),
[Tillyard 1928](#), [Engel & Grimaldi 2004](#)

The earliest known pterygote insect. Known only from the fragmentary mouthparts of one specimen, comprising a pair of robust mandibles with bladed tooth-like structures. Although fossil evidence is so far lacking, *Rhyniognatha* may have possessed primitive wings.

Comparing the jaws with those of modern insects, *Rhyniognatha* may have fed on higher plant tissues.

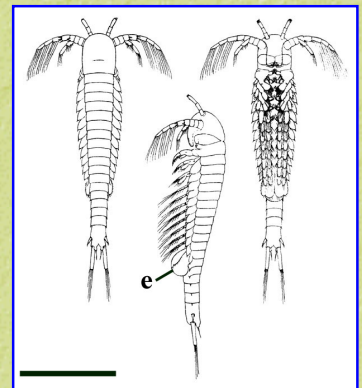


Lepidocaris rhyiensis

[Scourfield 1926](#) [1940c](#)

A small multi-segmented crustacean with 10 pairs of biramous leaf-like trunk appendages, long biramous antennae with plumose setae and lacking a cephalic shield in adults. Maxillae modified and look like the first 2 pairs of trunk limbs.

Micro-herbivore / detritivore, living in ephemeral freshwater ponds.



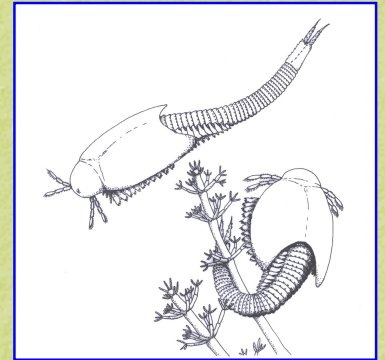
Crustaceans

Castracollis wilsonae

[Fayers & Trewin 2003](#)

8mm long, multisegmented crustacean. Thorax of up to 26 somites, each bearing legs. Up to 28 apodous abdominal segments. 2 series of thoracic legs. Anterior series: 11 pairs of long raptorial legs. Posterior series: 10-15 pairs of smaller phyllopodous legs. Head with large mandibles and long, symmetrical, biramous second antennae.

Similar to modern Tadpole Shrimps - detritivore / carnivore, living in ephemeral freshwater ponds.



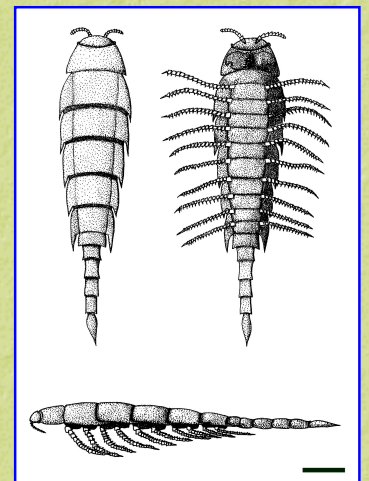
Euthycarcinoids

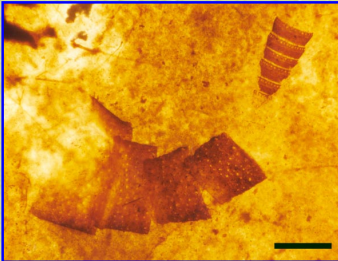
Heterocrania rhyniensis

[Hirst & Maulik 1926; Anderson & Trewin 2003](#)

Multi-segmented arthropod sharing features with crustaceans and myriapods. Body comprises 5 large dorsal segments, each with 2 corresponding ventral segments that bear a pair of

Micro-herbivore / detritivore, living in ephemeral freshwater ponds.



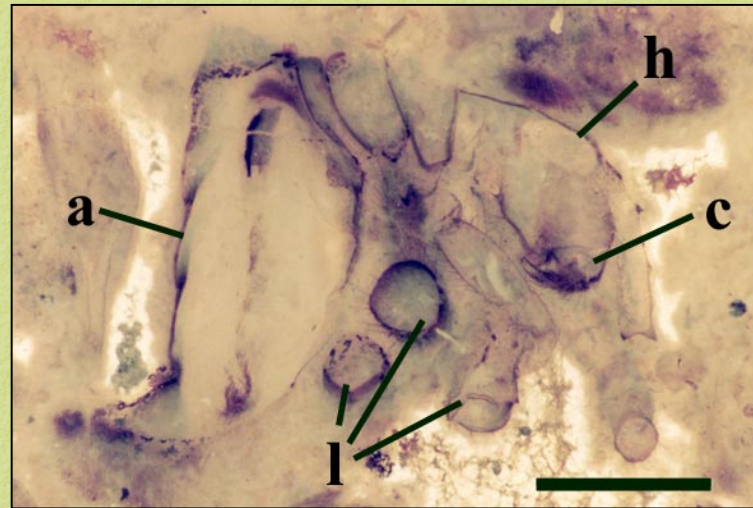
			multi-segmented legs.		
Arthropoda <i>incertae sedis</i>	<i>Rhynimonstrum dunlopi</i>	Anderson & Trewin 2003	Articulated tubular segments of cuticle, the leading edge of each with a ring of sockets for spines or setae. Sometimes associated with sheets of punctate cuticle and clusters of long robust setae.	Unknown	

*Note: A single specimen of a tiny arachnid described from the chert by [Hirst \(1923\)](#), *Palaeocteniza crassipes*, as being related to modern trap-door spiders is now regarded as a juvenile trigonotarbid ([Selden et al. 1991](#)).

CONTENTS PAGE



Trigonotarbid arachnids



Above: A curled up trigonotarbid, *Palaeocharinus rhyniensis*, in a thin section of Rhynie chert; showing segmented abdomen (a), head (h), chelicerae or 'fangs' (c) and cross sections of the walking legs (l) (scale bar = 1 mm).

[Introduction](#)

[Relationships](#)

[Identity](#)

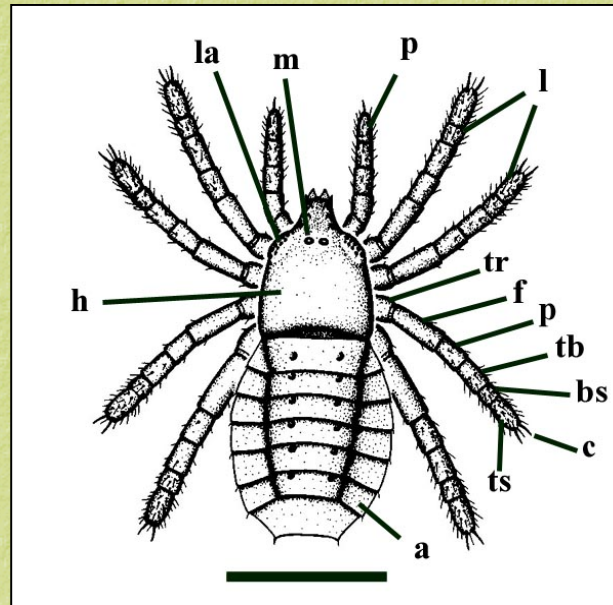
[Morphology](#)

[Reconstruction](#)

[Palaeoecology](#)

Introduction

Trigonotarbids are an extinct order of terrestrial arachnids related to modern day spiders. The earliest trigonotarbid known in the fossil record is from the Silurian Ludlow Bone Bed ([Jeram *et al.* 1990](#)). It was formally described by Jason Dunlop ([1996a](#)). The group ranges from the Late Silurian to the Early Permian; being most diverse in genera and species during the Late Carboniferous. During this time the group occupied a place in some of the earliest terrestrial ecosystems (Rhyne) as well as being an important faunal element of coal swamp communities. Fossil arachnids are relatively rare and only occur in sites of exceptional preservation where their unmineralised cuticle can be fossilised either due to unusual chemical conditions or rapidity of burial. The Lower Devonian trigonotarbids of Rhyne are amongst the most completely preserved and best known members of the group. They are so well preserved that features such as their respiratory organs (book lungs) ([Claridge & Lyon 1961](#)), mouthparts ([Dunlop 1994](#)) and even muscle tendons have been identified in some sections of the chert.



Above: Reconstruction of a trigonotarbid arachnid from the Rhyne chert, *Palaeocharinus rhyneensis*; showing segmented abdomen (a), walking legs (l), pedipalps (p) and head (h) with lateral (la) and median eyes (m). The walking legs may be subdivided into the trochanter (tr), femur (f), patella (p), tibia (tb), basitarsus (bs) and telotarsus (ts) with a paired apical claw (c). The chelicerae and the coxae can not be seen in this dorsal aspect of the animal. (after [Dunlop 1996b](#)) (scale bar = 2 mm).

Relationships

Although sharing a similar body plan with other arachnids, trigonotarbids are not spiders as such. They belong within a group of animals called the **chelicerates**. Other chelicerates include the horseshoe crabs (such as modern *Limulus*), scorpions, the extinct eurypterids and all other arachnids including mites. As the earliest recognised terrestrial animal fossil is an Upper Silurian trigonotarbid, understanding of the group obviously plays an important role in determining the timing and mechanism by which animals invaded the land.

There are a number of significant differences between trigonotarbids (informally called "trigs") and spiders which are tabulated below:

Spiders	Trigonotarbids
Silk producing spinnerets	Spinnerets absent
Smooth opisthosoma (with the exception of liphistid spiders)	Segmented opisthosoma
Lateral and median eyes consolidated on a single tubercle	Separate lateral and median eye tubercles

Identity

[Hirst \(1923\)](#) originally described five species of trigonotarbids from the Rhynie cherts under the generic names *Palaeocharinoides* and *Palaeocharinus*. These are *Palaeocharinoides hornei*, *Palaeocharinus rhyniensis*, *P. scourfieldi*, *P. calmani* and *P. kidstoni*. The two genera were distinguished respectively by an acute vs. a straight posterior margin of the sternum (a central plate located on the ventral side of the head region). Shear *et al.* (1987) rejected this as a diagnostic generic character and synonymised *Palaeocharinoides* with *Palaeocharinus*. The number of species should also be treated with caution as many were diagnosed as different from one another on very minor differences. Some of these apparent differences may have been introduced during the fossilisation process or could be accounted for by intra-specific variation. Of Hirst's trigonotarbid specimens, it would appear only two valid species are probably present: *Palaeocharinus rhyniensis* and *Palaeocharinus hornei*.

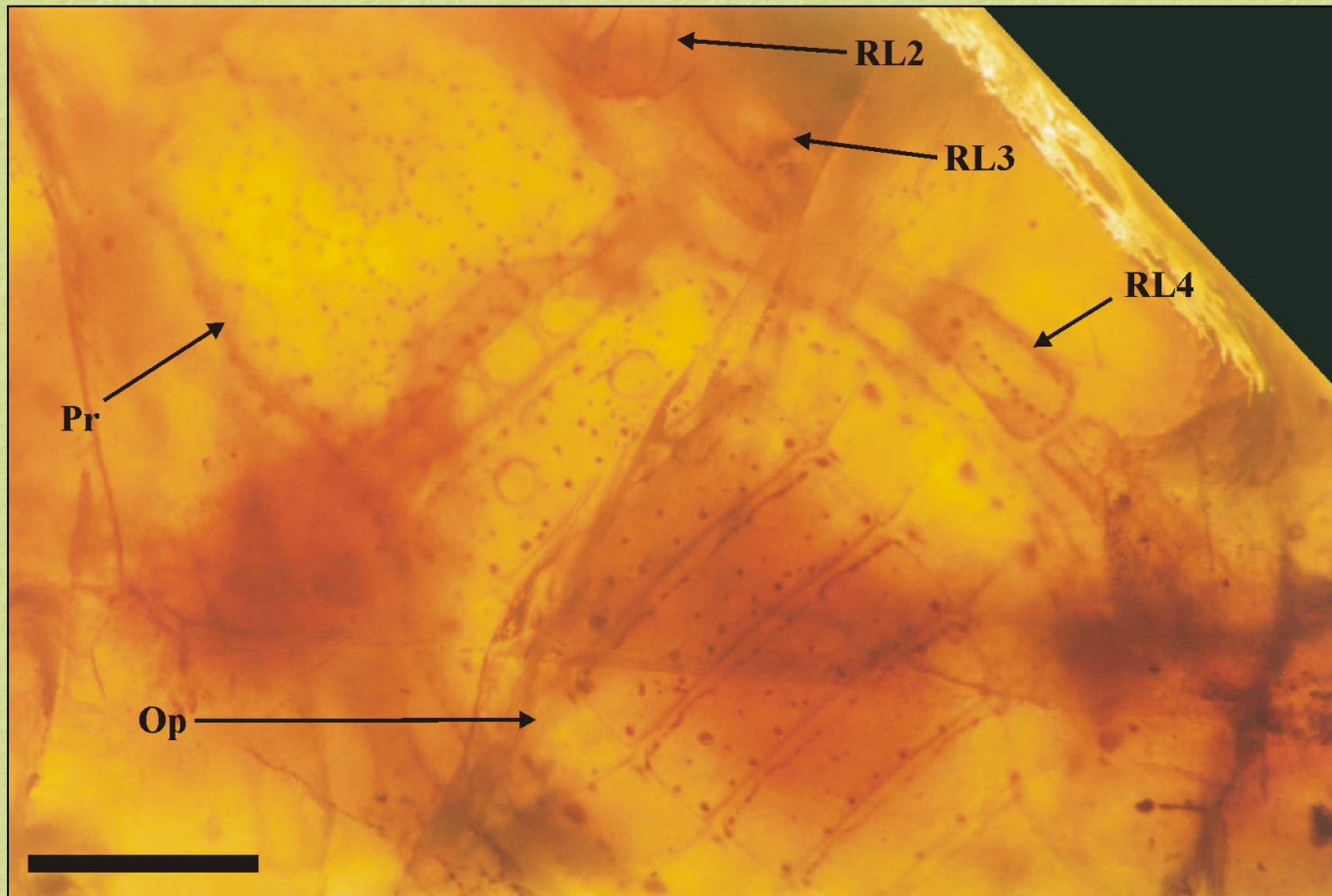
Recently a new species, *Palaeocharinus tuberculatus*, has been described from the Windyfield chert ([Fayers *et al.* 2004](#)), differing from Hirst's specimens in its larger size and distinctive tuberculate ornament (see inset below).

The following section gives the general morphology of the trigonotarbids known from the cherts at Rhynie.

Morphology

The Rhynie trigonotarbid arachnids described to date all belong to the family **Palaeocharinidae**, and possess a distinctive and characteristic morphology by which they can be identified. Overall trigonotarbids consist of a **prosoma** (head region) and an **opisthosoma** (body region) (see inset below). Each of these areas is explored in more detail below. The Rhynie 'trigs' are generally quite small in size. The most commonly encountered species (*Palaeocharinus rhyniensis* and *P.*

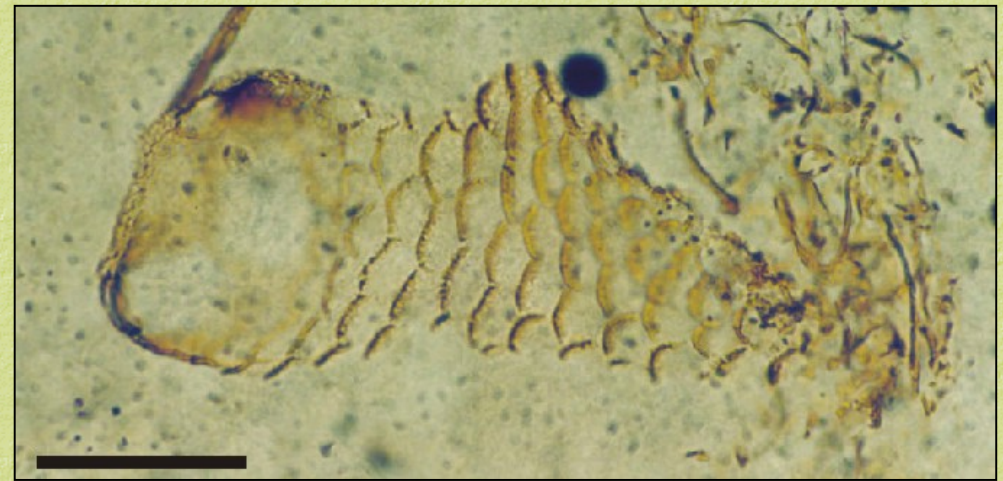
hornei) have a body length of up to 4 mm. *Palaeocharinus tuberculatus* is slightly larger having a maximum body length of at least 6mm. However, other trigonotarbid specimens have occasionally been found in the cherts with body lengths ranging between 14 mm and 20 mm. These larger forms (currently being described) appear to belong to a new species quite distinct from *Palaeocharinus* and possibly belong to a separate family.



Above: Dorsal view of a near-complete specimen of *Palaeocharinus tuberculatus* in Windyfield chert, showing prosoma (**Pr**), opisthosoma (**Op**), and the rear three right leg appendages (**RL2-4**) (scale bar = 1 mm).

One of the most diagnostic features of trigonotarbid arachnids is the microscopic scale-like sculpture seen variably developed on the cuticle or skin of the animal (see inset right). This can allow identification of fragments of cuticle where no whole body fossil exists, and is particularly useful in studies where material is limited (e.g. in thin sections of chert and fragments in organic concentrates extracted from sedimentary rocks).

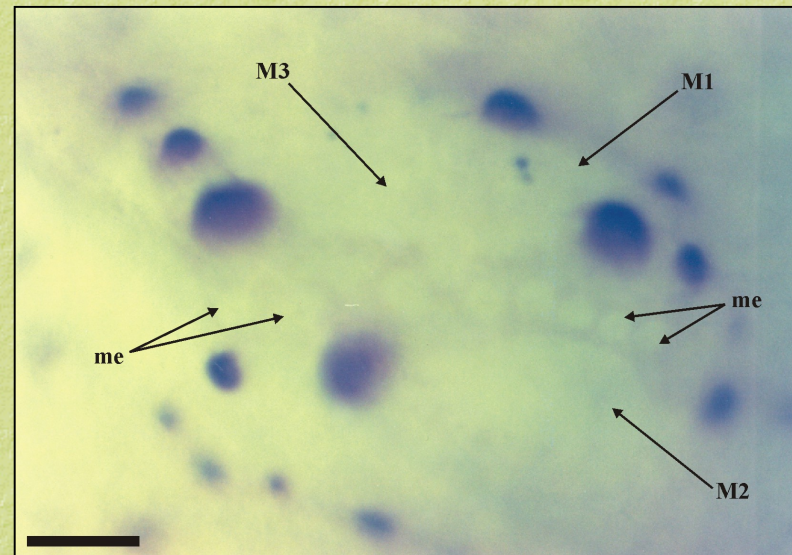
Right: Fragment of trigonotarbid cuticle in chert showing the distinctive scale-like sculpture (scale bar = 50 μm).



