Session 5 – Origin and evolution of life: evidence from ancient mineral deposits

The Rhynie Chert early land plants: palaeo-ecophysiological and taphonomic analogues

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Current interpretation of the early evolution of land plants is based on fossil plants preserved in exquisite detail within siliceous sinter deposited by the activity of terrestrial hot springs at Rhynie, Aberdeenshire, Scotland during the Lower Devonian (e.g. Powell *et al.*[7]). The Rhynie deposit's association with andesitic lavas and tuffs, Au–As mineralisation, quartz–adularia–sericite alteration assemblage and sinter deposits suggest that the cherts are the surface expression of a low-sulphidation, alkali-chloride hydrothermal system dominated by meteoric waters (e.g. Rice and Trewin[8]).

Significance

The Rhynie Chert yields an abundant and diverse early land plant flora that includes the earliest well-documented lycophyte (*Asteroxylon*), Rhyniophytes (e.g. *Rhynia*) and rhyniophytoid plants (e.g. *Aglaophyton*) that provide our best insight into early terrestrial ecosystems.[3] The flora, however, are unique and, with the exception of the lycopsids, have no closest living relatives.

Plants were preserved in great numbers, often *in situ*, anatomically in three-dimensions and to the cellular level as silica-laden hot spring waters permeated plant structures and cells (e.g. Trewin[9]). This exceptional anatomical preservation combined with environmental analogy to modern hot spring settings forms the basis for inferences of the plants palaeo-ecophysiology, preferred habitats, taxonomic affinities plus broader evolutionary patterns (e.g. Knoll and Walter[6]).

The Rhynie plants are not preserved in coeval clastic sedimentary environments on the Old Red Continent. This absence has been considered to reflect a taphonomic bias attributed to their low preservation potential, which arose because the plants had fleshy tissues comprising thin-walled cells (e.g. Powell *et al.*[7]). Alternatively, authors have suggested that the Rhynie plants were endemic, either being specialists highly adapted physiologically to stresses presented by the hot spring environment (e.g. Powell *et al.*[7]), or relictual, primitive species retreating from less stressed environments and competition from physiologically more advanced plants.[5]

Conversely, plants commonly preserved in coeval clastic sediments, which comprised a greater proportion of resistant woody tissues and which would thus have a high preservation potential, are absent from the Rhynie Chert. This true absence does appear to suggest that the Rhynie flora was growing and was preserved in settings hostile to such mesophytes.

Physical, chemical and biotic conditions of hot spring environments

Hot spring basins are extremely dynamic environments. Thermal gradients from vent pools to peripheral wetlands may vary from superheated to the freezing point. Cyclic periods of spring eruption and quiescence add temporal variations in temperature. Thermal ground lying above the local water table may impose soil temperatures on root systems in excess of 60°C. Spring water pH and chemistry vary greatly from spring to spring. Alkali-chloride springs (those that dominantly deposit silica) have neutral to alkali vent fluids (~pH 6·5–8·5) that, when discharged, cool and increase in pH due to degassing. Acid-sulphate pools may have vent fluids of ~pH 2. Dissolved constituents mean that the fluids are also brackish to saline and may contain heavy metals at phytotoxic concentrations. Soils develop slowly in thermal areas above altered country rocks and abandoned areas of sinter. These degrade to give (often monomineralic) mineral soils that lack organic components, retain little water (except that molecularly bound to opaline silica) and thus are often nutrient poor.

Plant adaptation and preservation in active hot springs

Plants have often well-defined ecological limits, particularly of temperature, pH and nutrient and water availability. Colonisation of environments at the periphery of geothermal features is, therefore, strongly influenced by the interplay between the physical and geochemical character of the local underlying geothermal system, surface topography relative to the local water table and hot spring eruption style and physical/chemical character.

A cursory assessment, in an active hot spring setting, of the associations between pool chemistry, patterns of plant colonisation and plant preservation reveals a bias to the preservation of hydrophytic, halophytic and alkaliphilic species. Such plants colonise areas of run-off associated with alkali-chloride, high silica springs. *Eleocharis rostellata* (Beaked spikerush) which colonises wetland areas influenced by alkali-chloride run-off is the species most commonly permineralised at present in Yellowstone. It lives semi-immersed in brackish, silica supersaturated waters of pH ~7–8·5 and temperature up to ~35°C. Roots and stems of the plant are readily silicified *in situ* after death and the plant accumulates silica during life. Another plant commonly associated with alkali-chloride high silica springs, the halophyte *Triglochin maritimum* (Seaside arrowgrass) is less often preserved as it favours growth on sinter aprons, where it often roots on microbial mats. In this setting, sporadic inundation by hot spring fluid favours decay over preservation due to aerobic decomposition and low silica deposition rates.

Areas of acid hydrothermal activity appear to present poor conditions for plant preservation despite supporting often abundant plant communities. Endemic thermophilic plant species such as *Eleocharis flavescens var. thermalis* (Warm spring spikerush) and *Juncus tweedyi* (Tweedy's rush) grow in geothermally influenced, acidic waters (temperature ~30°C, pH ~2·5–2·8). However, low spring discharge and silica deposition rates associated with such springs mean that plant preservation seldom occurs unless local water chemistry undergoes a rapid change to alkali-chloride, high silica type, or an alkali-chloride run off stream alters course.

Were the Rhynie plants adapted to alkaline, brackish or saltmarsh conditions and frequent flooding – i.e. highly stressed environments?

The alkali-chloride character of water upwelling from depth into and, if unaltered by near surface mixing, boiling or microbial interactions, erupting from vent pools of Rhynie hot springs would favour a local saltmarsh ecosystem. Sinter deposition entombing the flora indicates at least that alkali-chloride waters were responsible for killing and preserving local vegetation.

Taphonomic studies of microbes indicate that their organic and cellular preservation is at its greatest in low temperature aqueous environments (e.g. Cady and Farmer[1]) prompting the hypothesis that similar settings may be important in the widespread exceptional preservation of plants. As indicated above, in modern hot spring environments the plants most likely to be silicified are adapted not to high temperatures but rather saltmarsh/wetland conditions, where physiological adaptation is to frequent immersion by brackish/saline waters. Such habitats might be appropriate analogues for Rhynie.[2] This observation compares favourably with settings of plant preservation in the only other recorded Palaeozoic terrestrial hot spring, an Upper Devonian/Lower Carboniferous system in the Drummond Basin, Queensland, Australia where lycopsid and sphenopsid plants were preserved in semi-aquatic wetland environments.[10]

Whilst structural features of the Rhynie plants, cuticle, stomata, and vascular tissues, typify homoiohydry and the ability of a plant to regulate its water relations, detailed arrangements of cells demonstrate high water use efficiency, characteristic of water stressed (perhaps aquatic saline) environments (e.g. Edwards *et al.*[4]). Sedimentological data from the cherts are interpreted to illustrate colonisation of clastic sediments, plus those environments including sinter sheet surfaces and ephemeral geothermal pool environments where plants would suffer actual physiological drought.[7]

The combination of fossil, sedimentological, geochemical and analogue data suggest, therefore, that the Rhynie plants may have been rather adapted, stress tolerators rather than fortuitously preserved mesophytes. As such, they are not truly representative of coeval Lower Devonian vegetation.

References

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