Article:

Wellman, C.H. orcid.org/0000-0001-7511-0464 (2019) Palaeontology: The Rhynie chert is the gift that keeps on giving. Current Biology, 29 (3). R93-R95. ISSN 0960-9822

https://doi.org/10.1016/j.cub.2018.12.014

DISPATCH

Palaeontology: The Rhynie Chert is the Gift That Keeps on Giving

Charles H. Wellman
Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK
Correspondence: c.wellman@sheffield.ac.uk

The earliest record of a terrestrial testate amoeba is reported. This provides further evidence that early terrestrial ecosystems were more complex and modern in aspect than previously considered, in terms of biota, ecological interactions and biogeochemical cycling.

Lagerstätte are fossil-bearing deposits that yield extraordinary, exceptionally preserved fossils from organisms and/or parts of organisms that are not normally preserved **(AU:slight rewording OK?)**. A classic example is the Early-Devonian Rhynie-chert lagerstätte from Aberdeenshire in northeast Scotland [1]. The Rhynie chert was discovered in 1912 and remarkable new discoveries are still being made despite more than a century of intense research on these deposits. The Rhynie chert is part of a small outcrop of Lower Devonian rocks, some 407 million years old [1–2]. These rocks accumulated in an intermontane basin within the Caledonian Mountains on the southeast margin of the Euramerican 'Old Red Sandstone' continent. They comprise floodplain sediments associated with an axial river system that includes the deposits of rivers, lakes and small ponds; there is also a lava flow that attests to local volcanic activity. All appears relatively normal until you throw in the Rhynie cherts that are interspersed among these sediments. They are essentially preserved siliceous sinters deposited by hot springs. Rather remarkably, the sinter-forming siliceous liquids emanating from the hot springs appear to have rapidly entombed the surrounding biota, preserving it in situ with remarkable fidelity [3].

The result is that the Rhynie chert provides a unique example of an early terrestrial ecosystem preserved in situ and in its entirety. Thus, we have subaerial environments with plants in growth position, still harbouring the arthropods that lived among them and the fungi and lichen that grew alongside them. The soils are also preserved with their contents of rotting plants, roots, fungi (including mycorrhiza) and animals such as arthropods and nematodes. Even the ponds seem to have been frozen in time with their biota of charophytes and other green algae, aquatic fungi, cyanobacteria and the arthropods that swam in them. However, the Rhynie chert is not only remarkable for preserving the biota in situ [4], it also preserves the organisms with unbelievable fidelity. This includes organisms that are only rarely, if ever, preserved in normal conditions (for example, fungi and nematodes) [5–7] and parts of organisms seldom preserved (such as the enclosing callose wall of developing spores) [8].

If all this wasn't enough, the exceptional preservation of the Rhynie chert comes at a critical time in the Earth's History. The cherts are dated as Early Devonian in age [2], a period of time when primitive land plants were first beginning to diversify on the continents. The Rhynie chert not only allows us to study those early land plants in great anatomical detail, it also permits us to study them in situ and understand something of their ecological relationships with the other organisms with which they shared the landscape. Furthermore, at Rhynie, in addition to reconstructing the above-ground and below-ground (soil) ecosystems, we also have insight into the first aquatic ecosystems that flourished in the ponds and lakes of the terrestrial landscape.

But the Rhynie chert does not give up its secrets easily. The chert is buried below ground, and we rely on material previously collected by trenching. Furthermore, in order to study it the tough chert must be cut and thin sections ground to be **(AU:OK?)** wafer thin in order that they can be analysed through transmitted light microscopy. Serial sectioning then allows us to build up a three-dimensional picture of the organisms entombed in the chert.