Head Region

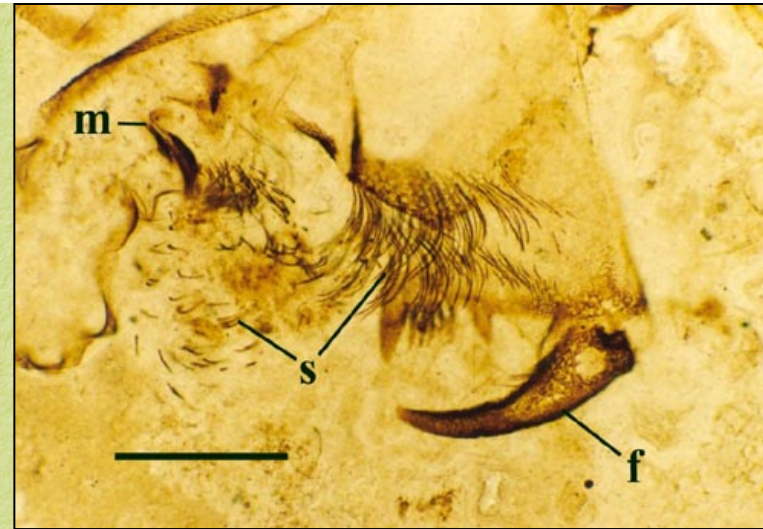
The head region or prosoma consists of a highly domed carapace with a distinctive pointed 'beak' towards the front (anterior). In the Palaeocharinidae this 'beak' shows two sub-parallel tubercled ridges that extend from the level of the **median eyes** to the anterior where they form a pair of acute spine-like processes. **Lateral eye tubercles** are present on either side of the carapace. In the Rhynie palaeocharinids each lateral eye tubercle possesses a series of major and minor eye lenses, comprising a staggered row of up to 10 minor lenses separating a larger lower lens and 2 larger upper lenses (see inset right).

Underneath the domed carapace hangs a pair of down and backwardly directed poison fangs or **chelicerae**; the morphological character from which the group derives its name (see inset below right). Towards the posterior of the carapace are the leg attachment points (**coxae**). The position of the leg appendages, associated with the prosoma is a further diagnostic characteristic of the Chelicerates.



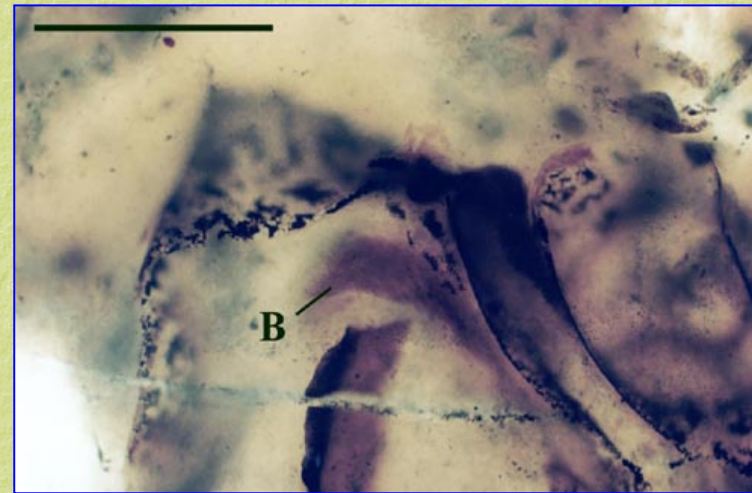
Above: Close up of the right lateral eye tubercle of *Palaeocharinus tuberculatus* showing the eye lenses. The dark circles are tubercles, a characteristic feature of this particular species. **Me**: minor eye lenses, **M1-3**: major eye lenses (scale bar = 100 μm).

Right: Close up on the mouthparts of *Palaeocharinus* showing position of mouth (**m**), dense setae (**s**) and a well preserved chelicera or fang (**f**) (scale bar = 250 μ m) (Copyright owned by The Natural History Museum).



Body Region

The body region of trigonotarbids is visibly segmented and also divided longitudinally into a medial and two lateral regions. This pattern of segmentation is quite unlike modern spiders in which the abdomen consists of a single fused area. Within the abdomen are housed the opisthosomal appendages. In the case of trigonotarbid arachnids these appendages take the form of lamellate **book lungs** (see inset right) used in respiration. The presence of book lungs indicates that these animals were unequivocally terrestrial organisms. The abdomen of trigonotarbids is terminated by a small, circular anal tubercle.



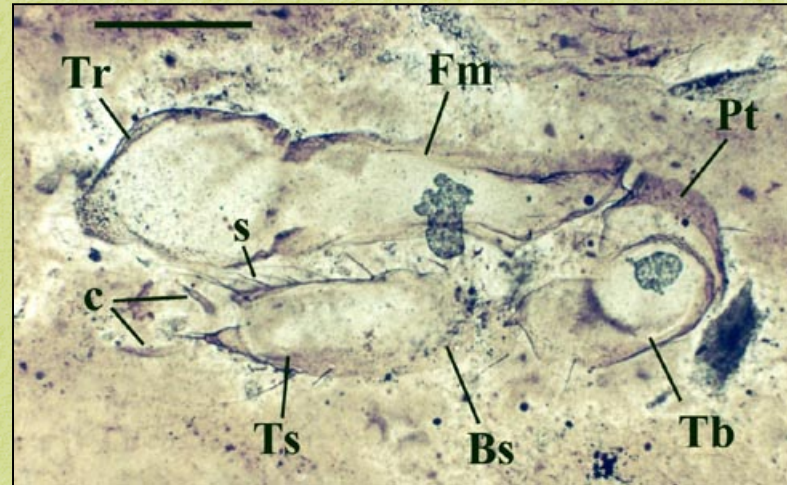
Above: Close-up of the anterior of the abdomen of *Palaeocharinus rhyniensis* (the same specimen in the heading photograph) showing the lamellate book lungs (**B**) (scale bar = 500 μ m). Click on the image for a close-up!

Prosomal Appendages

Just as in extant spiders, trigonotarbids possessed a pair of **chelicerae** (fangs), a pair of **pedipalps** and four pairs of

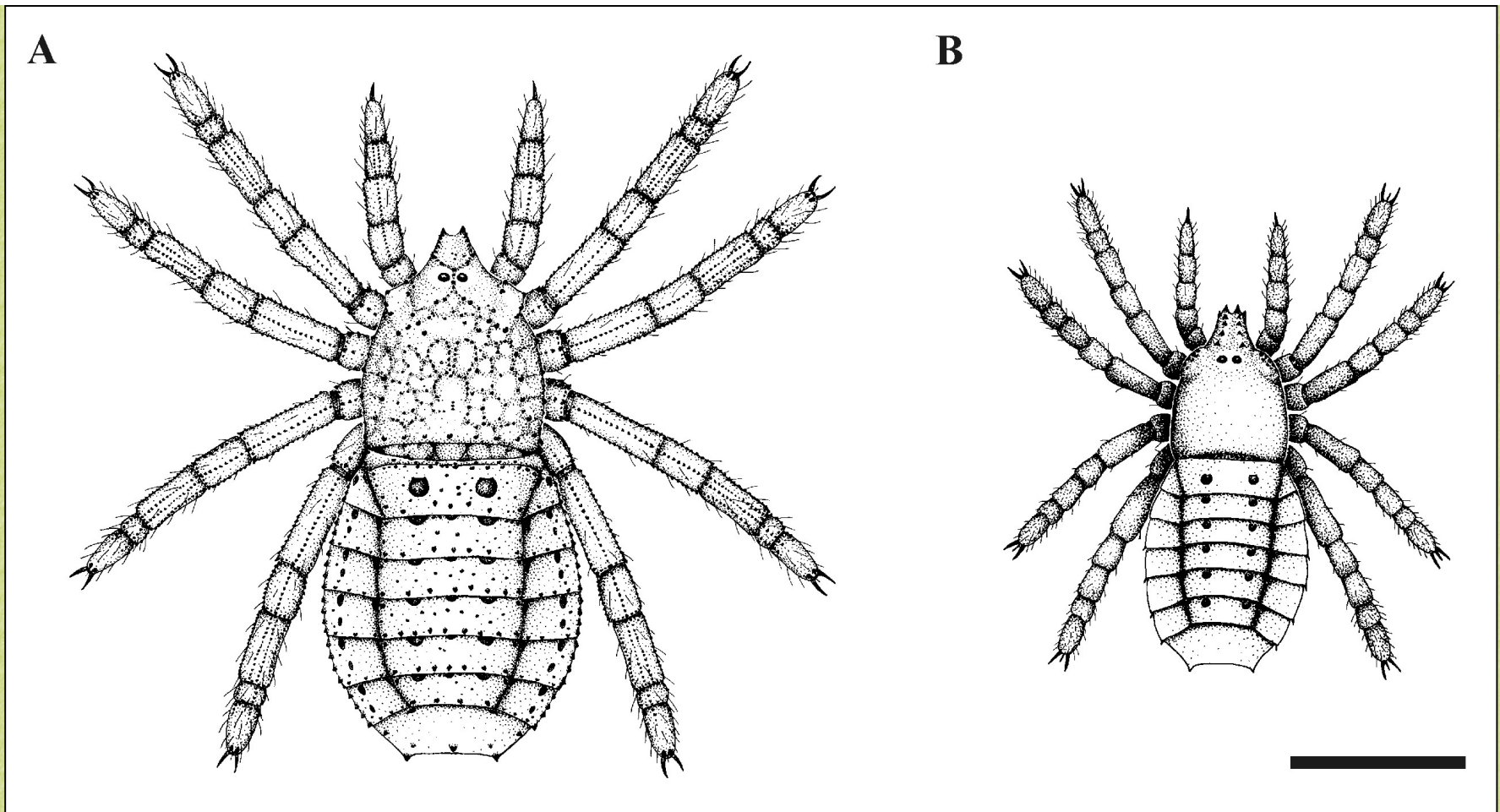
walking legs. The fangs were used in prey capture and the pedipalps may have had a sensory function, although in extant male spiders they are used in mating. Each of the individual leg segments or podomeres can be named. Starting from the insertion point they are as follows: **coxa**, **trochanter**, **femur**, **patella**, **tibia**, **basitarsus** and **telotarsus** (see reconstruction above and inset below). In trigonotarbids the most distal of the leg podomeres, the telotarsus, bears a pair of **tarsal claws** that were an adaptation for walking in the terrestrial environment. The more distal podomeres of the walking legs bear an increasing number of fine **setae** or hairs. These were used by the animal to augment its sensory array.

The legs of *Palaeocharinus tuberculatus* differ from the other *Palaeocharinus* species in that they possess distinctive longitudinal rows of tubercles. Many of these tubercles appear to flank and guard socketed sensory hairs.



Above: An isolated walking leg of *Palaeocharinus* showing almost a full series of podomeres (coxa missing); the trochanter (**Tr**), femur (**Fm**), patella (**Pt**), tibia (**Tb**), basitarsus (**Bs**) and telotarsus (**Ts**). The pair of apical claws (**c**) and setae (**s**) are also shown (scale bar = 250 μ m).

Reconstruction



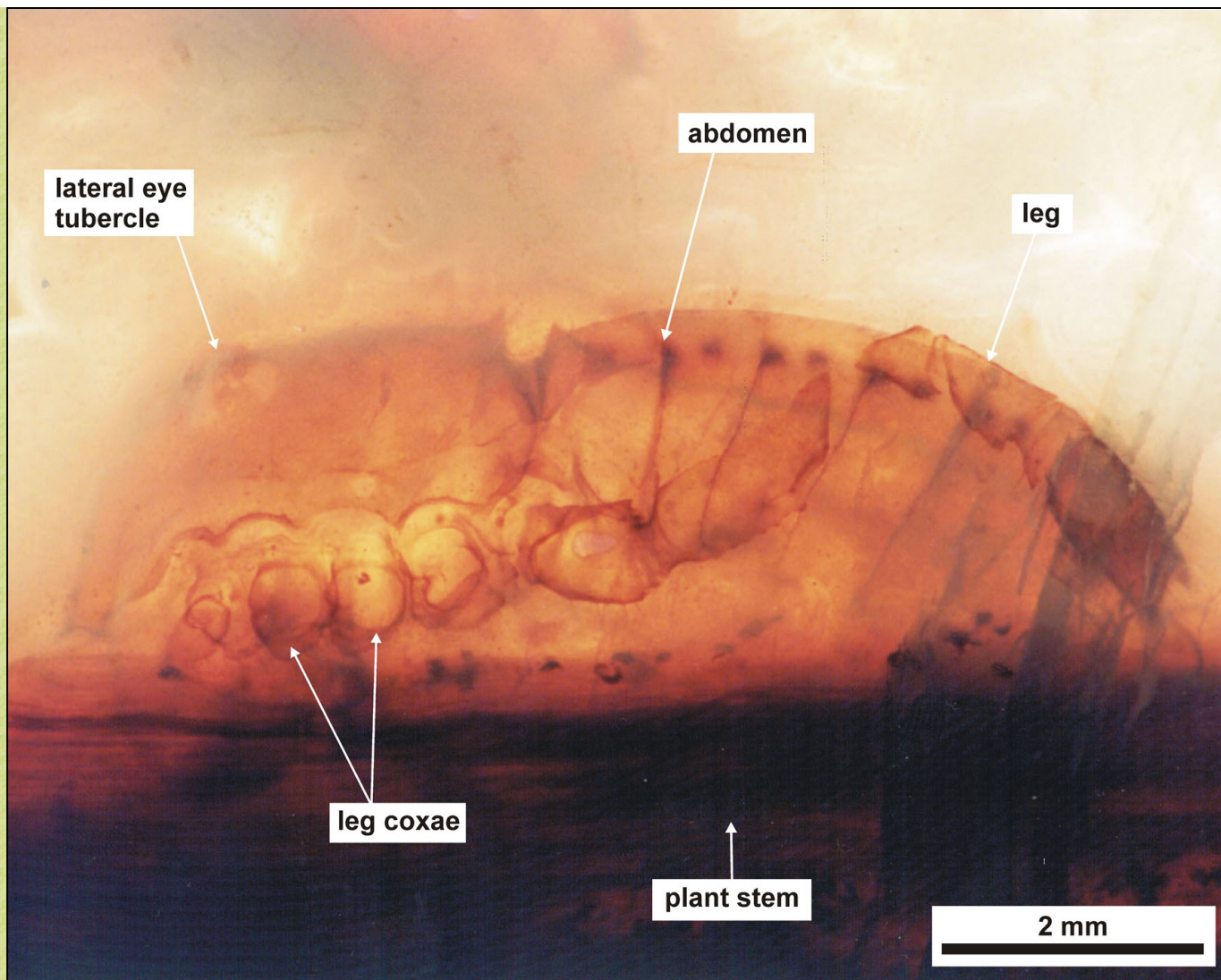
Above: Reconstructions of two of the Rhynie trigonotarbids (Palaeocharinidae) from a dorsal aspect: **A.** *Palaeocharinus tuberculatus* (after [Fayers et al. 2004](#)), **B.** *Palaeocharinus rhyniensis* (after [Dunlop 1996b](#)) (scale bar = 2 mm).

Right: 3-dimensional reconstruction of the Rhynie chert trigonotarbid *Palaeocharinus rhyniensis* (Click on the image for more views!) (Copyright owned by Jason Dunlop).



Palaeoecology

Trigonotarbid arachnids such as the Rhynie form *Palaeocharinus* did not possess the morphological structures termed spinnerets. Extant spiders have spinnerets and these are used to produce silk, one of the most important substances in terms of spider ecology. Silk threads spun from the spinnerets are used to build food-capturing webs, silk lines the burrows of trap door spiders, is used to wrap prey items and also to provide protective cocoons for the eggs. Some species even use the silk as a mode of transport. By letting out a long thread of silk into the prevailing wind small spiders 'balloon' and can travel great distances. This can aid widespread dispersal of the species. As trigonotarbids lack this innovation, their possible palaeoecological interpretation must be somewhat limited. Another group of extant arachnids which provide a more useful analogue to trigonotarbids are the opilionids, or 'harvestmen'. These ground living forms lack silk but instead immobilise their prey with a bite from poisonous fangs (chelicerae). It is conceivable the Rhynie trigonotarbids behaved in a similar manner since they possessed particularly robust and well-developed fangs.



Above: Lateral view of a near complete *Palaeocharinus* specimen preserved within the straw of a decayed plant stem. The dark base of the image represents the xylem strand of the plant.

The robust walking legs and downwardly directed fangs suggest that *Palaeocharinus* may have been a ground predator stalking the micro-habitat provided by the stands of Rhynie plants. It may well have sat in wait and ambushed its prey from the cover of fallen plant stems. Indeed some trigonotarbid fossils have been discovered within the cherts within the hollow stems and sporangia of the Rhynie plants ([Kevan et al. 1975](#)) (see inset above). They may have used these as cover from which to ambush their prey. Alternatively such locations may have provided ideal conditions for ecdysis or the moulting process to take place in.

CONTENTS PAGE



Harvestmen

[Introduction](#)

[Fossil Record](#)

[Morphology](#)

[Palaeoecology](#)

Introduction

A recent addition to the fauna of the Rhynie chert are harvestmen ('daddy long-legs'). These spider-like arachnids belong to the order **Opiliones**, and are primarily distinguished from other arachnids by the lack of a distinct division between the head and body, and the opisthosoma is segmented. Many are easily recognisable by their small ovoid bodies and long legs, hence their common name 'daddy long-legs' (see inset below). The order name comes from the Latin *opilio*, meaning shepherd, and may derive from the elevated position of the body on the long slender legs or the fact that male harvestmen guard the female during egg laying. Today harvestmen are a common and widespread group and tend to live in cool, damp terrestrial habitats such as in plant litter or wetland.



Above: A modern harvestman, *Mitopus morio*. This image was taken from the web site [BioImages](#), a virtual field guide illustrating the biodiversity of the UK (Copyright owned by Malcolm Storey).

