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Author for correspondence:
Alan Channing
e-mail: channinga@cardiff.ac.uk

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A review of active hot-spring analogues of Rhynie: environments, habitats and ecosystems

Alan Channing

School of Earth and Ocean Sciences, Cardiff University, Cardiff CF10 3AT, Wales, UK

AC, 0000-0002-1336-6744

The Lower Devonian Rhynie chert formed as silica sinter entombed an early terrestrial ecosystem. Silica sinter precipitates only from water flowing from alkali-chloride hot springs and geysers, the surface expression of crustal-scale geothermal systems that form low-sulfidation mineral deposits in the shallow subsurface. Active alkali-chloride hot springs at Yellowstone National Park create a suite of geothermally influenced environments; vent pools, sinter aprons, run-off streams, supra-apron terrace pools and geothermal wetlands that are habitats for modern hot-spring ecosystems. The plant-rich chert, which makes Rhynie internationally famous, probably formed in low-temperature environments at the margins of a sinter apron where frequent flooding by geothermal water and less frequent flooding by river waters created ephemeral to permanent wetland conditions. Here, the plants and associated microbes and animals would be immersed in waters with elevated temperature, brackish salinity, high pH and a cocktail of phytotoxic elements which created stresses that the fossil ecosystem must have tolerated. The environment excluded coeval mesophytic plants, creating a low-diversity hot-spring flora. Comparison with Yellowstone suggests the Rhynie plants were preadapted to their environment by life in more common and widespread environments with elevated salinity and pH such as coastal marshes, salt lakes, estuaries and saline seeps.

This article is part of a discussion meeting issue 'The Rhynie cherts: our earliest terrestrial ecosystem revisited'.

1. Introduction

The Rhynie chert of Aberdeenshire, Scotland, preserves the earliest and most detailed picture of a terrestrial ecosystem yet discovered. The Rhynie biota, which comprises abundant and diverse microbes (bacteria, micro-algae, fungi, protists) vascular plants, macro-algae and aquatic and terrestrial animals, was entombed as silica-rich waters flowed from hot-spring vent pools into surrounding terrestrial and aquatic habitats during the Lower Devonian (e.g. [1]). The various elements of the ecosystem were preserved in exquisite detail as the silica mineral opal-A (now transformed by diagenetic processes to the rock chert) precipitated from the cooling hot-spring waters. External surfaces of organisms immersed in the hot-spring waters became encrusted in opal-A precipitate (known as silica sinter). This formed a relatively robust and structurally stable matrix, while dissolved silica permeated their tissues and cells prior to opal-A precipitation at the cellular level by the process of silica permineralization (e.g. [2,3]). The exceptional preservation at Rhynie was possible because the local ecosystem was most commonly fossilized where it lived in a 'geological-instant' without any transport-induced damage and frequently prior even to the onset of substantial cell and tissue decay.

(a) Regional setting and tectonic framework of the Rhynie chert

Hot-spring chert deposits are not a common feature of the rock record (e.g. [4]) as their formation requires a quite specific set of geological conditions to be met.

Hot springs are the surface expression of crustal geothermal and/or hydrothermal circulation systems (e.g. [5]). These are created where waters in the subsurface interact with bodies of hot rock or magma setting up large-scale circulation cells that transport/redistribute heat via convection of fluids through porous rocks or along major fracture pathways such as faults. The distribution of hot-spring areas worldwide indicates that geothermal systems are most common in areas where plate tectonic processes such as subduction, mountain building and rifting lead to elevated crustal temperatures, magma generation and volcanism (e.g. [6]).

Scotland in the Devonian period conforms to this basic spatial model of geothermal system distribution (e.g. [7–9]). During the Early Devonian, Britain lay on the southern margins of the palaeocontinent Laurussia (also known as Euramerica and the Old Red Continent) in a semi-arid to arid zone 30–20° south of the equator. Laurussia had recently formed by collisional/compressional plate tectonic processes (subduction and mountain building) during the preceding Ordovician and Silurian periods that were related to the closure of the Iapetus Ocean during the Caledonian Orogeny (e.g. [10]). Britain was largely terrestrial (e.g. [11]) comprising an upland core, the Caledonian Mountains (Scotland, northern England, central and north Wales), lowland coastal plains (south Wales, southern Britain) and shallow shelf seas (southwest Britain).