Initial work on the Rhynie chert focussed on reconstructing the plants and studying their anatomy. This was undertaken by Kidston and Lang (1917–1921) in a ground-breaking series of monographs that radically altered the way scientists understood early land plants [9]. But our knowledge of the Rhynie plants did not stop with these monumental monographs. The laborious production of new thin sections over the years has served up new plants (we now know of seven) as well as new anatomical information, such as the remarkable discovery of germinating spores, gametophytes, their sex organs, and even sperm [10–12]. The discovery of animals living among the plants, in the form of primitive spiders and other arthropods, was announced in the 1920s [13–14]. Again, the more chert we study, the more animals we find [15]. Recently this has included a harvestman spider [16] and even nematodes living within rotting plants in the soil and litter horizons [7]. However, it is among the microbiota that most recent advances have been made. In their final monograph in 1921, Kidston and Lang [9] reported that the cherts also yielded various bacteria, fungi and algae. In recent years attention has been drawn to this often-neglected aspect of terrestrial ecosystems — the microbial realm. There has been a continuous stream of new discoveries of bacteria (including cyanobacteria) [17], fungi [5–6], algae [18] and even peronosporomycetes (oomycetes, or water molds) **(AU:OK?)**[19].

In this issue of Current Biology Strullu-Derrien et al. [20] add to our understanding of the microbiota of the Rhynie chert. They describe fossils interpreted as testate amoebae belonging with the arcellinid amoebozoans (Figure 1). This is not the earliest report of testate amoebae. They are widely known from upper Proterozoic rocks some 750 million years old. But these are all marine forms that inhabited the oceans before plants had even colonised the land. So at some point testate amoebae left the sanctuary of the oceans and transitioned onto the land. In living ecosystems arcellinid amoebozoans are present in rivers, ponds, peat bogs and soils. Here they occur in abundance, and are of great ecological importance, particularly because they play such a prominent role in biogeochemical cycling. So our Rhynie testate amoebae show us that these organisms invaded the land simultaneously with land plants, or soon after they**(AU:OK?)** first appeared. The Rhynie testate amoebae also add to the growing list of organisms described from the Rhynie chert that is forcing our realization of just how modern in aspect this early terrestrial ecosystem was in terms of biota, ecological interactions and biogeochemical cycling.

If we consider the ponds in which the arcellinid amoebozoans are interpreted as living we can begin to piece together a complex food web. In the water column, we have a phytoplankton comprising unicellular algae (such as the prasinophyceans) and cyanobacteria. Attached to the substrate we have multicellular charophyte algae alongside filamentous cyanobacteria; all are photosynthesising away. Living off the plant debris we have various aquatic arthropods and now also our arcellinid amoebozoans [20]. Chytrids and other aquatic fungi also abound.

However, when interpreting the Rhynie chert we must always bear in mind some caveats. Just about every Lower Devonian terrestrial deposit worldwide is notable for yielding abundant fish fossils — the Devonian is, after all, known as ‘the age of the fishes’. But at Rhynie there are no signs of fish fossils, either in the cherts that preserved the ponds or even in the river and lake deposits that comprise the vast majority of rock sequence. When we ponder on how modern the Rhynie chert aquatic biotas appear, we must remember that we are dealing with a very strange environment indeed [3]. The Rhynie deposits accumulated in a volcanically active region with the associated lava flows of volcanos and the sinter deposits of hot-springs. Could it be that the peculiar ecosystem of Rhynie is one that is highly adapted to a hot-springs environment rather than one that reflects more normal aquatic environments of the time? The Rhynie chert may be the gift to palaeontologists that keeps on giving, but its meaning is not often**<u>(AU: slight rewording OK?)</u>** so easy to interpret.