Fossil Record

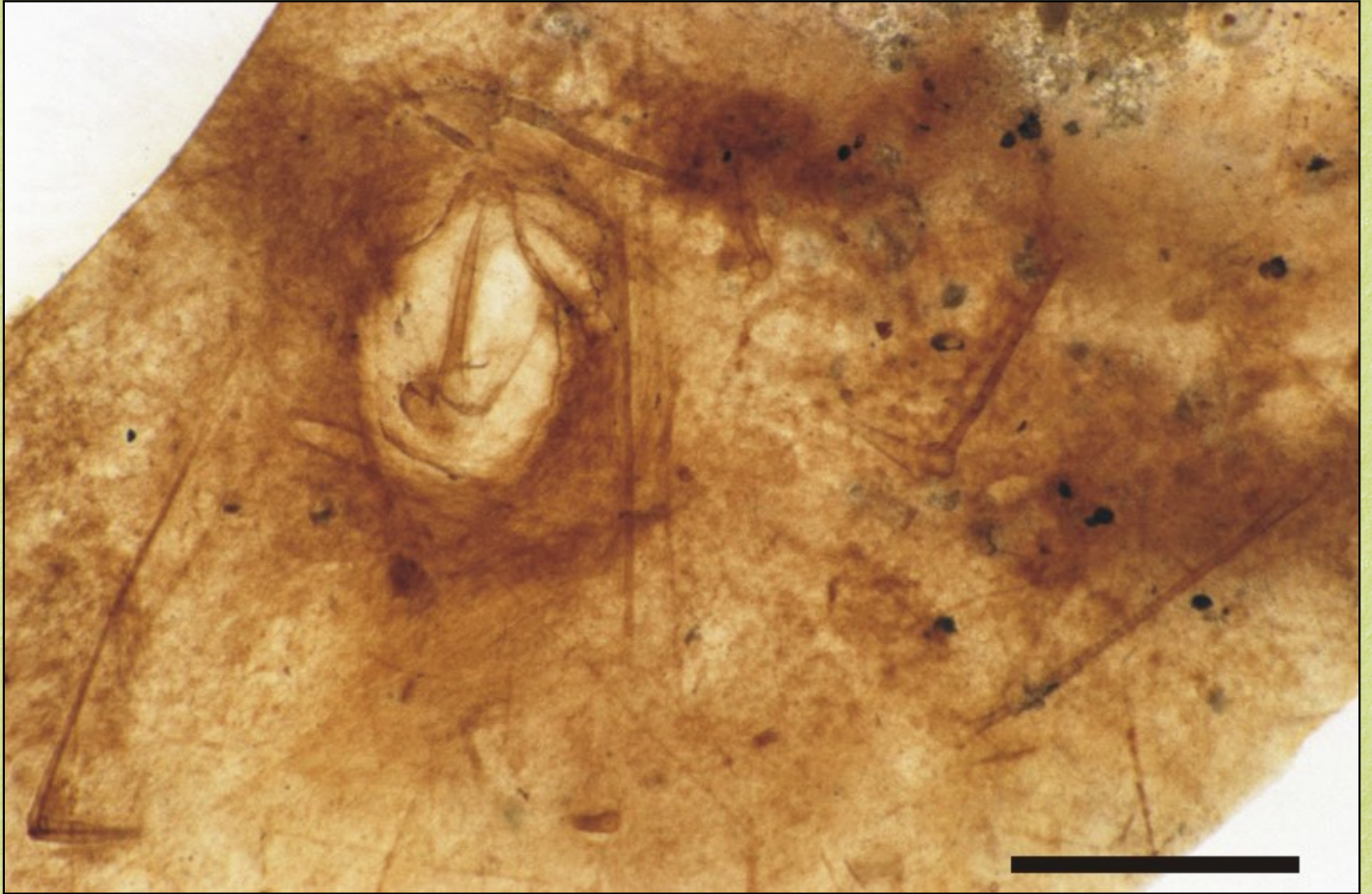
As with other arachnids, and indeed other terrestrial arthropods with un-mineralised exoskeletons, harvestmen are generally rare in the fossil record. A few Palaeozoic and Mesozoic examples are known, such as from the Lower Carboniferous of Scotland (e.g. [Wood *et al.* 1985](#)); but most fossils have been found in rocks of Tertiary age, particularly the Florissant Formation of Colorado, USA (e.g. [Cokendolpher & Cokendolpher 1982](#)), and from Baltic, Dominican and Bitterfeld ambers (e.g. [Cokendolpher & Poinar Jr 1998](#); [Dunlop & Giribet 2003](#)). Three specimens of fossil harvestmen have recently been discovered in the Rhynie chert (two male and one female), and have attracted much interest, not only because they represent the earliest known harvestmen in the fossil record but also because they contain the silicified remains of the earliest known preserved genitalia of a terrestrial animal ([Dunlop *et al.* 2003](#)).

A formal description and diagnosis for the Rhynie chert harvestmen has been written by Jason Dunlop and other authors ([Dunlop *et al.* 2004](#)). These authors believe the fossil specimens represent a single species, to which they have assigned the name *Eophalangium sheari*.

Morphology

The Rhynie chert harvestmen are fairly small. The female specimen has a body length of approximately 6mm; the males are somewhat smaller with an opisthosoma length of approximately 1.2mm (see insets below). The female specimen exhibits a well developed median eye tubercle, and one of the male specimens possesses the distinctive long slender legs seen in many

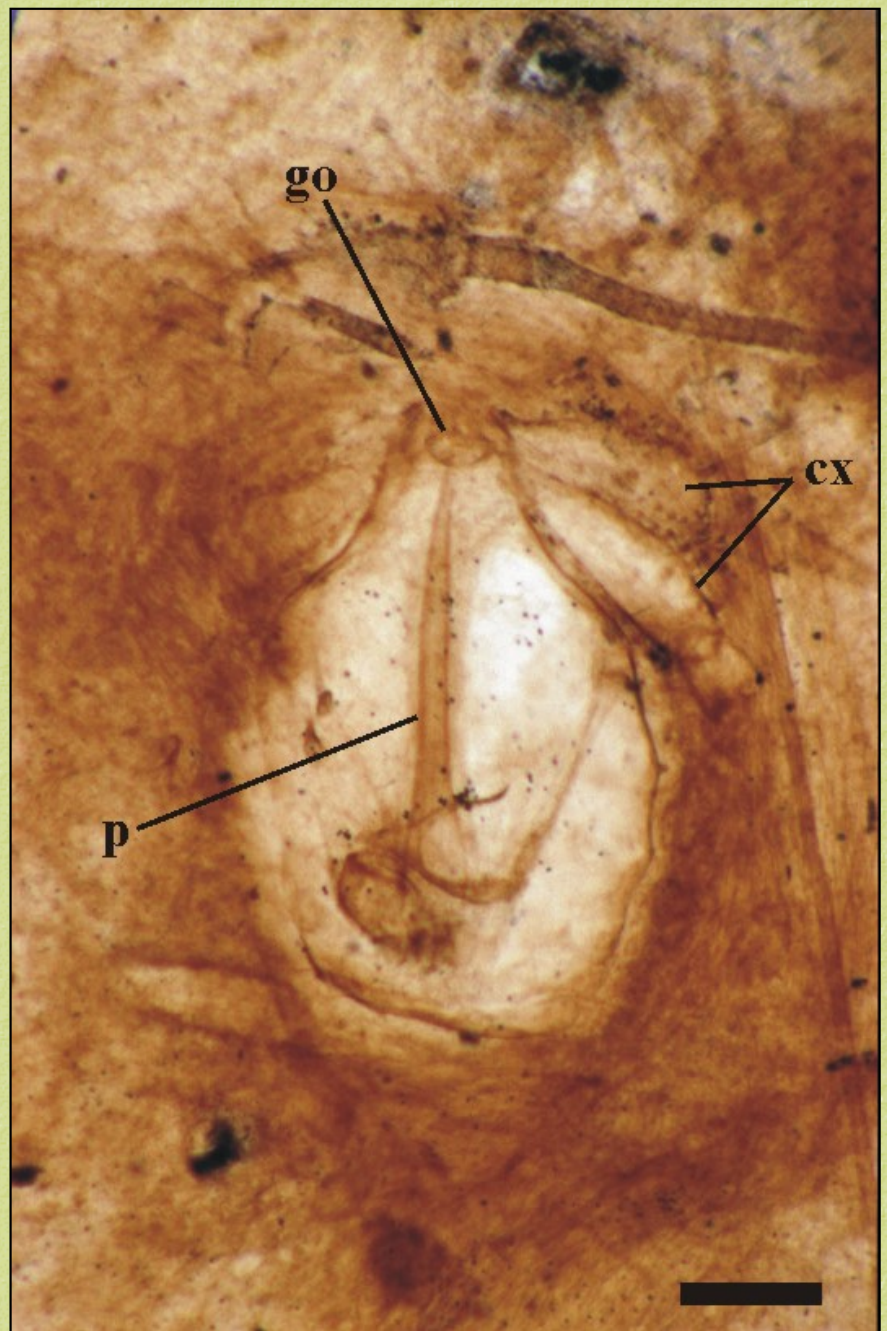
extant harvestmen (with the exception of the Cyphophthalmi) (see inset below). The specimens are essentially 'modern' in their appearance, particularly with regards to the morphology of the penis and ovipositor (see insets below).



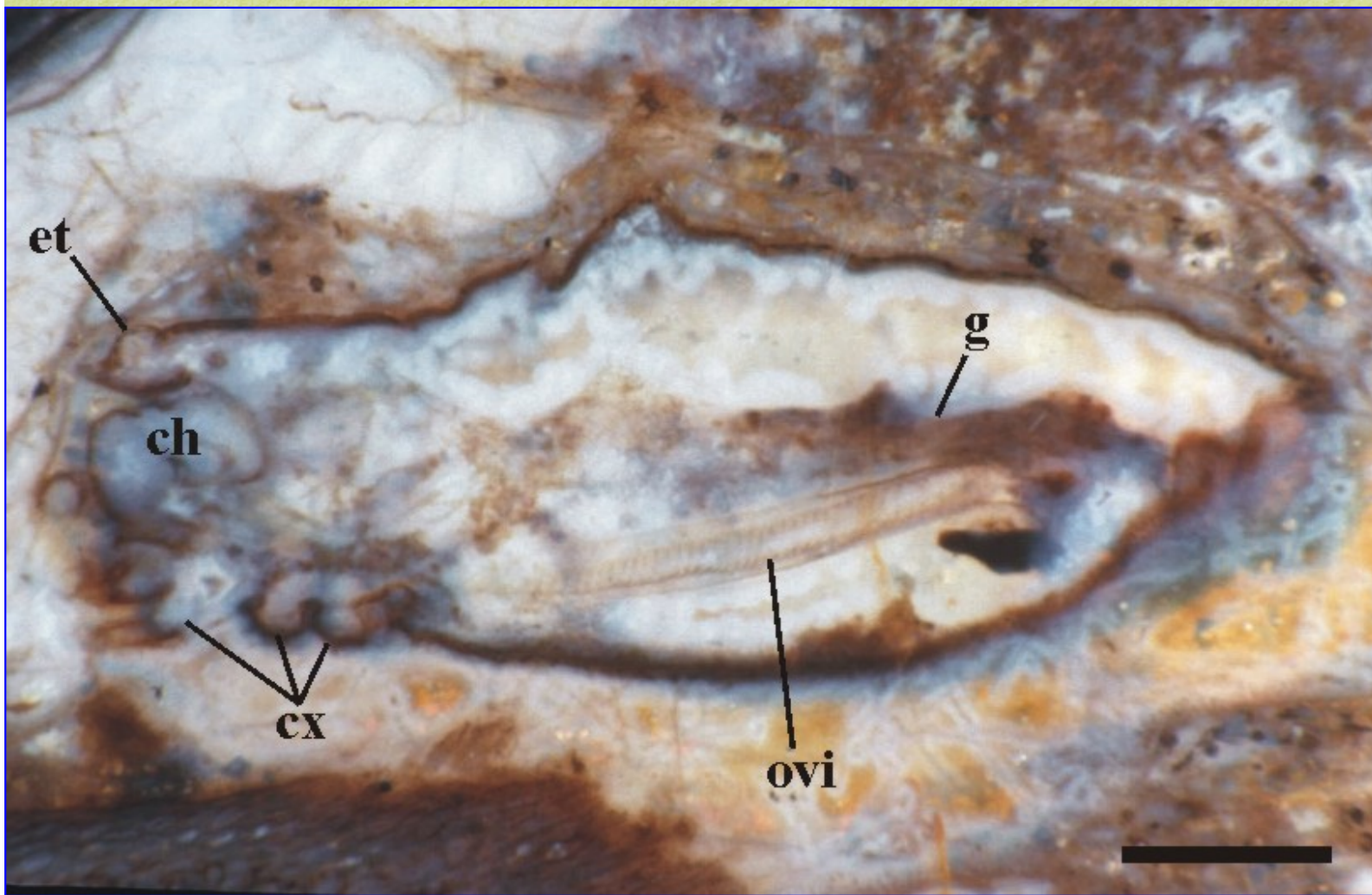
Above: Male harvestman in Rhynie chert. Ventral view of opisthosoma and posterior-most coxae (upper left of centre) with numerous long leg podomeres in the surrounding chert matrix (scale bar = 1mm) (Copyright owned by University Münster).

The opisthosoma of the male exhibits a well preserved penis and **gonopore** or genital opening (see inset right). The gonopore occurs between the fourth leg coxae, and behind this within the body cavity is the penis. The latter comprises a tapering rod-like cuticular structure, and details such as sensory setae and possible muscle tendons are preserved ([Dunlop *et al.* 2003](#)).

Right: Close up of male (ventral view) showing posterior-most coxae (**cx**) and opisthosoma (sternites missing) with the gonopore opening (**go**) and internal penis (**p**) (scale bar = 200 μ m) (Copyright owned by University Münster).

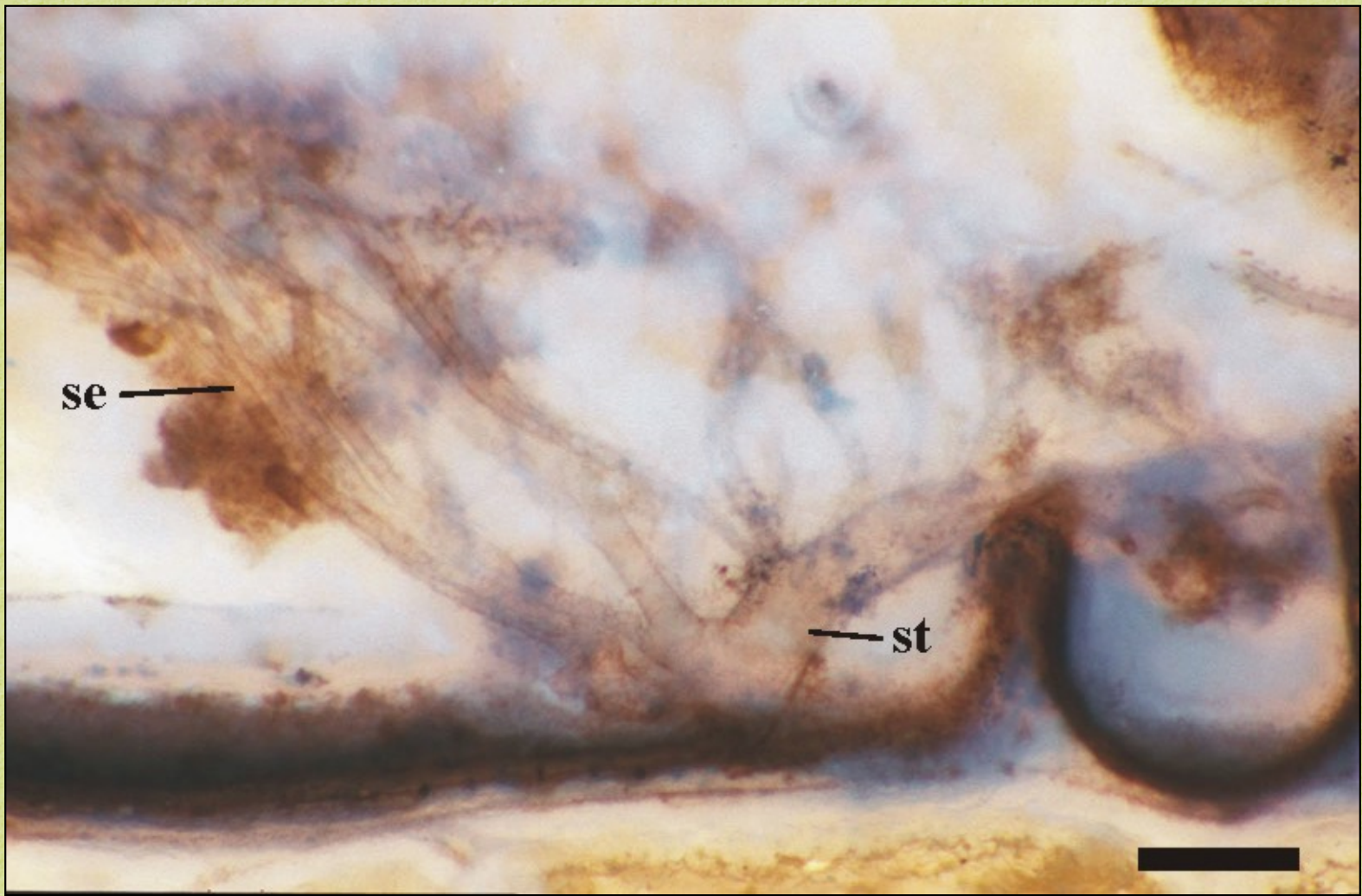


The ovipositor within the opisthosoma of the female appears distinctly annulated (see inset below) and exhibits numerous short sensory setae, and together with the presence of long legs is particularly reminiscent of a particular modern harvestman clade, the **Eupnoi**. This suggests the Rhynie fossils are either representatives of the eupnoid group of harvestmen or an extinct sister taxon, either way they are unequivocally members of the harvestman crown-group.



Above: Longitudinal section through the body of a female harvestman showing the eye tubercle (**et**), chelicerae (**ch**), leg coxae (**cx**), and within the opisthosoma the gut trace (**g**) and ovipositor (**ovi**). Click on image for a close-up (scale bar = 1mm) (Copyright owned by University Münster).

The female harvestman fossil exhibits other internal structures within the opisthosoma, as well as the ovipositor. These include a gut trace, its content comprising mainly dark brown-coloured amorphous organic matter (see inset above); and the respiratory structures (see inset below). The respiratory structures, the **trachea**, comprise a series of cuticular tubes originating from the ventral surface of the anterior opisthosoma, directly behind the fourth leg coxae. Their position and morphology are almost identical to those seen in modern harvestmen ([Dunlop *et al.* 2003](#)) and indicate the animal was definitely a fully terrestrial organism.



Above: Longitudinal view through the anterior opisthosoma of a female (posterior-most leg coxa to the right) showing the stem trachea (st) and secondary trachea (se) (scale bar = 200µm) (Copyright owned by University Münster).

Palaeoecology

Extant harvestmen are omnivorous. They generally feed on dead plant and animal matter (**saprovorous**) but will also kill small arthropods and invertebrates. Harvestmen lack silk-producing spinnerets and therefore do not spin webs to catch their prey. They also eat faecal matter and organic detritus (**detritivores**) and fungi. *Eophalangium sheari* probably had a similar diet.

The well developed branching trachea in *Eophalangium sheari* indicates the Rhynie harvestmen, like their modern counterparts, were unequivocally terrestrial animals; and is the earliest known example of this type of air-breathing apparatus in arachnids. The tubular respiratory organs in opilionids is quite different, for example, from the lamellate book lungs seen in true spiders and the extinct [trigonotarbids](#). Since arachnids (along with all animal groups) began life in the sea, the marked differences in 'lung' morphology indicates their **terrestrialisation** did not occur as a single event, their different respiratory systems evolving independently of each other.