During the Late Silurian to Early Devonian following the peak of mountain building and regional metamorphism related to the Caledonian Orogeny the uplifted orogenic belt became topographically unstable. Largely compressional tectonic forces were superseded by orogenic collapse and transpressional/transtensional forces (e.g. [8,12,13]) that led to widespread left-lateral strike-slip faulting and localized extensional faulting that promoted basin formation and crustal thinning. Rhynie, which occurs in the Grampian Highlands of Scotland, lay in an intermountain setting to the southeast of the most elevated upland regions of the collapsing and eroding orogen. Crustal thinning due to transtensional and extensional forces lead to elevated crustal heat flow and ultimately to plutonism and magmatism. Silurian to Devonian post-orogenic granites intruded into the Grampian Highlands Terrane (e.g. in western and central Aberdeenshire) between *ca* 415 and 408 Ma [9,14,15] provide one potential heat source for the Rhynie geothermal system [8]. An alternative heat source is the basaltic-andesitic tuffs and lavas (dated at 411.5 ± 1.3 Ma by Parry *et al*. [15]) intercalated with the Lower Devonian sediments below the chert bearing rocks of the Rhynie basin. These presumably flowed from a geographically close-by vent or fissure linked to a subsurface magma chamber. A date of 407.6 ± 2.2 Ma obtained by analysing adularia (a potassium (K) feldspar) precipitated in a subsurface vein of the Rhynie geothermal system [16] provides a direct estimate of the age of the geothermal and hot spring activity at Rhynie.

Based on palynological work [17–20] the Rhynie cherts and the sediments that contain them have been assigned to a single-spore biozone, the *polygonalis–emsiensis* Sporomorph Assemblage Biozone (PE zone), which indicates hot-spring activity occurred in the early (but not earliest) Pragian to earliest Emsian stages of the Early Devonian. Recent revisions of the ICS Chronostratigraphic Chart [21] place the base of the Pragian at 410.8 ± 2.8 Ma and the base of the Emsian at 407.6 ± 2.6 Ma. Within errors, all the latest age estimates for the Rhynie cherts fall within the internationally defined age range of the *polygonalis–emsiensis* Biozone.

Water input to the Rhynie geothermal system came from dominantly meteoric (rainwater) sources (evidenced by $\delta^{18}O$ ratios of fossiliferous chert samples) with a lesser component derived from magmatic fluids/gasses [8,22]. Recharge areas presumably lay in the uplands beyond the Rhynie Basin. Despite the arid to semi-arid regional climate evidenced by caliche formation in the Rhynie and adjacent Turrif basins (e.g. [23,24]) and lacustrine evaporite deposits on the adjacent Northern Highlands Terrane [25] the Rhynie sedimentary sequence is dominated by water-lain clastic sediments (fluvial sands/silts and overbank floodplain muds, lacustrine shales etc.) indicating that pluvial conditions were a common feature of the region's climate during the period of basin filling (e.g. [8,12,13]).

Ascent of fluid from subsurface geothermal convection cells to Earth's surface is promoted by extensional tectonics. The Rhynie Basin, a NE–SW orientated half-graben or pull-apart structure with a fault-bounded NW margin formed as a response to the local extensional tectonic regime. Fluid up-flow was focused on the basin margin fault, which acted as a conduit for deep geothermal fluids migrating from SE to NW (e.g. [8,22]). This caused the localization of hot-spring activity adjacent to the NW basin margin at Rhynie and at a related but geographically separate hot-spring centre at Windyfield [26]. The local extensional regime was sufficiently long lived to allow the deposition of *ca* 1500 m of Lower Devonian sediments in the northern part of the Rhynie Basin [13].

The maximum duration of geothermal activity at Rhynie is constrained by the length of the *polygonalis–emsiensis* Sporomorph Assemblage Biozone, which is a *ca* 4 million year-long interval. However, surface hot-spring activity (represented by the Rhynie chert Unit and slightly younger Windyfield cherts) has only been recorded towards the top of the Rhynie Basin stratigraphy in the Dryden Flags Formation [13] suggesting that a considerable time had elapsed prior to the onset of hot-spring activity. Comparison with other younger geothermal circulation systems and hot-spring areas suggests that they can be active on the scale of tens of thousands to hundreds of thousands of years. The Yellowstone National Park, USA, geothermal system appears to have been active for approximately 500 kyr [27] with sinter deposits [28] and alteration minerals [29] and silica cemented sediments [30,31] created by geothermal activity during the last interglacial period (between *ca* 150–45 kyr ago) recorded from widespread locations. Active thermal features in Yellowstone [32,33] and in Iceland [34] appear to have formed only since the last deglaciation (*ca* 12–11 ka). Rates of sinter accretion recorded from modern geothermal areas including Yellowstone [33,35–39], New Zealand [40,41] and Iceland [42] seldom exceed 10 cm per year, with rates of 1–5 cm per year being more typical. At comparable accretion rates the 10–20 cm thick chert beds commonly recorded at Rhynie (e.g. [43–45]) would have been created on yearly to decadal timescales rather than days or weeks.