References

1. Rice, C.M., Trewin, N.H. and Anderson, L.I. (2002). Geological setting of the Early Devonian Rhynie cherts, Aberdeenshire, Scotland: an early terrestrial hot spring system. J. Geol. Soc. London 159, 203–214.
2. Wellman, C.H. (2006). Spore assemblages from the Lower Devonian 'Lower Old Red Sandstone' deposits of the Rhynie outlier, Scotland. Trans. R. Soc. Edinb. Earth Sci. 97, 167–211.
3. Channing, A. (2017). A review of active hot-springs analogues of Rhynie: environments, habitats and ecosystems. Philos. Trans. R. Soc. Lond. B Biol. Sci. 373, 20160490.
4. Powell, C.L., Trewin, N.H. and Edwards, D. (2000). Palaeoecology and plant succession in a borehole through the Rhynie cherts, Lower Old Red Sandstone, Scotland. Geol. Soc. Lond., Special Publications 180, 439–457.
5. Taylor, T.N., Klavins, S.D., Krings, M., Taylor, E.L., Kerp, H. and Hass, H. (2004) Fungi from the Rhynie chert: a view from the dark side. Trans. R. Soc. Edinb. Earth Sci. 94, 457–473.
6. Krings, M., Harper, C.J. and Taylor, E.L. (2017). Fungi and fungal interactions in the Rhynie chert: a review of the evidence, with a description of Perexiflasca tayloriana gen. et sp. nov. Philos. Trans. R. Soc. Lond. B Biol. Sci. 373, 20160500.
7. Poinar, G., Kerp, H. and Hass, H. (2008). Palaeonema phyticum gen. n., sp. n. (nematode: Palaeonematidae fam. N.), a Devonian nematode associated with early land plants. Nematology 10, 9–14.
8. Wellman, C.H., Kerp. H. and Hass, H. (2006). Spores of the Rhynie chert plant Aglaophyton (Rhynia) major (Kidston and Lang) D.S. Edwards, 1986. Rev. Palaeobot. Palynol. 142, 229–250.
9. Kidston, R. and Lang, W.H. (1917–1921). On Old Red Sandstone plants showing structure from the Rhynie Chert bed, Aberdeenshire (Parts I –V). Trans. Roy. Soc. Edinb. 51, 761–784; 52: 603-627, 643-680, 831-854, 855-902.

10. Lyon, A.G. (1957). Germinating spores in the Rhynie chert. Nature 180, 1219–1221.

11. Remy, W. and Remy, R. (1980). Devonian gametophytes with anatomically preserved gametangia. Science 208, 295–296.

12. Kerp, H., Trewin, N.H., and Hass, H. (2004). New gametophytes from the Early Devonian Rhynie chert. Trans. R. Soc. Edinb. Earth Sci. 84, 411–428.

13. Hirst, S. (1923). On some arachnid remains from the Old Red Sandstone (Rhynie Chert bed, Aberdeenshire). Ann. Mag. Nat. Hist. 12, 455–474.

14. Scourfield, D.J. (1926). On a new type of crustacean from the Old Red Sandstone (Rhynie chert bed, Aberdeenshire) Lepidocaris rhyniensis gen. et sp. nov. Philos. Trans. R. Soc. Lond. B Biol. Sci. 214, 153–187.

15. Dunlop, J.A. and R.J. Garwood. (2018). Terrestrial invertebrates in the Rhynie chert ecosystem. Philos. Trans. R. Soc. Lond. B Biol. Sci. 373, 20160493.

16. Dunlop, J.A., Anderson, L.I., Kerp, H. and Hass, H. (2004). A harvestman (Arachnid: Opiliones) from the Early Devonian Rhynie cherts, Aberdeenshire, Scotland. Trans. R. Soc. Edinb. Earth Sci. 94, 341–354.

17. Krings, M., Kerp, H., Hass, H. Taylor, T.N. and Dotzler, N. (2007). A filamentous cyanobacterium showing structured colonial growth from the Early Devonian Rhynie chert. Rev. Palaeobot. Palynol. 146, 265–276.

18. Edwards, D.S. and Lyon, A.G. (1983). Algae from the Rhynie Chert. Bot. J. Linnean Soc. 86, 37–55.

19. Krings, M., Taylor, T.N., Taylor, E.L., Kerp, H., Hass, H., Dotzler, N., and Harper, C.J. (2012). Microfossils from the Lower Devonian Rhynie chert with suggested affinities to the Peronosporomycetes. J. Paleontol. 86, 358–367.

20. Strullu-Derrien, C., Kenrick, P., Goral, T., and Knoll, A.H. (2018). Testate amoebae in the 407 million-year-old Rhynie chert. Curr. Biol. 29, XXXX-XXXX.

Figure 1. **(Author, please provide a brief descriptive title to go with the legend.)**
A section of Rhynie chert preserving pond deposits with a bacterial mat containing an enmeshed fossil testate amoebae (arcellinid amoebozoan). Scale bar, 100 µm. Image courtesy of C. Strullu-Derrien.

In Brief:

The earliest record of a terrestrial testate amoeba is reported. This provides further evidence that early terrestrial ecosystems were more complex and modern in aspect than previously considered, in terms of biota, ecological interactions and biogeochemical cycling.