The possession of a 'penis' is an adaptation required for sperm transfer on land. Normally sperm would rapidly dry out in a terrestrial environment, but being able to transfer sperm directly into the female overcomes this problem. Like modern harvestmen, during egg laying the Early Devonian female harvestman would have extended its ovipositor and 'injected' its eggs directly into damp soil or plant litter. Clearly the reproductive behaviour seen in modern harvestmen was well established by

the Early Devonian.

CONTENTS PAGE



Mites



Above: Ventral view of a tydeid mite, *Palaeotydeus devonicus*, from the Rhynie chert found within an empty sporangium; showing mouthparts (**m**), walking legs (**l**) and opisthosoma (**o**) (scale bar = 50 μ m) (Copyright owned by University Münster).

[Introduction](#)

[Relationships](#)

[Identity](#)

[Morphology](#)

[Palaeoecology](#)

[Other useful references](#)

Introduction

Mites are from the second largest order of the arachnids called the [Arcari](#), an order that also includes the ticks. These arthropods are generally very small in size very often being less than a millimeter in length, but the largest trombiform mites can reach up to 12mm in size. Mites range from the Early Devonian to the present day. The earliest member of this group comes from the Rhynie chert and was originally described by [Hirst \(1923\)](#). The fossil record of mites is particularly sparse and like most other arachnids they occur mainly in sites of exceptional preservation where their soft unmineralised cuticle can become fossilised. Although others are known from the Devonian (e.g. [Norton *et al.* 1988](#)) the majority of fossil mites are best known from the Oligocene Baltic amber.

Relationships

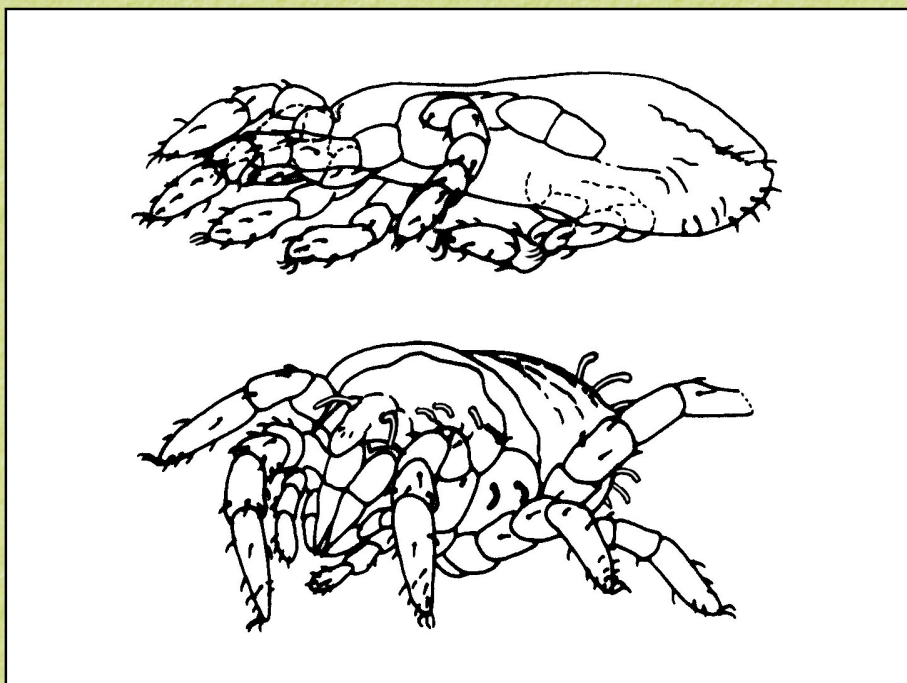
As with other arachnids (including true spiders, harvestmen (opilionids), trigonotarbids and scorpions), mites are part of a group of animals called the **chelicerates**, which also includes horseshoe crabs (e.g. the modern *Limulus*) and the extinct eurypterids. Although superficially similar to spiders and harvestmen there are however a number of characteristic differences that separate them; the two main differences are tabulated below:

Mites	Spiders	Opilionids (harvestmen)
Lack distinct division between head and body.	Clear division into a head and body.	Lack distinct division between head and body.
Smooth opisthosoma.	Smooth, fused opisthosoma (with the exception of liphistid spiders).	Segmented opisthosoma.

Identity

One species of mite was originally recorded from the Rhynie chert, *Protacarus crani* ([Hirst 1923](#)). Since then [Dubinin \(1962\)](#) transferred four of the specimens originally assigned to *Protacarus* to four new species: *Protospeleorchestes pseudoprotacarus*, *Pseudoprotacarus scoticus*, *Palaeotydeus devonicus* and *Paraprotacarus hirsti*. For the purposes of this resource page, however, we will concentrate on the first

described species, *Protocarus crani*.



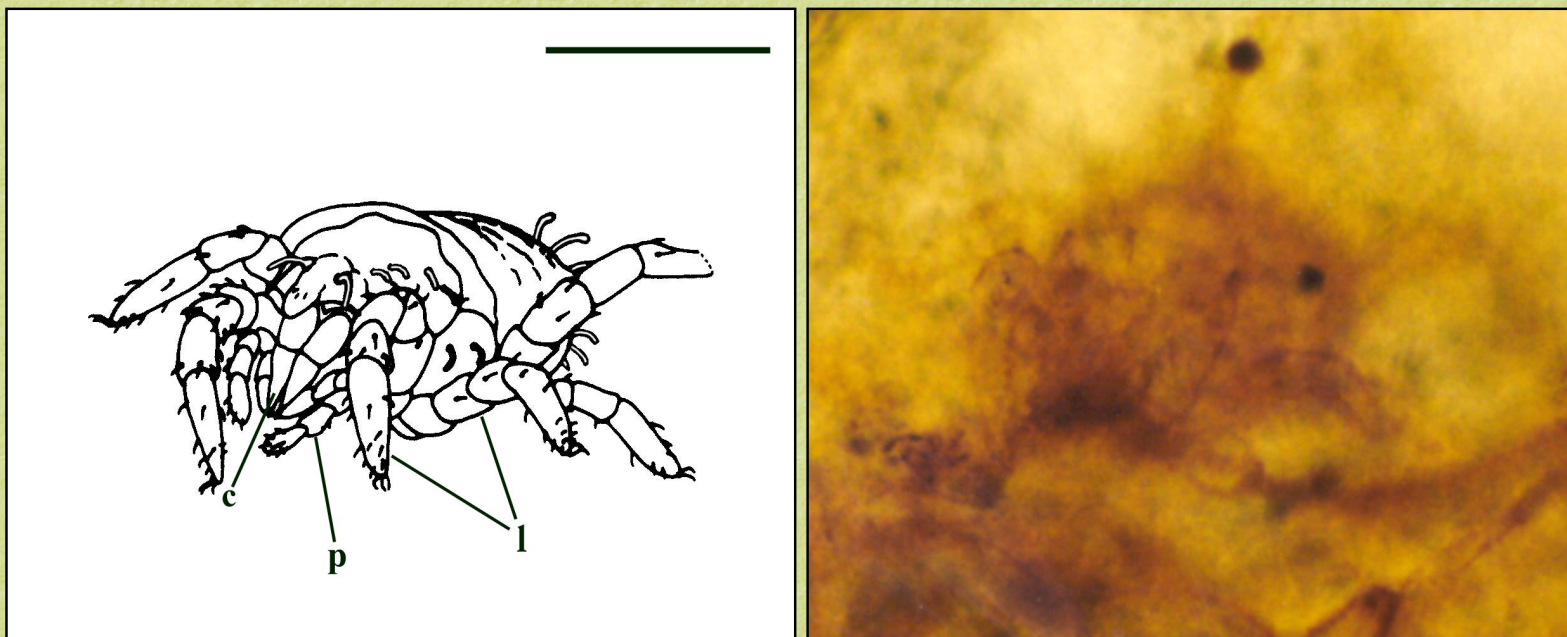
Above: *Pseudoprotacarus scoticus* ([Dubinin 1962](#)) (top) and the holotype of *Protacarus crani* ([Hirst 1923](#)) (bottom).

Protacarus has been placed as a member of a sub group of the Arcari, the family **Pachygnathidae** which still survives today. This is a group of primitive soft-bodied mites of which the extant forms commonly live in soil and damp forest litter.

Note: When the specimens of Protacarus crani and the other Rhynie mites were first prepared they were found by fragmenting small blocks of chert into tiny shards. The shards of chert that were found to contain the mite were then mounted onto glass slides. Since these fossils are in uneven shards of chert and often preserved in 3D, they cannot be easily photographed with any clarity at high magnification, therefore most of the images seen on this page are taken from line drawings after [Hirst \(1923\)](#) and [Dubinin \(1962\)](#) (e.g.: see inset below right).

Morphology

The Rhynie mite *Protacarus* has a characteristic and distinctive morphology that easily distinguishes it from other Rhynie arachnids, namely the trigonotarbid. Overall, mites including *Protacarus* show no segmentation on the opisthosoma and no distinct division between the head and the rest of the body. The size is minute, the fossil mites found ranging from 290 to 450 microns in length (see insets below).



Above: The holotype of *Protacarus crani* (right) with line drawing for comparison (left) showing the whole animal with segmented walking legs (**l**), pedipalps (**p**) and chelicerae (**c**). Due to the nature of the chert sample and the orientation and minute size of the fossil, the actual specimen (image on the right) does not lend itself well to photography (scale bar = 100 μ m) (Copyright owned by The Natural History Museum)

Protacarus does not exhibit the same scale-like cuticle sculpture as that seen in the Rhynie trigonotarbids. The body is divided into an anterior **proterosoma** and a posterior **hysterosoma**, the junction being taken in front of the posterior two pairs of legs. The proterosoma is subdivided into the gnathosoma (bearing the mouthparts, chelicerae and pedipalps) and propodosoma which bears the first two pairs of walking legs. *Protacarus* lacked eyes. The hysterosoma is broadly subdivided, comprising the metapodosoma (the region bearing the last two pairs of walking legs) and the opisthosoma. The hysterosoma exhibits transverse furrows and the dorsal surface exhibits very fine fan-like hairs or **setae** (see inset above left).

The paired chelicerae ("jaws") are relatively large and highly modified, the terminal segment being strongly cutinised, having a pointed tip and appearing very stylet-like. Lateral and posterior to the chelicerae are the pedipalps. These comprise six jointed segments or podomeres with three claw-like hairs on the terminal segment (the tarsus). There are four pairs of walking legs, each comprising just six jointed segments. Again the walking legs possess claw-like hairs at the tips of the terminal segments. The walking legs and the pedipalps show very fine hairs or setae which most likely formed part of the animal's sensory array (see inset above left).

Palaeoecology

The extant Arcari are particularly diverse in terms of their structure and habitat. They are the only arachnid order which contains plant-eating species. A number of species are parasitic, and several are aquatic; occurring in fresh-water and even marine habitats. The mites that include the family Pachygnathidae are in part saprophagous (living off dead organic remains) and mainly found living in damp plant litter; it is quite possible that *Protacarus* lived in a similar habitat. Many of the Rhynie mites have been found within empty sporangia. The morphology of the mouthparts of *Protacarus* suggests it may have also fed off the sap of living plants by

puncturing the epidermis with its stylet-like chelicerae then imbibing the fluid through the wound. In some thin sections of chert, axes of plants have shown pathological damage and what appear to be enlarged cells in the epidermis and cortex filled with opaque organic material that may reflect a response to such an attack ([Kevan *et al.* 1975](#)).

Other useful references

For a review of the phylogenetic importance of the Rhynie chert mites see [Bernini \(1986\)](#).

CONTENTS PAGE



Myriapods

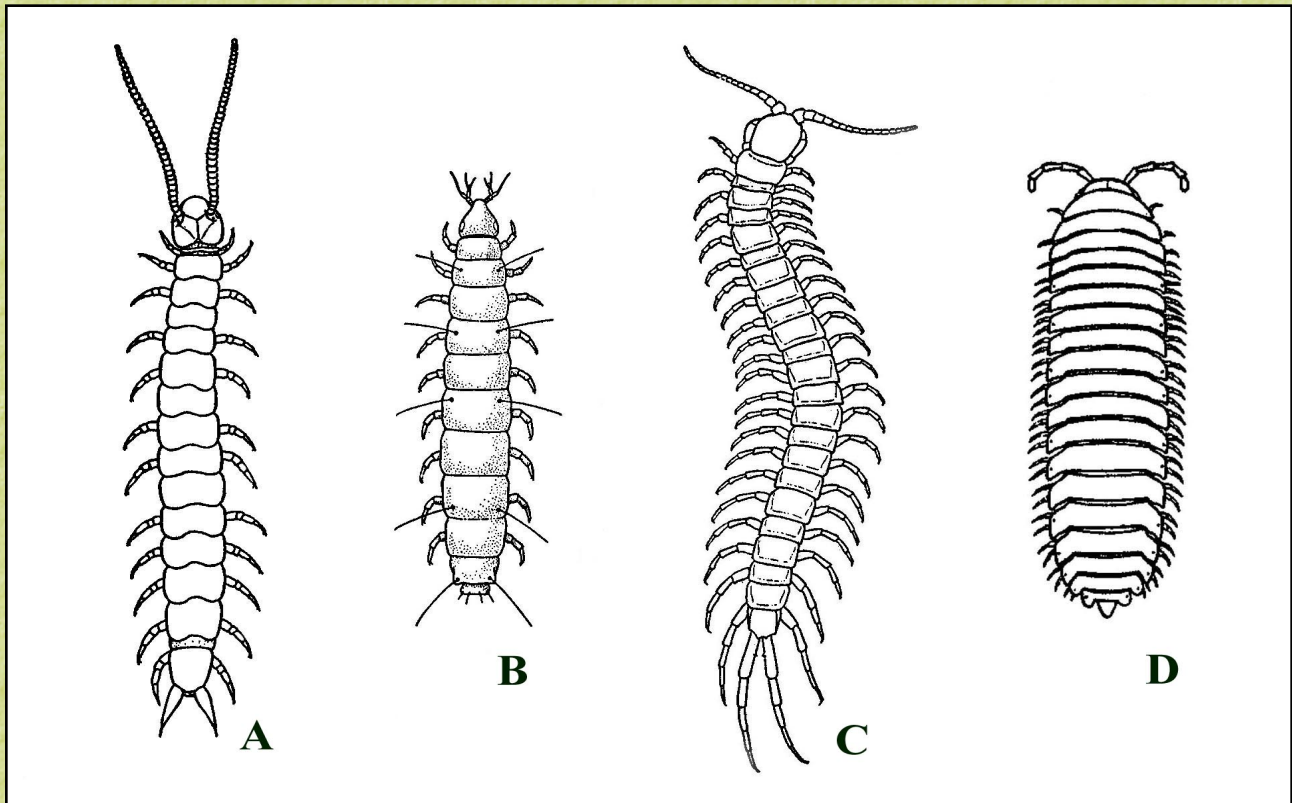
[Introduction](#)

[Fossil Record](#)

[Identity](#)

Introduction

Fossils of a group of arthropods called the **Myriapoda** have also been discovered in the Rhynie chert. Myriapods lack external gills, instead they possess an internal tube-like respiratory system called the **tracheae**, a feature that has enabled the group to pervade the terrestrial environment. The myriapods are distinguished from other mandibulate ('jawed') arthropods by their large number of legs and also the fact that these animals are divided into two parts, a distinct body and head. Myriapods include the extant centipedes, millipedes and the tiny litter-dwelling symphylans and pauropods (see inset below), and also some enigmatic extinct forms such as the arthropleurids.



Above: Some examples of extant myriapods (not shown to scale):

A: *Scutigera immaculata*, a symphylan; **B:** a pauropod; **C:** *Otocryptops sexspinosa*, a scolopendromorph centipede; **D:** a polydesmoid millipede (after [Snodgrass 1952](#)).

Fossil Record

Myriapods have a very sparse fossil record, primarily a reflection of the environments in which they live and the poor preservation potential of their non-mineralised exoskeletons. The earliest myriapod-like fossils recorded are from Cambrian marine deposits. Possible myriapod burrows are also recorded from the Late Ordovician. However, the first unequivocal terrestrial myriapod fossils are millipedes (Archidesmids) recorded from Mid Silurian rocks of Scotland ([Wilson & Anderson 2004](#)). Other terrestrial myriapods (including centipedes and arthropleurids) are recorded from rocks of the Late Silurian of Shropshire, UK (e.g.: [Jeram et al. 1990](#), [Shear & Selden 1995](#)). Cenozoic examples are known primarily from Oligocene amber. Mesozoic myriapod fossils are quite rare. In Palaeozoic rocks myriapods are quite well known from the Devonian and particularly the Carboniferous. To date a number of myriapodous arthropods have been discovered in the Rhynie chert and appear to have formed a significant component of the Early Devonian biota.

Identity

Of the Rhynie myriapod material that has been described at least one is an unequivocal centipede, *Crussolum* sp. ([Anderson & Trewin 2003](#)) whereas others are of, as yet, uncertain affinities. Other new material that has been discovered more recently in the Windyfield chert is currently being described and when published will be added to these resource pages in due course. The new discoveries include at least one new species of centipede, and the first arthropleurids to be found at Rhynie! Click on the hyperlinks below for images and brief descriptions of some of the animals described to date.

- [Centipedes](#)
- [Myriapoda *incertae sedis*](#)

CONTENTS PAGE



Collembolans

[Introduction](#)

[Fossil Record](#)

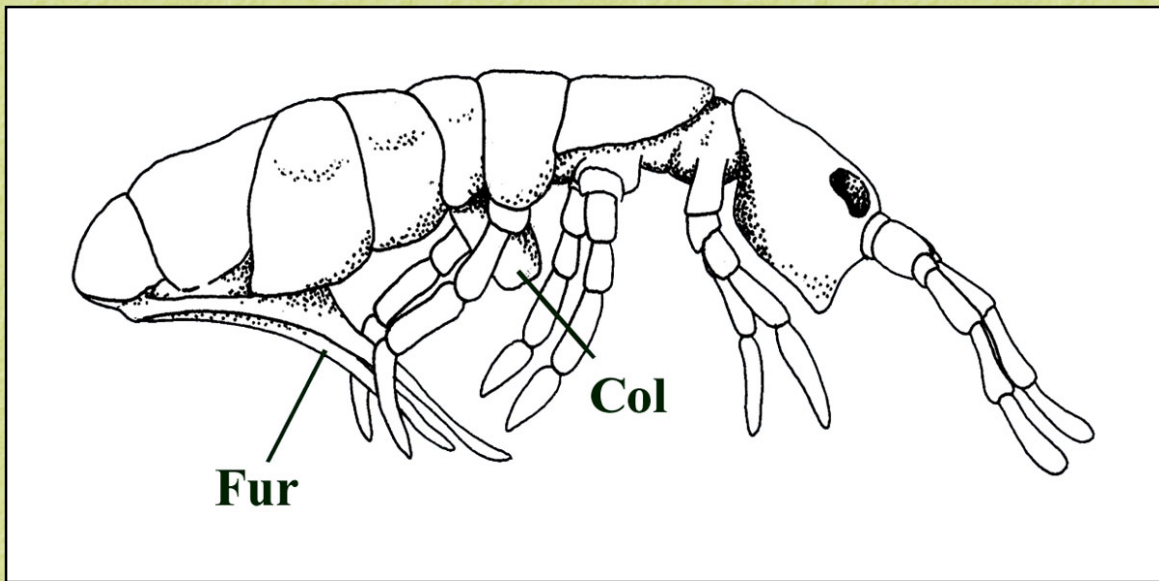
[Morphology](#)

[Palaeoecology](#)

[Other useful references](#)

Introduction

Collembolans or 'springtails' are a group of small arthropods that, together with the Protura, comprise the Class Parainsecta. As with true insects the Parainsecta are hexapods in that they possess three pairs of walking legs. However they differ in the fact that the abdomen of true insects comprises eleven segments whereas the collembolans have only six abdominal segments. The Protura on the other hand possess between nine and twelve segments on the abdomen. In the past the collembolans, proturans and two other groups; the diplurans and the thysanurans were all grouped together as the apterygotes or the wingless insects. It is now generally accepted by entomologists, however, that the first three groups are in fact offshoots of the main insectan evolutionary stem and have therefore since been given separate taxonomic status from the Class Insecta. Thus the frequently repeated claim that the earliest known 'insect' is found in the Rhynie chert refers to a collembolan, and the 'insect' taxonomic status depends on taxonomic opinions.