2. From rocks to palaeoenvironments and habitats

The discoverer of the Rhynie locality, Dr William Mackie, explored the area while preparing a geological map published in 1913 [46]. Mackie collected a variety of samples of cherty rocks from the area between 1910 and 1912. Some he discovered to contain clasts of altered volcanic rocks. Others were sandstones cemented with silica. These rocks are now interpreted as hydrothermally altered and silicified igneous rocks and silicified Devonian sandstones (e.g. [8,22]). Chert samples, when sectioned, were often found to contain 'plant and animal remains'. These fossiliferous cherts, Mackie hypothesized, had been formed by the activity of geysers or hot springs during the declining phases of local volcanism. More recent investigations of the Rhynie Basin have confirmed Mackie's initial interpretation (e.g. [8,12,23]).

(a) Subsurface rocks—the plumbing system of the Rhynie hot springs

Observations of hot springs and geysers worldwide reveal a bimodal distribution of vent water pH, with many features containing acid water in the range (pH 2–4) or alkaline waters (pH 7–9) but few containing waters in the range pH 4–7 [47]. This finding relates to the geothermal circulation systems that lay in the shallow crust beneath the land surface. Two end member geothermal system types exist. Where compressional plate tectonics leads to the creation of subduction zones, thrust faulting and volcanic arcs, waters flowing to the surface in hot springs tend to be acidic and rich in dissolved sulphate as geothermal systems tend to sit above shallow volcanic magma chambers and fluid chemistry is dominated by acidic volatiles (e.g. SO_2, HSO_4 and HCl) being released from magma. Conversely, in regions where extensional tectonics prevail (as is the case at Rhynie), magma chamber volatiles influence water chemistry far less and instead geothermal circulation cells carry alkaline waters rich in dissolved chloride (e.g. [5,6]).

Geothermal circulation cells are responsible for the creation of significant economic mineral deposits and also, when active, offer a potential source for renewable geothermal energy. As such, they have a long history as a research focus. Exploration geologists searching for economically exploitable gold (Au), silver (Ag), mercury (Hg) ore deposits have created detailed conceptual models for the crustal geothermal–hydrothermal systems that can lead to shallow subsurface vein systems and surficial deposits (e.g. [48–50]). These are known as epithermal mineral deposits and, as with the circulation cells, there are two end member mineral deposit models. Acid sulphate circulation cells create high sulfidation epithermal deposits, while alkaline chloride waters create low-sulfidation epithermal deposits.

The 'plumbing' system of the Rhynie chert conforms to the low-sulfidation model (e.g. [8,22]). This has major implications for the physical and chemical properties of water flowing from the Rhynie hot-spring vent pools into the preservation environments of the ecosystem [3,4,51]. Alkali-chloride geothermal systems typically have topographically elevated recharge areas where surface waters infiltrate permeable rocks. Because the waters are cool, they descend into subsurface aquifers. Here, if they interact with a heat source they become hotter and more saline and are able to dissolve the rocks through which they are flowing. Dissolution of silicate minerals of the country rocks creates a fluid that can liberate and carry metals (e.g. Au, Ag, Hg, Cu (copper), Zn (zinc), Tl (thallium)) and metalloids (e.g. As (arsenic), Sb (antimony), plus Si (silicon), sodium (Na), chloride (Cl) and K). The hot and therefore buoyant fluids begin to rise in the crust towards the surface outflow areas of the geothermal system, hot springs and geysers (e.g. [5,6]). Fluid/rock interactions in the subsurface lead to distinctive host rock alteration minerals that are diagnostic of the geothermal systems alkali-chloride chemistry. At Rhynie, sediments and lavas exhibit alteration to quartz, adularia, calcite and illitic/chloritic clays. Some of the dissolved elements (silicon plus metals, metalloids) may precipitate in the subsurface in vein systems and breccias creating low-sulfidation mineral deposits. At Rhynie, this mineralization is concentrated in chert, quartz- and minor carbonate-bearing breccias and veins. These rocks locally exhibit anomalous levels of elements including Au, As, Hg, Sb and Tl (e.g. [8,22]).