Above: A modern collembolan or 'springtail'. Notice the ventral fork-like furcula or 'spring' (**Fur**) towards the back of the animal and the ventral tube-like colophore (**Col**). Compare this image with the *Rhyniella* images below.

The collembolans (with the exception of a few genera) are also distinguished by a curious ventral abdominal 'jumping organ' - the **furcula** which the animal uses to vault into the air when it is threatened - hence the common name 'springtail'. This is attached to the fourth abdominal segment and is held in tension by means of a special 'catch' called the **tenaculum** on the third abdominal segment. Another curious characteristic of collembolans is the **colophore**, a ventral tube attached to the first abdominal segment. The exact function of this organ remains unknown but may be a means of allowing the animal to regulate its water balance. The colophore was originally thought to be used for adhesion - hence the name 'collembolan' taken from the Greek words *coll* and *embol* meaning 'glue peg'.

Fossil Record

The fossil record of the collembolans and indeed the proturans is particularly sparse, in fact proturans have not been described from the fossil record at all. The collembolans have been in existence since the Early Devonian; with most fossil representatives having been described from Oligocene amber but the earliest recorded fossil species is from the Rhynie chert. To date one species has been identified; ***Rhyniella praecursor***, described by [Hirst and Maulik \(1926\)](#) (from four specimens of the animal's head) and is traditionally famed for being the earliest recorded fossil 'insect'. Initially its affinity was treated with some skepticism, however [Tillyard \(1928\)](#), demonstrated that *Rhyniella* was indeed a collembolan based on the morphology of the antennae and mouthparts. Further discoveries of more complete specimens by the Rev. W. Cran and D. J. Scourfield established beyond a doubt a collembolan affinity ([Scourfield 1940a, b](#)).

Rhyniella shows very similar characteristics to two extant collembolan families; the Hypogasturidae and the Entomobryiidae. The similarity is so striking, it has led some authors in the past to question whether the *Rhyniella* specimens are modern contaminants ([Crowson 1970](#)), but since they are all completely silicified

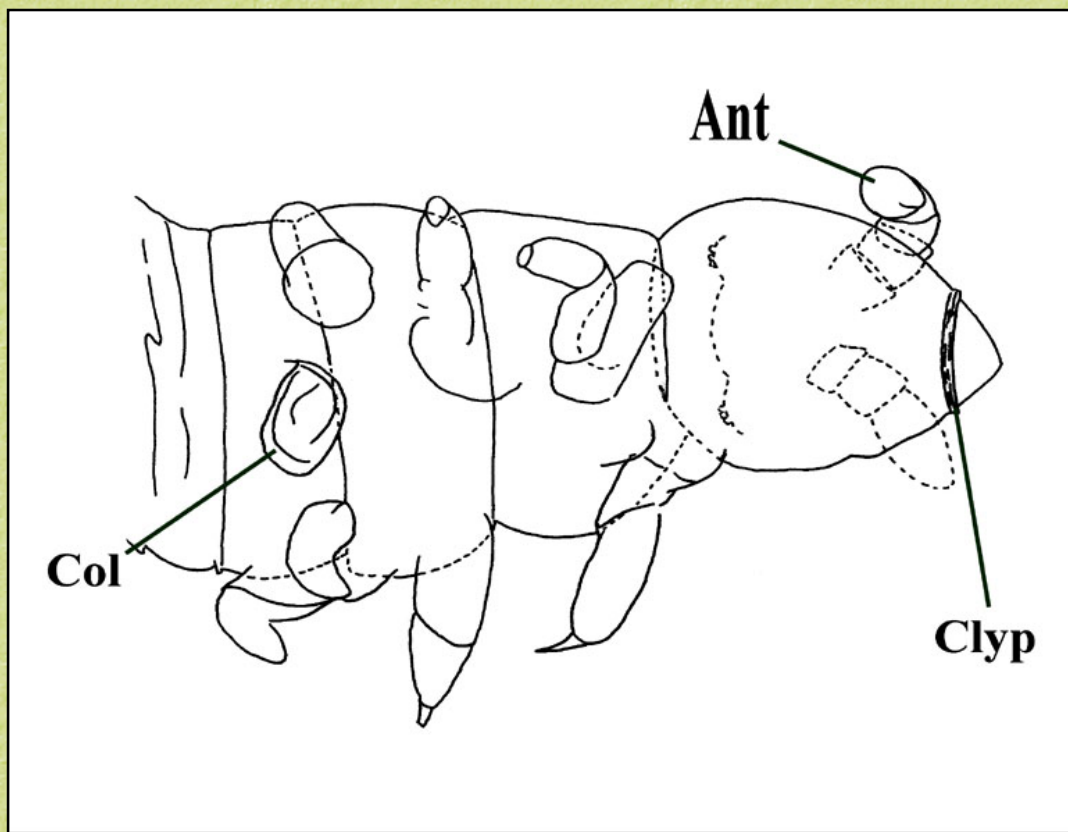
and enclosed within the rock, they are undoubtedly contemporaneous with the chert and are therefore Devonian in age.

Although strictly speaking the collembolans are no longer regarded as true insects by most entomologists, this in no way detracts from the significance of this fossil in terms of the evolutionary history of hexapods and the insects and also the emergence and construction of early terrestrial biotas.

Note: When the specimens of Rhyniella praecursor were first prepared in the 1920's they were found by fragmenting small blocks of chert into tiny shards. The shards of chert that were found to contain Rhyniella were then mounted onto slides. Since these fossils are in uneven shards of chert, they cannot be easily photographed with any clarity, therefore the following images on this page are taken from line drawings after [Hirst and Maulik \(1926\)](#) and [Scourfield \(1940a, b\)](#).

Morphology

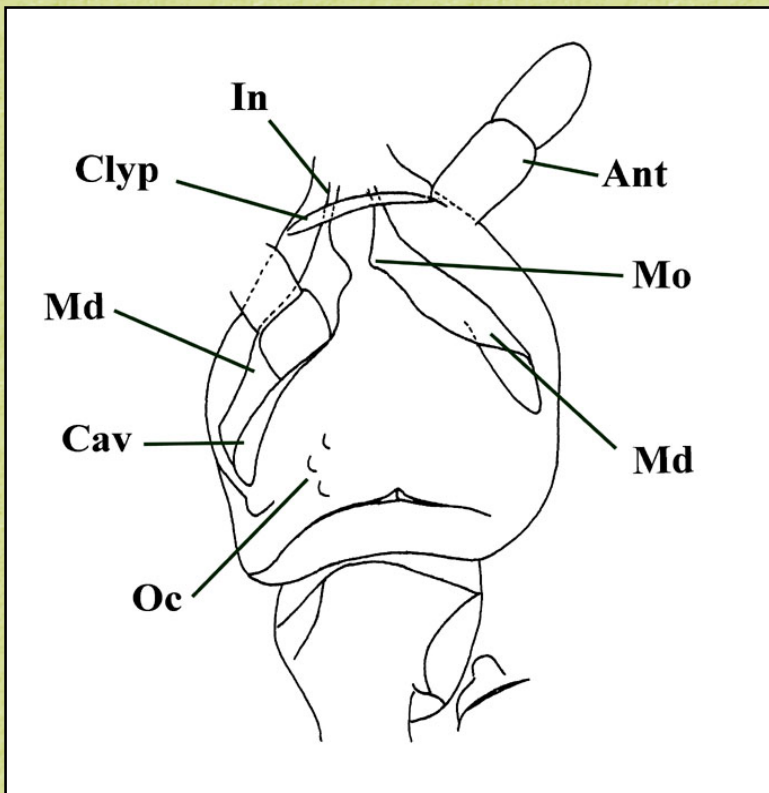
The general morphology of Rhyniella praecursor appears very much similar to the general body plan of many modern collembolans. It was rather small, apparently being between 1-2mm in length. The **head**, **thorax** (the region that bears the walking legs) and parts of the **abdomen** have been identified and described (see inset below). The body segments behind the head do not appear to have been fused together and were sub-cylindrical. Work on new specimens by [Whalley and Jarzembowski \(1981\)](#) showed that Rhyniella possessed a furcula. The following gives a brief account of the morphology of the known body elements.



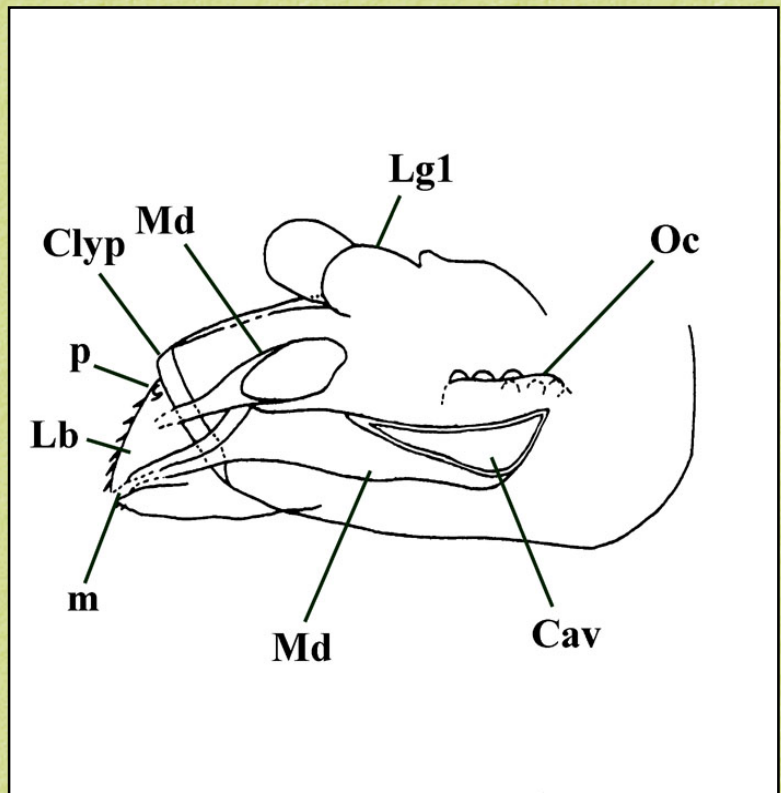
Above: *Rhyniella praecursor* showing head, thorax and first two abdominal segments. Full series of leg appendages (3 pairs) shown together with the collophore (**Col**), antenna (**Ant**) and clypeus (**Clyp**) (after [Scourfield 1940b](#)).

Head Region

The head varies between 300 and 400 microns in length and is heart-shaped with the pointed end to the anterior. It has an arched strongly cutinised **clypeus** commonly appearing in specimens as a conspicuous dark brown band (see inset below left). A **labrum** is present (a small ventral piece of cuticle that protects the mouthparts) attached to the clypeus by two small rounded projections and appears to have been covered by tufts of fine hairs or setae (see inset below right). A pair of **ocelli** or 'eyes' are present, each apparently comprising at least six tiny hemispherical tubercles on the dorsal part of the head behind the antennae. The antennae are simple, rather shorter in length than the head capsule, each comprising four segments. The terminal segment may possess tiny sensory structures.



Above: Dorsal view of head showing parts of the left and right antennae (**Ant**), clypeus (**Clyp**), mandibles (**Md**) with the opening to the mandibular cavity (**Cav**) and the left ocelli (**Oc**). The incisor (**In**) and molar (**Mo**) areas of the mandibles are also illustrated (after [Hirst & Maulik 1926](#) and [Scourfield 1940](#)).



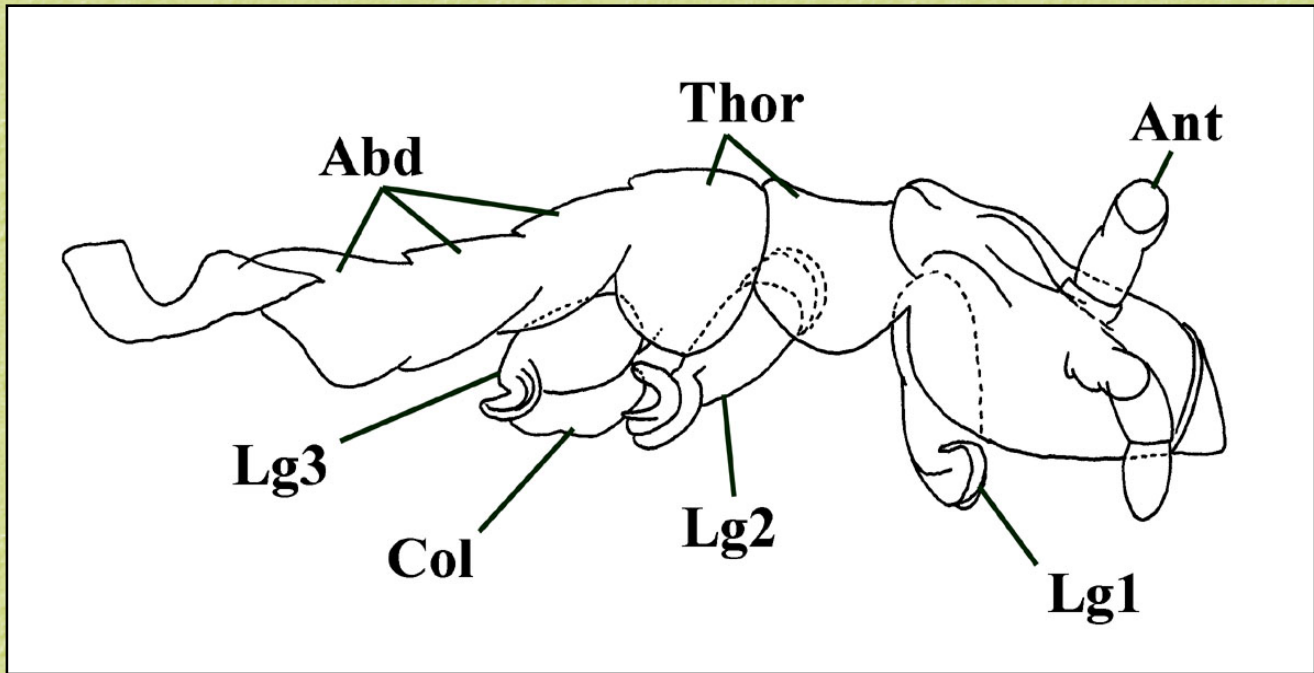
Above: Slightly ventral view of head showing mandibles (**Md**) and mandibular cavity (**Cav**). Labrum (**Lb**) attached to clypeus (**Clyp**) by two small processes (**p**). Position of mouth (**m**), ocelli (**Oc**) and part of first left leg (**Lg1**) also shown (after [Scourfield 1940](#)).

The mouth parts are of interest. These are entirely located within the head capsule. The most conspicuous feature are the **mandibles**. These are relatively elongate (see insets above left and right) and become split towards the anterior into a distinct incisor and molar region. The tips of the incisors have not been seen but were probably stylet-like and most likely lacked teeth. In one particular specimen the molar area of one mandible shows very faint parallel lines. This suggests the molar area originally supported some very fine ridges as 'teeth'. The posterior end of the mandibles show a conspicuous cavity into which muscles were originally inserted. Other mouthparts are unfortunately not particularly clear, though a number of specimens show what may be parts of the **maxillae** and possible lingual elements.

Thorax and appendages

The thorax is the region of the body between the head and the abdomen that supports the walking legs, and may be divided into three parts; the prothorax, mesothorax and metathorax. The prothorax bears the first pair of walking legs. In *Rhyniella* this segment is not very clear and seems to be very much reduced and lacking a tergum giving the impression that the first pair of legs originates between the back of the head and

the following segment (the mesothorax). The mesothorax and metathorax are well developed (see inset below); these two segments bearing the second and third pairs of walking legs respectively.



Above: *Rhyniella praecursor* showing head with antennae (**Ant**), thorax (**Thor**) with three pairs of legs (**Lg1-3**) (left leg series only shown) and part of the abdomen (**Abd**). A poorly preserved colophore (**Col**) is also present (after [Scourfield 1940b](#)).

The legs of *Rhyniella* (three pairs in all) appear to have been similar to each other. Due to relatively poor preservation, the complete morphology of the walking legs remains unknown. It does seem, however, that each leg ended with a distinct single claw. These terminal claws appear to have been relatively long but simple in their structure.

Abdomen

As with modern collembolans *Rhyniella* possessed six abdominal segments. It appears to have also possessed a furcula ([Whalley & Jarzembowski 1981](#)). In a number of specimens the first abdominal segment has a poorly preserved structure on its ventral surface that may represent the colophore (see insets above).

Palaeoecology

Modern collembolans or springtails are found in a variety of habitats ranging from beaches, caves, grassland, trees and forest floors to the surface of ponds. They have even been found in Antarctica. In fact unlike many other arthropods it appears collembolans have actually adapted to flourish in relatively cold environments. On the whole, however, most species seem to prefer cool humid conditions, particularly in soils with an abundance of plant litter. They are mainly saprophagous (living off dead organic, particularly plant, matter) and some species attack young plants. A few modern species are carnivorous feeding on nematodes and other collembolans. In many modern terrestrial ecosystems collembolans play an active role in the breakdown and recycling of dead plant material and, as a result, help in the formation of soils.

It is quite likely that *Rhyniella* fitted a similar ecological niche within the Rhynie fauna, perhaps living among *Rhynia* and *Aglaophyton* stands feeding on soil micro-organisms, spores and breaking down rotting plant litter. This would imply an important interaction between *Rhyniella* and the Rhynie flora in that it may have helped significantly in the formation of soils during the Early Devonian. It is also interesting that the few specimens of *Rhyniella* to be discovered appear to be mainly associated with cherts formed within a more aquatic setting (that is, the chert matrix containing the fossils often shows open meshes of filamentous algae, fungal hyphae, cyanobacteria and coprolites). Although it is likely these animals or their moults were washed into localised ponds and areas of standing water, *Rhyniella* may have been able to live on the surface of ponds buoyed up by surface tension like some modern semi-aquatic collembolan species.