(b) Surficial rocks—sinters, hot-spring sub-environments and ecosystem habitats

Observation of active hot-spring areas reveal a second bimodally distributed phenomenon related to pH and the underlying geothermal system, the presence or absence of silica sinter. Low-pH, acid-sulphate geothermal areas and individual hot springs lack sinter aprons while sinter is extremely common in alkali-chloride hot-spring areas (reviewed by Sillitoe [5]). Acid-sulphate hot springs tend to precipitate a different, but again diagnostic suite of minerals such as kaolinite clays and sulphate minerals of the alunite–jarosite group and native sulfur (e.g. [5,52]). These diagnostic minerals are largely absent from cores drilled at Rhynie. Instead cores reveal stacked sequences of up to 50 or more silica sinter horizons within relatively short vertical intervals (e.g. [43,44]). Powell *et al.* [43], for instance, recorded 52 sinter beds within a 35 m thick sequence of fluvial and lacustrine sediments in Rhynie Core 19C. Much of the intervening sediment is cemented by silica creating cherty sandstones and siltstones. This widespread cementation represents silica precipitation in the shallow subsurface as alkali-chloride geothermal fluid percolated laterally and vertically through porous sediments (e.g. [45]). Hence, the Rhynie deep subsurface, shallow subsurface and sinter depositional areas of the surface environment are dominated by indicators of alkali-chloride geothermal fluids.

As alkali-chloride geothermal waters flow to the surface, chloride acts conservatively tending to remain in solution. This means that, as they flow from vent pools (figure 1*a*–*c*), waters are brackish (oligohaline) in character, containing *ca* 1.5 parts per thousand NaCl. Vent waters (typically near boiling), once erupted, rapidly cool to ambient temperature. This process decreases the solubility of dissolved silica forcing supersaturation and rapid precipitation in the form of the amorphous silica mineral opal-A (e.g. [3,4,51]). The precipitated silica forms geochemical sedimentary rocks, sinters (figure 1*a*–*c*), and encrusts organisms leading to moldic preservation that can faithfully replicate surface morphology and three-dimensional organization from the micro- (individual microbial cells) to macro-scale (in modern examples entombing decimetre diameter tree bases). Silica, which is transported in solution as monosilicic acid $Si(OH)_4$, also permeates the organic structure of organisms (figure 1*f*,*g*) depositing colloidal opal-A particles that can create rigid mineral frameworks in inter- and intracellular sites that stabilize tissues against collapse (e.g. [2,3]).

Erupted fluids, which may have near neutral pH (7–8), degas as they flow away from vent pools. The loss of CO and CO_2 forces increases in pH, to in excess of pH 9 (e.g. [3]). Loss of water by condensation and evaporation can outpace loss of dissolved elements by mineral precipitation and,

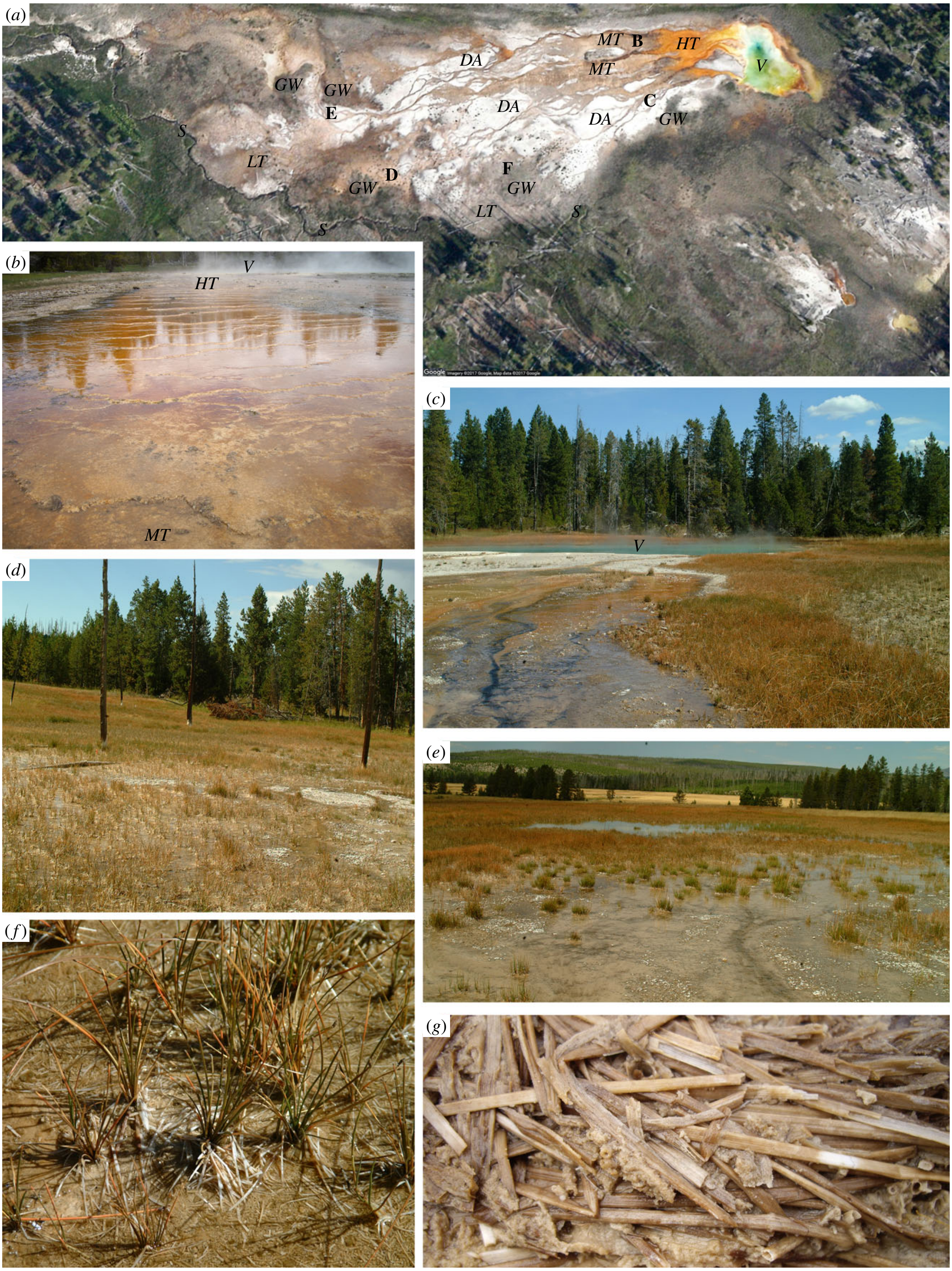

Figure 1. (*Caption overleaf.*)

therefore, while water temperature is falling towards ambient, salinity, pH, silica supersaturation and concentrations of remaining dissolved metals and metalloids may be increasing with distance flowed from vent pools. This presents a set of stresses which organisms living in and around geothermal features (figure 1*a*–*f*) must tolerate (e.g. [3,4,51]). As the hot-spring fluids are a prerequisite for silicification of organisms in this setting, and because hot-spring fluids come inextricably linked to abiotic stressors, there is a tendency for hot-spring fossil assemblages to contain a high proportion of extremophiles (figure 1*b*) related to high temperature environments (e.g. [53]) and rather specialized organisms tolerant of milder (but not inconsiderable) physico-chemical stresses (figure 1*c*–*f*) at lower temperatures (e.g. [4]).

Figure 1. (*Overleaf*.) Habitats associated with alkali-chloride, sinter-depositing hot springs at Yellowstone National Park. (*a*) Google Earth satellite image of Big Blue Hot Spring and associated apron and geothermal wetlands, Elk Park, Norris Geyser Basin, Wyoming (bold letters B–F indicate sites of *b*–*f*). Periphery of image shows local lodgepole pine (*Pinus contorta*) dominated forest beyond the influence of geothermal waters. Big Blue vent pool (*V*) erupts near-boiling, alkali-chloride, silica-rich waters via run-off streams colonized by high temperature (*HT*) microbial mats (orange and dark brown). Water flows onto the accreting and prograding sinter apron and cools in mid-temperature (*MT*) microterrace pools (beige) colonized by cyanobacteria and at lower temperatures, chlorophyte algae and higher plants. Dry apron (*DA*) surfaces between run-off streams and wet apron areas appear white. The apron margin is fringed laterally and distally by geothermal wetland (*GW*) dominated by *Eleocharis rostellata*. Areas of lodgepole pine invaded by wetland conditions contain dead standing and fallen trunks (*LT*). Geothermally influenced habitats are delimited distally by dilution as geothermal outflow enters surface waters streams (*S*). Vegetation diversity and abundance shows a marked increase from geothermally influenced banks to 'normal' banks. (*b*) Shallow terraces with elevated rimstone edges cause pooling and cooling of run-off providing habitat for microbial mats. (*c*) Apron margin pools with sinter substrate colonized by *E. rostellata* via stolons. Forest fringe beyond the vent pool shows strong partitioning of the local ecosystem between geothermally influenced and dryland environments. (*d*) Geothermal wetland area developed at formerly forested site with standing but dead lodgepole pines. (*e*) Distal sinter apron margin with clumps of *Triglochin maritimum* (seaside arrow grass) in the foreground and monotypic stands of *E. rostellata* surrounding a deeper wetland pool containing mats of chlorophyte algae. (*f*) Geothermal wetland surface, living *E. rostellata* has fallen stems that are partially silicified. Sediment surface is dominated by silicified (permineralized) stem fragments. (*g*) Holocene sub-fossil wetland soil dominated by *E. rostellata* stem fragments.