Other useful references

Since Scourfield's time further works have been written relating to *Rhyniella*. Among others, useful texts have been written by: [Kevan *et al.* \(1975\)](#); [Rolfe \(1980 & 1985\)](#); [Whalley & Jarzembowski \(1981\)](#); [Crowson \(1985\)](#); [Greenslade & Whalley \(1986\)](#); [Greenslade \(1988\)](#) and [D'Haese \(2003\)](#).

CONTENTS PAGE



Euthycarcinoids

[Introduction](#)

[Fossil Record](#)

[Morphology](#)

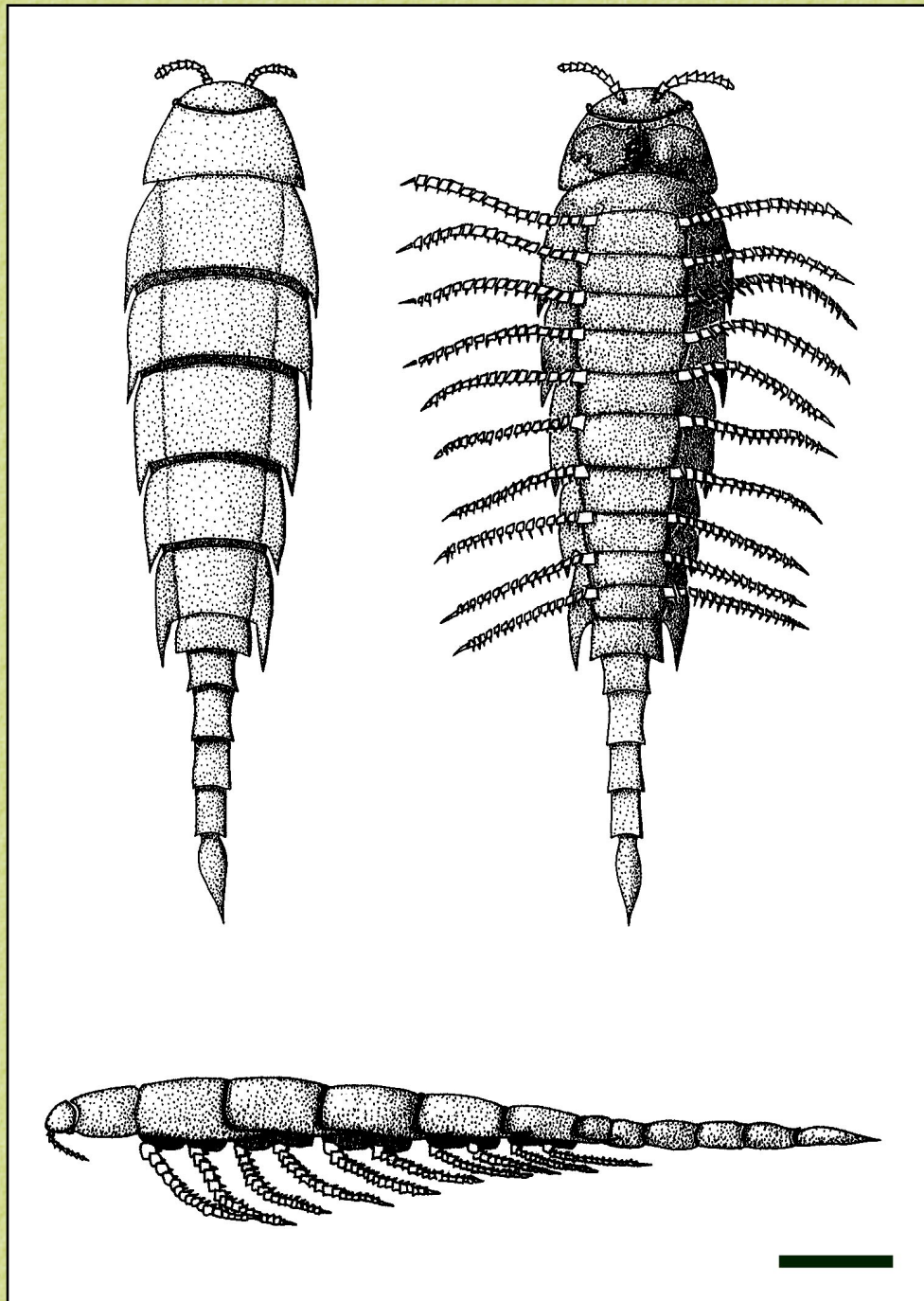
[Palaeoecology](#)

Introduction

A recent addition to the aquatic fauna of the Rhynie chert is a group of bizarre organisms which are termed euthycarcinoids. The euthycarcinoid body plan comprises a **preabdomen** with a variable number of segments or **somites**. On the ventral side these form distinct plates or **sternites** whereas on the dorsal side the plates (**tergites**) being fused appear larger and fewer in number so that two or sometimes three sternites appear to correspond with one tergite. Characteristically the appendages of the preabdomen are multi-segmented, almost antenna-like, with one leg pair per sternite. An **apodous postabdomen** with a variable number of segments ends in a pointed or styliform tail or **telson**. The systematic placement of euthycarcinoids remains somewhat problematic, since they show similarities with crustaceans and uniramous arthropods, including insects.

One species of euthycarcinoid has been found in the chert, *Heterocrania rhyniensis* ([Hirst & Maulik 1926](#)). It was originally assigned to the genus *Crania* after the collector and discoverer Rev. William Cran, but was subsequently changed to *Heterocrania* as the name *Crania* was preoccupied by a genus of brachiopod.

When first discovered, the affinity of *Heterocrania* was unknown, the fossil only being known from fragmentary remains lacking sufficient diagnostic features. It was only with the recent discovery of more complete specimens in the Windyfield chert that it became clear the animal was a euthycarcinoid ([Anderson & Trewin 2003](#)) (see inset below).



Above: Reconstruction of the Rhynie chert euthycarcinoid *Heterocrania rhyniensis* (scale bar = 2mm) ([Anderson & Trewin 2003](#)).

Fossil Record

Euthycarcinoids are relatively rare as fossils. They are an extinct group of arthropods with a fossil record spanning from the Late Silurian to the Middle Triassic. The earliest euthycarcinoid fossil was described

by [McNamara and Trewin \(1993\)](#) from the Tumblagooda Sandstone of Western Australia. The youngest fossil has been described from the Middle Triassic of Australia ([Edgecombe & Morgan 1999](#)). Upper Carboniferous euthycarcinoids have been recorded from Mazon Creek fauna ([Schram & Rolfe 1982](#)) and also in Europe ([Anderson *et al.* 1997, 1999](#); [Secretan 1980](#); [Wilson & Almond 2001](#)). *Heterocrania* is the first euthycarcinoid known from Devonian rocks.

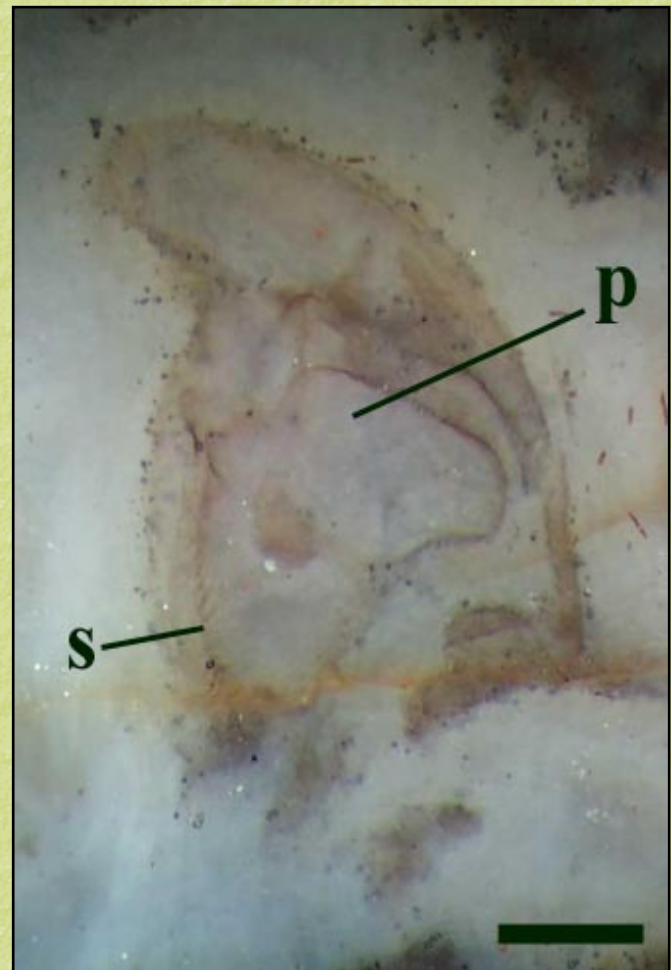
Morphology

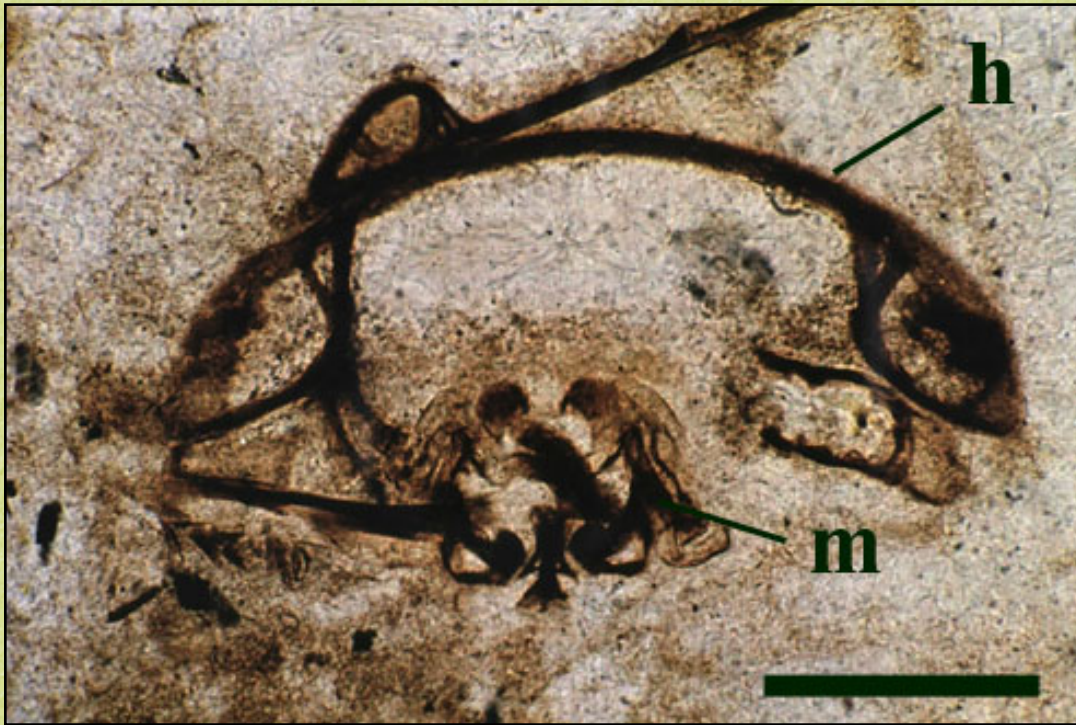
Heterocrania is a small euthycarcinoid, to date being the smallest of its kind described. In life it probably attained a length of approximately 15mm.

Head

The cephalic segment or the head of *Heterocrania* is domed, and flattened on the ventral surface (see inset below). The latter bears a pair of sub-rectangular plates, probably representing mandibles. The inner edge of these plates, where they meet, possess striated ridges (see inset right).

Right: Fragment of the cephalic segment of *Heterocrania rhyniensis* showing one of the ventral plates (**p**) with a striated inner margin (**s**) (scale bar = 500µm).





Above: Transverse cross section through the head capsule of *Heterocrania rhyniensis* showing the domed dorsal surface (**h**) and what are most probably mouthparts (**m**) (scale bar = 500 μ m)
(Copyright owned by The Natural History Museum).

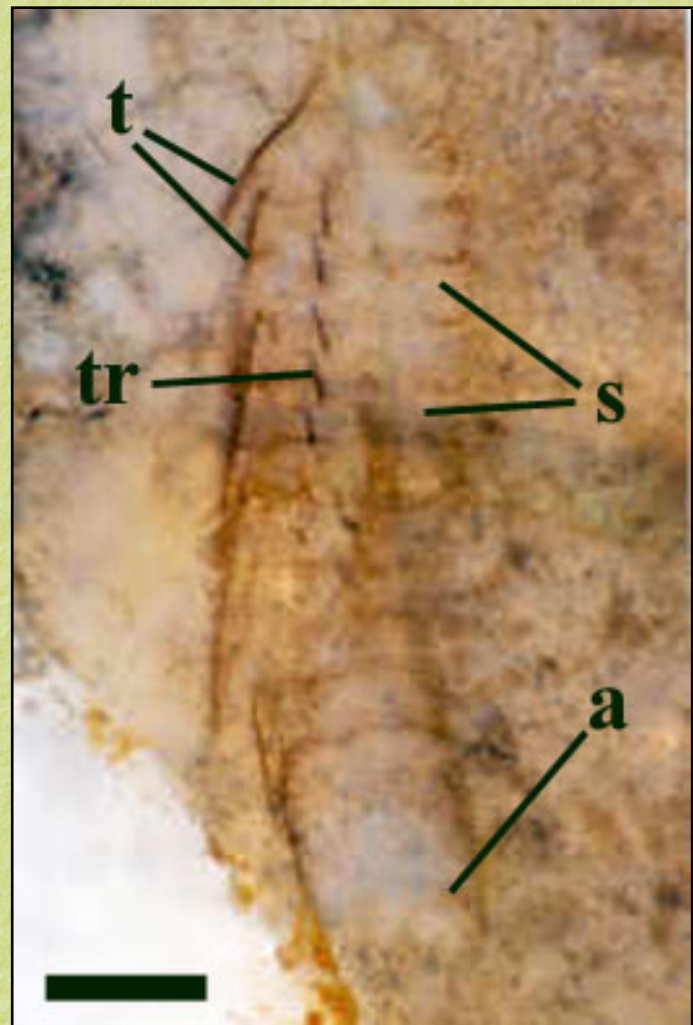
Preabdomen

The preabdomen of *Heterocrania* is multi-segmented, comprising a series of two distinct ventral plates or sternites corresponding to a larger, fused tergite of which there were probably five in all (see inset right). Each sternite bears a pair of leg appendages.

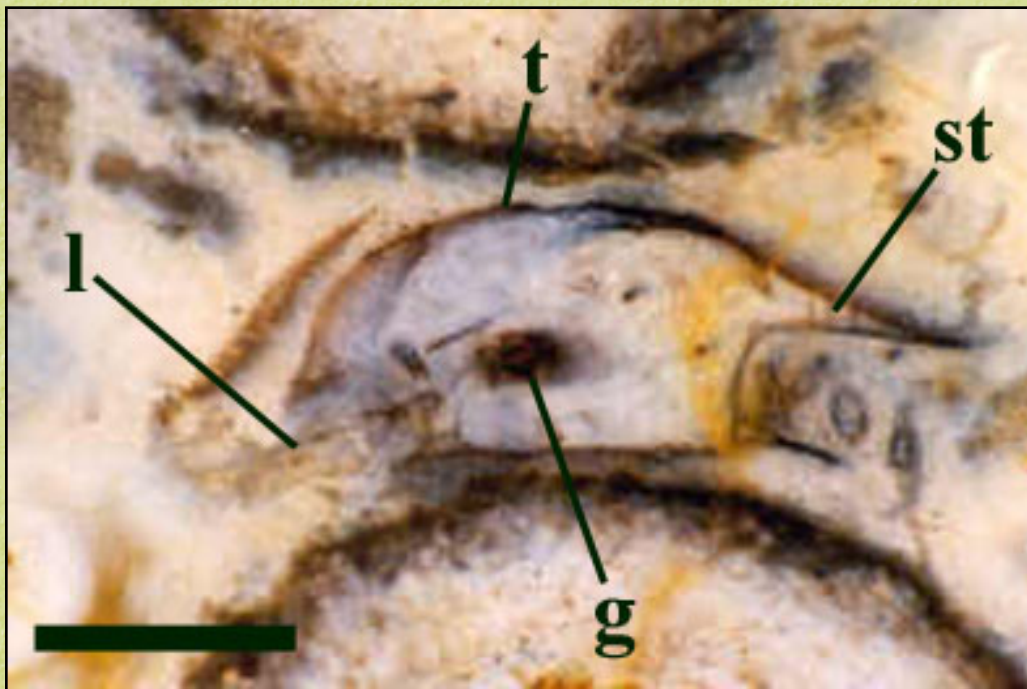
The tergites are convex and markedly wider than the flattened sternites, the lateral margins of the tergites forming shelf-like projections ([Anderson & Trewin 2003](#)). In transverse cross section, these lateral projections appear to be reinforced by cuticular struts

separating the upper and lower surfaces of the tergite cuticle (see inset below). In some thin sections of the animal curious rod-like tubes are present internally, with a disposition of one pair per sternite (see inset right) and appear to correspond with the position of the bases of the leg appendages, for which they probably provided support.

In a few specimens an internal sub-cylindrical gut trace occurs, comprising amorphous organic detritus (see inset below).



Above: An almost complete specimen of *Heterocrania rhyniensis* in longitudinal section seen in dorsal aspect (the dorsal surface has been lost during sample preparation). This shows the margins of the fused tergites (**t**) with the corresponding sternites at depth in the section (**s**). The curious rod-like tubes are also shown (**tr**), together with the anterior segments of the postabdomen (**a**) (scale bar = 1mm).



Above: Transverse cross section through the preabdomen of *Heterocrania rhyniensis* showing the convex tergite (**t**) with lateral shelf-like projections supported internally by cuticular struts (**st**). One of the leg appendages is visible (**l**) together with probable gut contents (**g**) (scale bar = 500 μ m).

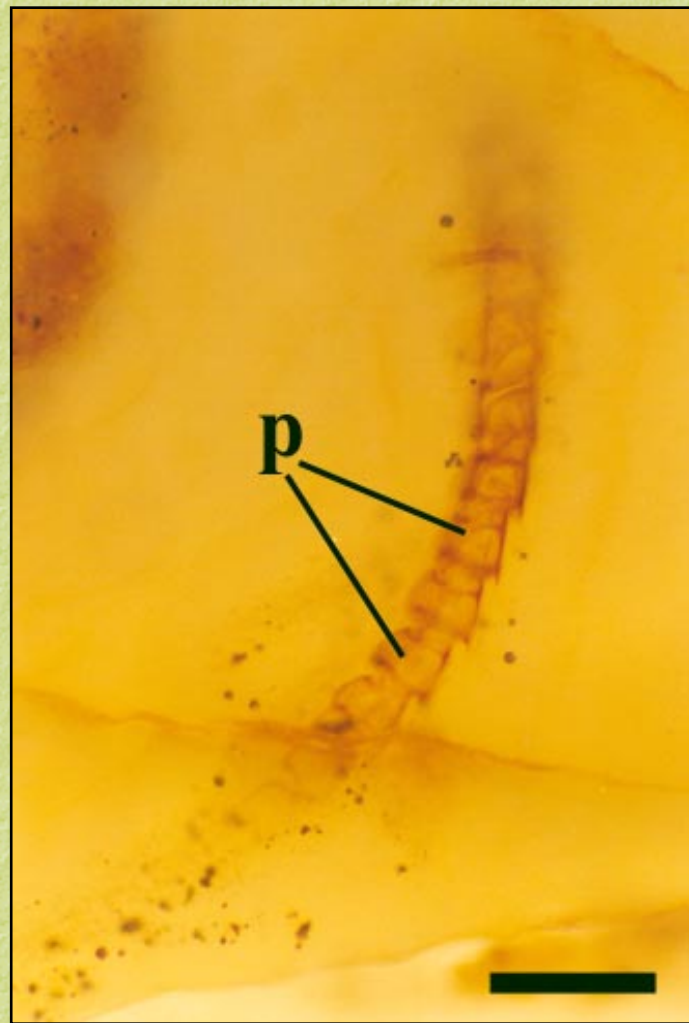
Postabdomen and Tail

The postabdomen of *Heterocrania* comprises five apodous homologous segments. This arrangement suggests the euthycarcinoid belongs to the family **Kottixerixidae**. The tail or telson is of unknown length but appears to be similar in morphology to most other euthycarcinoids in being pointed and styliform.

Leg Appendages

Heterocrania possesses ten pairs of leg appendages, one pair attached to each of the preabdominal sternites. Each leg appendage comprises sixteen individual box-shaped segments or **podomeres** of consecutively decreasing size and each leg ends in a sharp distal spine. The podomeres bear a short, ventrally positioned, articulated spine or spur. The leg pairs decrease in their relative length towards the posterior or the preabdomen.

Right: A leg appendage of *Heterocrania rhyniensis*, showing the individual box-shaped podomeres (**p**) (scale bar = 250µm).



Palaeoecology

In the Rhynie chert *Heterocrania* is typically associated with the crustacean *Lepidocaris*, the probable charophyte *Palaeonitella*, coprolites, algal and cyanobacterial filaments and often occurs in cherts displaying a clotted or 'mulm-like' texture. *Heterocrania* is therefore interpreted as an aquatic organism.

The morphology of the leg appendages suggests the animal was not suited to a predominantly swimming or nektonic lifestyle, as evidenced by the lack of paddle-like flattened podomeres and setae. Although *Heterocrania* may have been capable of limited swimming, it was probably more suited to burrowing or crawling on the substrate of freshwater ponds, feeding on organic detritus ([Anderson & Trewin 2003](#)).

CONTENTS PAGE



The Ancient Environment and Modern Analogues:

Modern Analogues:

Large-scale features

The spatial distribution of the biota with respect to the hot springs, apart from available soil moisture, nutrients and sunlight, is dependant primarily on two environmental factors: water temperature and pH. Both these factors are important, especially in hot spring areas, because different forms of life have specific tolerances to both, and thus temperature and pH tend to govern which plants and animals may flourish. These constraints would also have been applicable at Rhynie 400 million years ago.

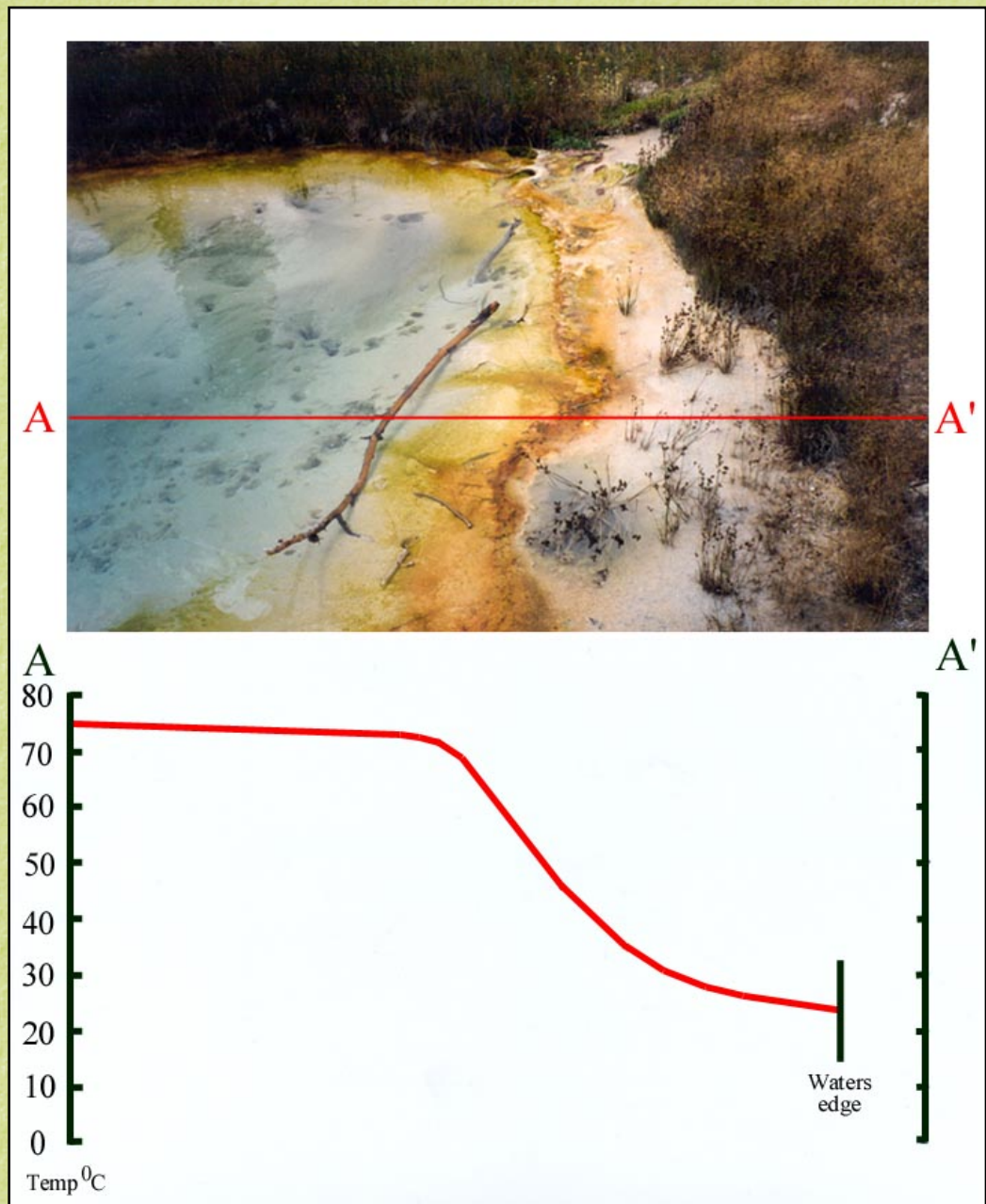
The following table gives a general idea of the upper temperature limits of a number of animals, plants and micro-organisms (after [Brock 1994](#)):

Group	Upper temperature limits (°C)
Animals	
Fish	38
Insects	45-50
Ostracods (crustaceans)	49-50
Plants	
Vascular plants	45

Mosses	50
Eukaryotic micro-organisms	
Protozoa	56
Algae	55-60
Fungi	60-62
Prokaryotes	
<i>Bacteria</i>	
Cyanobacteria (O ₂ producing photosynthetic bacteria)	70-73
Other photosynthetic bacteria (do not produce O ₂)	70-73
Heterotrophic bacteria (use organic nutrients)	90
<i>Archaea</i>	
Methane-producing bacteria	110
Sulphur-dependant bacteria	115

Eukaryotic organisms are unable to adapt to high temperatures, the upper limit (for fungi) being 60-62°C and for plants and animals less than 50°C. Above 62°C only prokaryotes may live, of which the photosynthetic, thermophyllic, cyanobacteria can only tolerate temperatures up to 73°C. At the highest temperatures, over 100°C, where water is boiling, only the heat-adapted, hyperthermophyllic Archaea survive.

Not surprisingly, therefore, in these hydrothermal areas the **thermal gradient** can often be visually identified by the biota present. The hot pool in the inset right is a typical example, the clear blue water on the left represents the hotter parts of the pool (below boiling, at around 75°C), probably colonised, if at all, by heterotrophic bacteria and Archaea. The narrow yellow to orange zone (a maximum distance of 55cm) ranges from 72°C on the left to 46°C on the right and is colonised primarily by photosynthetic cyanobacteria. Beyond this to the edge of the pool the temperature drops to approximately 30°C in the 'milky white' water to 24°C at the waters edge where vascular plants, primarily sedges, abound. Notice the rapid change in temperature over less than one metre to the pools edge and, therefore, how close plants and animals can actually live to these hydrothermal features. The pH also tends to become more alkaline, from a neutral pH 7 in the centre of the pool to pH 9 at the edge.



Similarly, changes in biota and the colour of cyanobacterial mats are also evident in overflow channels from geysers and hot springs, marking the temperature limits of the biota and hence the decrease in water temperature (see inset below).

Above: Seismograph pool at West Thumb Geyser Basin, Yellowstone National Park, showing the thermal gradient as the water temperature drops from the centre of the pool (left) to the waters edge. The yellow to orange band represents a sharp drop between 72 - 46°C, the colour caused by the growth of photosynthetic cyanobacteria.



Above: Heart Spring, near the Lion Geyser Complex (centre right background), Yellowstone National Park. This image shows the changes in colours, from pale yellow, to orange to brownish green, created by cyanobacteria in the overflow channels, marking the progressive drop in water temperature from the spring. Notice how close plants are growing to the spring on the right of the photograph. Sinter is being precipitated around the edge of the spring and over the water surface (the bright white ledges) and also on the overflow apron in the centre left of the image. The foreground comprises degraded, desiccated and brecciated sinter.



In cooler areas of overflow aprons and around pools, plants can grow in variable numbers and in variable diversity depending upon the substrate, available nutrients, moisture and pH. For example, one of the earliest vascular plants to colonise sinters in many areas of Yellowstone National Park is *Triglochin* and typically occurs as patches of monotypic stands (see insets left and below left). Even as these plants are growing their roots and bases of stems may be coated in precipitated silica. Old exhumed sinters occasionally show these and similar plants preserved in silica (click on inset left for an example). Other mature sinter surfaces may become incorporated into organic and mineral-rich soils and are capable of supporting more diverse biotas.

Left: Sinter surface, with a thin veneer of standing water, colonised by a stand of *Triglochin*. The bases of the plant stems often show a thin powdery coating of precipitated silica (Click on the image for examples preserved in sinter). Photograph taken near the main overflow channel from Giantess geyser, Yellowstone National Park.

Often, during periods of heightened hydrothermal activity, together with changes in the subterranean 'plumbing system', water levels of springs may rise, and overflow courses may alter. During such events, areas colonised by plants, previously away from hot water discharges, may suddenly become inundated, killing the plants and any fauna that cannot escape. Rapid precipitation from cooling, flowing, silica-charged waters can, and do, preserve such 'death

assemblages' in sinter.

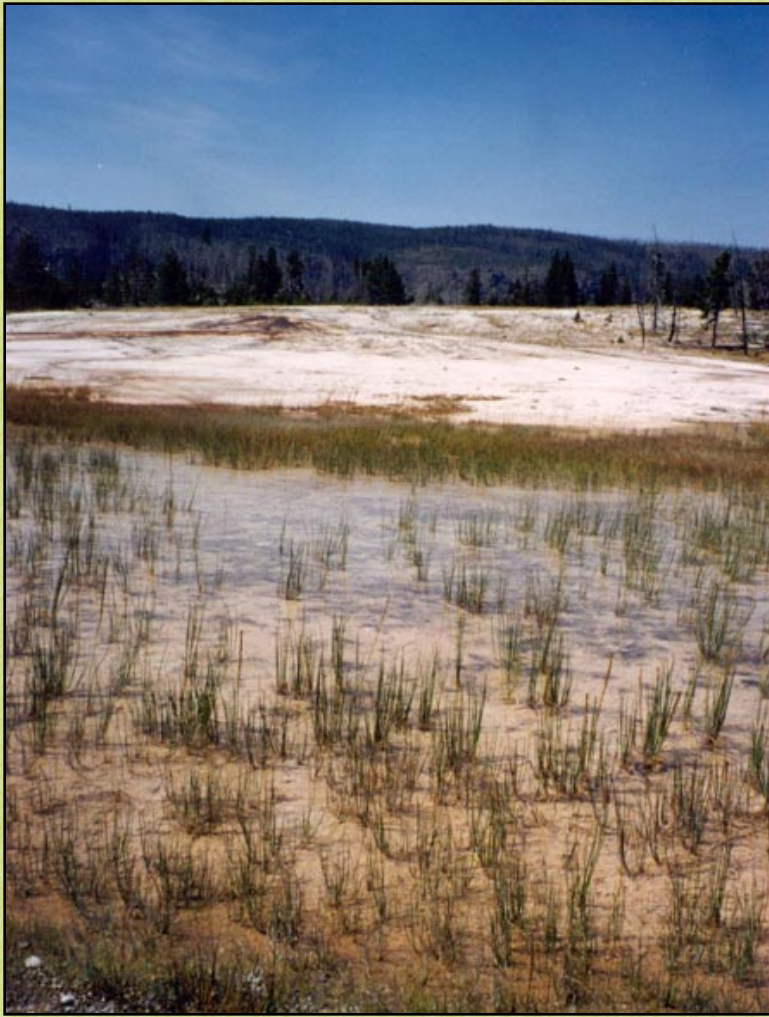
Even in cool streams fed by overflow channels from springs and geysers 10's to 100's of metres up-stream, the evaporation of waters still super-saturated with silica will deposit silica crusts on stream beds and around the bases and roots of plants ([Trewin *et al.* 2003](#)) (see inset right).



Above: Botryoidal clusters of silica (white) precipitated around the bases of stems and roots along a stream near White Dome Geyser, Yellowstone National Park.

In some areas, the cooled overflow from geysers and hot springs may become ponded forming shallow, ephemeral bodies of water (see inset left), forming a variety of wetland habitats that, together with tolerant species of plants, may also be home to various aquatic invertebrates.

Hot springs and geyser vents may become dormant due to changes in the subterranean 'plumbing' of the hydrothermal system and may thus become



'cool pools' capable of supporting a variety of aquatic flora and fauna (see inset below).

Left: Poned run-off from Daisy geyser (middle distance) creating a localised wetland habitat on a degraded sinter surface, Yellowstone National Park.



Above: A hot spring with an outflow channel (bottom centre), Yellowstone National Park. When the photograph was taken, the centre of this pool had a maximum water temperature of 54°C, well within the temperature range for cyanobacteria, and also the upper temperature range for algae and protozoans. The surface of the pool is colonised by a thick, rubbery cyanobacterial mat, buoyed by trapped gas bubbles (click on image for a close up!). Plant stems are held rigid within this mat and it is cohesive enough to support the weight of small invertebrates. The white patches on the mat are comprised of very fine, precipitated silica.

In the few examples of habitats and subenvironments given here, given the right conditions and a continuous influx of silica-charged water (cooled or otherwise), the biota and deposits of all have the potential to become silicified and incorporated in sinter for inclusion in the rock record.

From the variety of textures and biota found within individual beds of the Rhynie chert, most, if not all of the subenvironments mentioned here, or their 400 million year old equivalents, are probably represented.

BACK

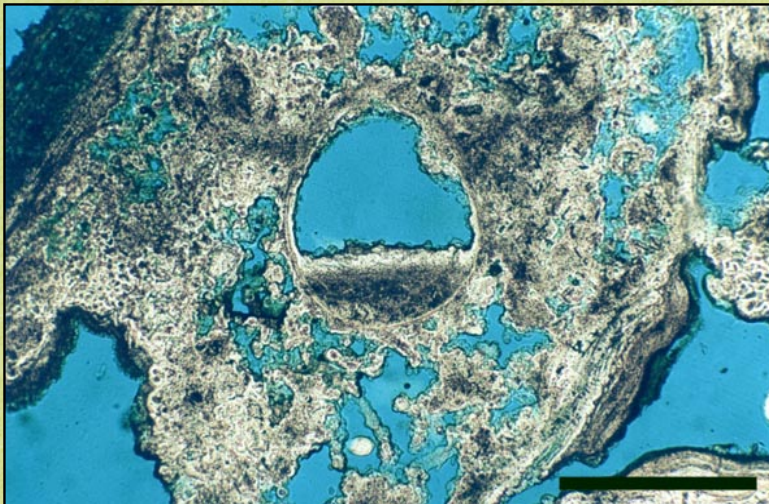


The Ancient Environment and Modern Analogues

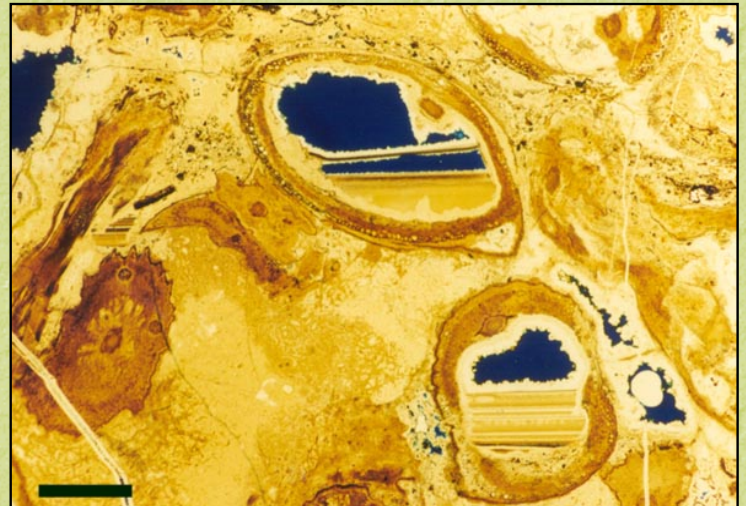
'Micro-features'

Looking at thin sections of various types of modern sinters and comparing them with textures and preservation styles seen in thin sections of the Rhynie chert can also be instructive:

Note: The blue colour in the following images represents pore space in-filled by blue-dyed epoxy resin.



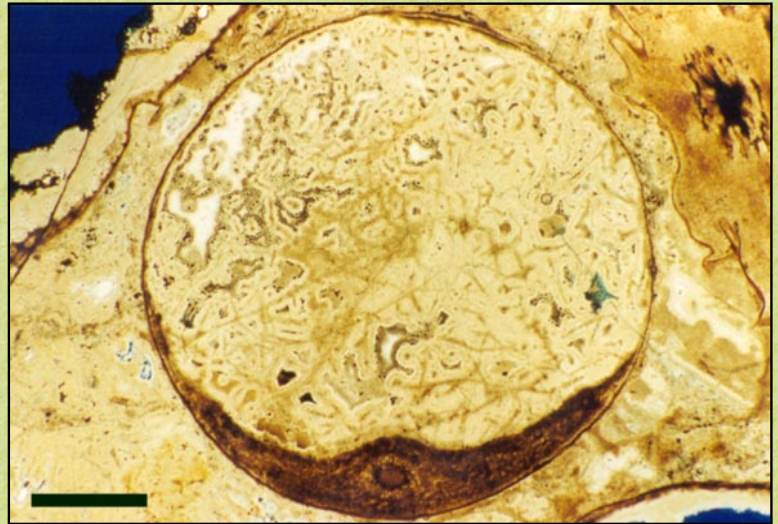
Above: Straws and partially decayed plant stems held in an open framework of amorphous, 'clotted' sinter. The straw in the centre of the image contains a geopetal layer of sediment and silica cement. Sinter from Elk Flats, Yellowstone National Park (scale bar = 250µm).



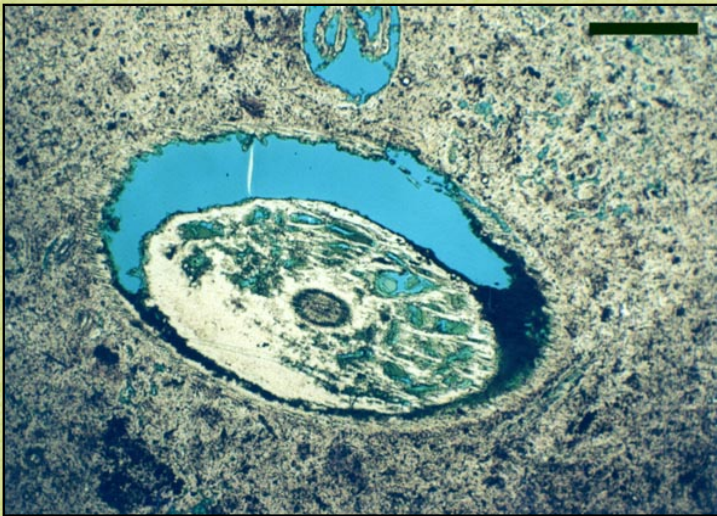
Above: Straws of *Aglaophyton* and partially decayed plant stems held in an open framework of amorphous, 'clotted' chert. The two straws in this sample of Rhynie chert exhibit similar geopetal textures to that in the modern sinter shown in the image on the left (scale bar = 3mm).



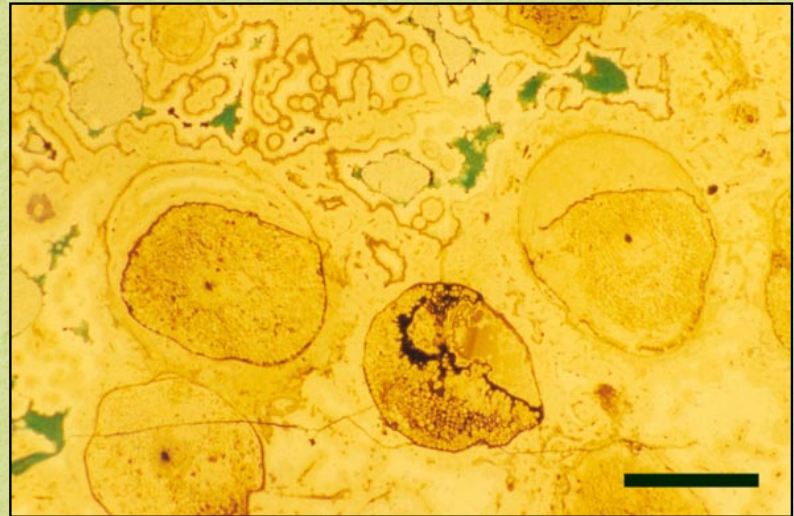
Above: Silicified, partially decayed plant stem missing much of the cortex, the resulting void is traversed by a mesh of silicified microbial filaments. Stream bed sinter near White Dome Geyser, Yellowstone National Park (scale bar = 250 μ m).



Above: Decayed stem of *Aglaophyton* with the xylem strand and remainder of the internal cells collapsed to the base of the stem. The resulting void is traversed by a mesh of filaments (probably fungal hyphae) (scale bar = 1mm).



Above: A plant axis that has partially decayed and shrunk away from the cuticle before being silicified. Sinter from Elk Flats, Yellowstone National Park (scale bar = 500 μ m).



Above: Partially decayed axes of *Rhynia gwynne-vaughanii* that have shrunk away from the cuticle before being silicified (scale bar = 2mm).





Rhynie Chert: Botanical Significance

The Significance of the Rhynie Plants

At the end of the Silurian there began a rapid burst of evolution in plants. Within just 25 million years during the Devonian period, recognised as being one of the two intervals of greatest expansion in plant evolution, land plants evolved complex vascular systems, leaves which specialised in photosynthesis, and roots and stems for support. Most significantly sporangia were developed and seed-bearing plants evolved. More over, the biochemical and physiological processes required to support such complex organisms also developed.

The exceptional preservation of the flora in the Rhynie chert provides botanists and palaeobotanists with a unique window of a time early on in this period of rapid evolution, about 400 million years ago, during the Early Devonian. It gives scientists an insight into the morphology and detailed internal anatomy of these early land plants (in fact in some cases cellular preservation is so exquisite, that the anatomy of a number of the Rhynie plants, for example *Rhynia gwynne-vaughanii* and *Aglaophyton major*, is better known than many living plant species!). The Rhynie plants also provide clues as to the probable evolutionary pathways that gave rise to modern plants and also the mechanisms by which plants adapted to terrestrial habitats.

The Significance of the Rhynie Prokaryotes

Another reason the Rhynie chert is important to palaeobotanists, botanists, and life and earth scientists in general, is the presence of fossilised bacteria and cyanobacteria, some of which may have been thermophillic, thriving within hot springs and their outflow channels.

Prokaryotic organisms provide a fascinating glimpse of the beginnings of life on Earth. Many modern mycoplasmas (organisms related to bacteria, but of simpler structure and smaller size) are capable of independent existence and are probably very similar to the first living things. Anaerobic bacteria may resemble organisms which lived when free oxygen was not available. Cyanobacteria, being aerobic must

have evolved as oxygen began to diffuse into the atmosphere. Once oxygen was available, cyanobacteria would have been responsible for increasing its concentration as a bi-product of photosynthesis.

Certain types of bacteria found in modern hot springs thrive in boiling water, in alkaline and even highly acidic waters, and many cyanobacteria tolerate temperatures up to 73°C. As such, the study of these organisms living in extreme conditions in hydrothermal areas, and their fossilised forms in the Rhynie chert, is not only important in understanding how life evolved on Earth but may also have implications for future studies in the search for life on other planets.





Rhynie Chert: Zoological Significance

The Late Silurian saw the invasion of terrestrial environments by invertebrates, in particular groups of [arthropods](#), including myriapods (such as millipedes, centipedes and the extinct arthropleurids) and arachnids. A rapid burst of evolution from this time to the end of the Devonian not only saw the expansion of these and other arthropod groups, most notably the development of winged insects, but also, significantly, the evolution of air-breathing vertebrates and their adaptation to terrestrial habitats.

The Early Devonian Rhynie chert was deposited early on in this period of evolution and diversification about 400 million years ago. The exceptional preservation of the Rhynie fauna allows zoologists and palaeontologists to examine these early terrestrial, and freshwater, invertebrates in terms of their anatomy, and to determine how the various arthropod groups evolved and adapted to live in these new habitats. For example how centipedes and arachnids separately developed the means to breath air: centipedes developed an internal network of tubes or trachea; whereas in arachnids (esp. trigonotarbids) the anterior abdominal appendages where developed into filliform book-lungs.

By studying the associated *in situ* biota in the individual chert beds, much information can also be gathered on the interactions between fauna, flora and the inorganic environment, thus helping to build a picture of early terrestrial and freshwater ecosystems.

[BACK](#)



Rhynie Chert: Geological Significance

As well as the palaeontological and palaeobotanical significance of the Rhynie chert konservat lagerstätte, there are also other aspects of this unique deposit that are important to geologists.

At 400 million years old, the Rhynie chert is the earliest known, unequivocal, metalliferous, siliceous hot spring deposit that preserves surface 'sinters' and evidence of geyser activity. Hot spring deposits, and particularly their surface expressions, are relatively rare in the rock record. As such the Rhynie chert and its associated sedimentary rocks gives geologists one of the few examples of an ancient hot spring complex.

The Rhynie chert is also important to geologists in understanding the processes through which organisms may be included in the fossil record; such as **taphonomy** (processes affecting organic remains after death and prior to burial), **biostratinomy** (processes affecting organic remains during deposition and burial) and **diagenesis** (processes affecting the rocks and their included organic remains after burial). For example, studying this deposit and the preservation of its biota helps in an understanding of the processes of silicification and how silica can preserve organic remains.



The Biota of Early Terrestrial Ecosystems: The Rhynie Chert

Suggestions For Tutors

Welcome! The guidelines for tutors given in this site have been structured into three components: Course content, Levels of attainment and Course assessment and subdivided as shown in the contents list. Tutors may proceed sequentially through this site by using the navigation buttons at the bottom of each page or alternatively may go directly to any specific item by clicking on the hyperlinks in the list below.

Click here to access the accompanying [resource site](#) and [bibliography](#) covering the subject area, though on returning to this page tutors may need to sign-in again.

Site Navigation

In conjunction with the hyper-linked table of contents below, use the forward and back icons on your web browser to navigate the site.

Contents

1. [Course content](#)
 - [General geological / palaeontological content](#)
 - [Specialist subject content](#)

2. [Levels of attainment](#)

[Final Honours level](#)

[Junior Honours level](#)

[Specialist topic in a non-geological course](#)

[Basic University level](#)

[Pre-University level](#)

3. [Course Assessment](#)

[Assessment Methods](#)

[Report / Essay titles](#)

[Seminar topics](#)

[Examination questions](#)

[Practicals - image interpretation](#)

***Footnote:** Tutors may wish to follow the course suggestions provided above, or prefer to structure the information and assessment to suit the requirements of their own institution.*

The authors of this course would welcome any feedback from tutors that would help improve the course, but cannot supply standard essays or answers to questions.





The Rhynie Hot Spring System: Geology, Biota and Mineralisation

The Proceedings of a Conference organised by the Rhynie Research Group,
University of Aberdeen

Held 17 - 20 September 2003

Edited by Nigel H. Trewin and Clive M. Rice

The peer-reviewed proceedings of the above Conference have been published as Volume **94(4)** of *Transactions of the Royal Society of Edinburgh: Earth Sciences*. The Early Devonian Rhynie and Windyfield cherts of Scotland contain the most diverse terrestrial fauna of this age anywhere in the world. In this volume the history of research and the regional geology of this ancient hot-spring system are reviewed, and exciting new elements of the biota are described, such as a harvestman spider and the gametophytes of *Rhynia*. Reviews are presented of the sporophyte plants, the fungi, and of the biota of the Windyfield chert. Modern analogues of the Rhynie hot springs are represented by studies of modern hot-spring deposits in New Zealand and Yellowstone National Park. This volume brings together the results of diverse research themes related to this world-renowned deposit

Published by:

The RSE Scotland Foundation (on behalf of the [Royal Society of Edinburgh](#)), December 2004, 246pp, paperback. ISBN: 0 902198 29 7 [ISSN: 0263-5933].

Price:

£35 inclusive of postage and packing.

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Contents:

N. H. TREWIN & C. M. RICE - Preface

N. H. TREWIN - History of research on the geology and palaeontology of the Rhynie area, Aberdeenshire, Scotland.

C. M. RICE & W. A. ASHCROFT - The geology of the northern half of the Rhynie basin, Aberdeenshire, Scotland.

M. BARON, S. HILLIER, C. M. RICE, K. CZAPNIK & J. PARNELL - Fluids and hydrothermal alteration assemblages in a Devonian gold-bearing hot-spring system, Rhynie, Scotland.

S. R. FAYERS & N. H. TREWIN - A review of the palaeoenvironments and biota of the Windyfield chert.

J. A. DUNLOP, L. I. ANDERSON, H. KERP & H. HASS - A harvestman (Arachnida: Opiliones) from the Early Devonian Rhynie cherts, Aberdeenshire, Scotland.

L. I. ANDERSON, W. R. B. CRIGHTON & H. HASS - A new univalve crustacean from the Early Devonian Rhynie chert hot-spring complex.

K. S. HABGOOD, H. HASS & H. KERP - Evidence for an early terrestrial food web: coprolites from the Early Devonian Rhynie chert.

- A. J. ROSS & P. V. YORK - A catalogue of the type and figured specimens of Hexapoda from the Rhynie chert (Early Devonian) at the Natural History Museum, London, UK.
- D. EDWARDS - Embryophytic sporophytes in the Rhynie and Windyfield cherts.
- H. KERP, N. H. TREWIN & H. HASS - New gametophytes from the Early Devonian Rhynie chert.
- C. H. WELLMAN, H. KERP & H. HASS - Spores of the Rhynie chert plant *Horneophyton lignieri* (Kidston & Lang) Barghoorn & Darrah, 1938.
- R. KELMAN, M. FEIST, N. H. TREWIN & H. HASS - Charophyte algae from the Rhynie chert.
- T. N. TAYLOR, S. D. KLAVINS, M. KRINGS, E. L. TAYLOR, H. KERP & H. HASS - Fungi from the Rhynie chert: a view from the dark side.
- B. JONES, R. W. RENAULT & M. R. ROSEN - Taxonomic fidelity of silicified filamentous microbes from hot-spring systems in the Taupo Volcanic Zone, North Island, New Zealand.
- K. A. CAMPBELL, T. F. BUDDLE & P. R. L. BROWNE - Late Pleistocene silica sinter associated with fluvial, lacustrine, volcanoclastic and landslide deposits at Tahunaatara, Taupo Volcanic Zone, New Zealand.
- A. CHANNING & D. EDWARDS - Experimental taphonomy: silicification of plants in Yellowstone hot-spring environments.





'410 million years ago in Scotland: Fossils from the Rhynie chert'

Royal Society's Summer Science Exhibition 2004

[BE AMAZED - The Royal Society's Summer Science Exhibition 2004](#)

During July this year the fossil plants and animals found in the Rhynie chert we brought back to life (well, almost!) at the Royal Society's Summer Science Exhibition in London. The Rhynie Research Group were invited to exhibit their research on the chert and its remarkably preserved biota, and provide a glimpse of what life was like on land 410 million years ago during the Early Devonian period. For further details of the exhibition, click on the link above.

Here are some images taken of the exhibit, including a visit by H.R.H. The Prince of Wales!



Above: Front view of the exhibit, the centrepiece being a diorama showing how the Rhynie area may have looked 410 million years ago.



Above: The exhibitors. From left to right: Dr Stephen Fayers, Dr Nigel Trewin, Miss Ruth Kelman, Dr Clive Rice.



Above: View of the exhibit from the left.



Above: View of the exhibit from the right.



Above: Close-up of the diorama showing life-size models of *Asteroxylon*, *Nothia*, *Horneophyton*, *Rhynia* and *Aglaophyton*.



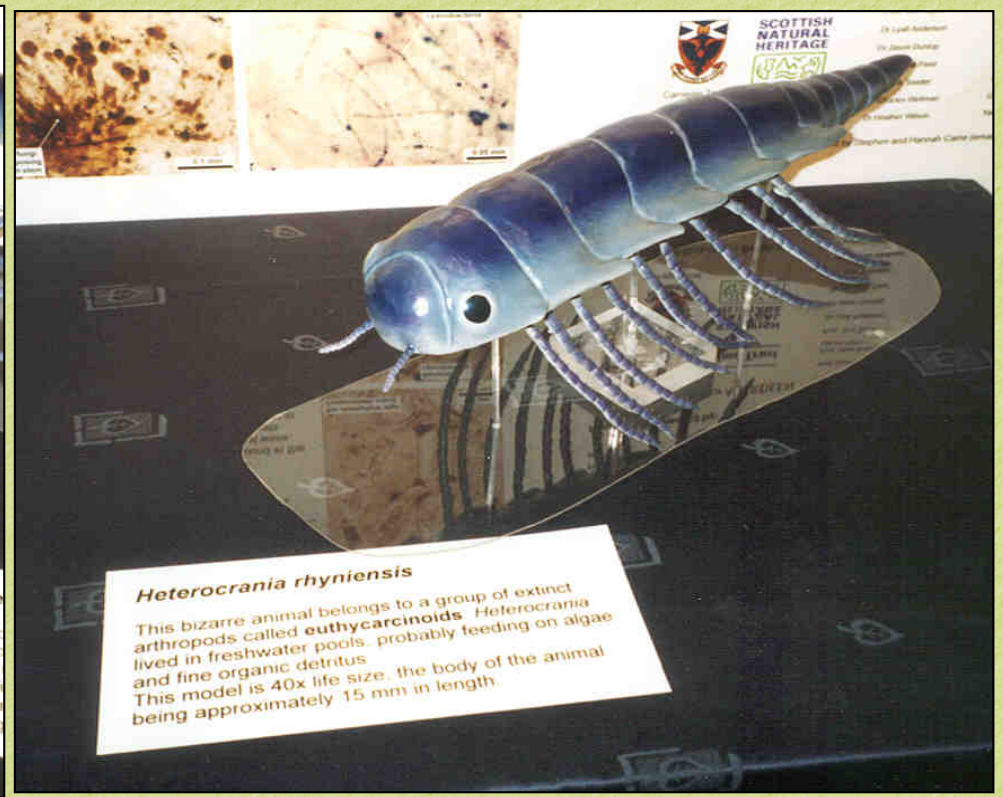
Palaeocharinus tuberculatus

This spider-like arachnid was a terrestrial predator eating other small arthropods and invertebrates. This model is 40x life size. The body of the animal being approximately 7 mm in length.

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Above: Model of the [trigonotarbid](#) arachnid *Palaeocharinus*.



Heterocrania rhyiensis

This bizarre animal belongs to a group of extinct arthropods called **euthycarcinoids**. *Heterocrania* lived in freshwater pools, probably feeding on algae and fine organic detritus. This model is 40x life size. The body of the animal being approximately 15 mm in length.

Above: Model of the [euthycarcinoid](#) *Heterocrania*.



Above: A visit by H.R.H. The Prince of Wales (image provided courtesy of the Royal Society).



Above: Explaining the diorama.



Above: One of the evening functions attended by fellows of the Royal Society.

We would like to thank the Royal Society for their hospitality, Hans Kerp ([Palaeobotanical Research Group, University of Münster](#)) for some of the images used on the poster display, and also [Stephen Caine](#) who sculpted the models and provided the diorama for the exhibit.