(c) Water chemistry and physical properties in geothermally influenced aquatic settings

Recognition that the Rhynie chert is a hot-spring sinter deposit, the surface expression of a low-sulfidation epithermal deposit that was created by opaline silica precipitating from alkali-chloride hot-spring waters, allows us to constrain, with some certainty, the chemical and physical properties of the hot spring waters flowing at the surface into areas where silica sinter (now transformed to chert) accumulated and where the same waters preserved the local ecosystem by encrustation and permineralization. Stressed habitats associated with alkali-chloride sinter depositing springs can be observed at any of the world's active geothermal areas allowing physico-chemical parameters affecting potential fossils to be measured. Below I provide details for Yellowstone geothermal areas, but comparable characteristics are reported from other geothermal areas such as the Taupo Volcanic Zone, New Zealand (e.g. [4,54–56]), Iceland (e.g. [4,57,58]), El Tatio, Chile (e.g. [59,60]) and East African Rift (e.g. [61,62]). A typical sinter-depositing, alkali–chloride hot spring has vent fluid approaching boiling point (70–100°C), with a circum-neutral to alkaline pH (6.5–8) that contains major elements such as Na (sodium) (300–450 ppm), Cl (500–650 ppm) and Si (200–750 ppm) plus a suite of trace elements including heavy metals and metalloids (e.g. Au, Ag, Cu, Zn, As, Sb, Hg and Tl). High water temperature in vent pools limits organisms to extremophile archaea and bacteria (e.g. [38,53]).

As water erupts from the vent, a number of processes occur that modify the physical and chemical properties of the fluid. Vent fluids contain Si concentrations that are close to or exceed saturation at vent temperature. Outflow from the vent is accompanied by cooling and evaporation, which increases saturation further promoting rapid silica precipitation to form sinter composed of the hydrated, non-crystalline silica mineral opal-A (SiO_2 n. H_2O). Precipitation close to vent pools creates sinter terraces, sheets and aprons (figure 1*b*) that accrete vertically to form vent mounds (commonly several metres high) and prograde laterally (figure 1*a*–*e*) into surrounding environments (e.g. [63]). Apron surfaces can develop a variety of surface features, depending on topography, flow-rates and eruption style. Typical features include broad low angled surfaces where sheet-flow conditions are present and stair-step terraces with sinter rims that cause ponding of thermal water forming shallow supra-apron pools (figure 1*b*). Run-off channels, again with sinter-rim margins, carry water from point sources on the vent pool margins (figure 1*c*) onto apron surfaces (e.g. [64]). Water temperature in streams and pools is dictated by distance from vent pool and rates of flow. In proximal areas of the apron, temperature approaches that of vent fluids but it falls rapidly downstream to the range 65–45°C. The biota of apron pools and streams shows a zonation based largely on the local temperature gradient. As temperature drops below *ca* 70°C, filamentous and mat-forming cyanobacteria (figure 1*b*) colonize sinter surfaces (e.g. [53]) and become fossilized within sinter. Mat-formation and fossilization leads to internally laminated sinter fabrics. Water in these settings remains super-saturated with regard to silica despite sinter formation. Salinity and pH, however, both increase as vent water flows across aprons and cools. Degassing of dissolved CO and CO_2 promoting pH increases, and water volume loss via condensation and/or evaporation increasing NaCl concentration. Dissolved metals and metalloids co-precipitate with silica during sinter formation (e.g. [65]); however, measurements of water chemistry in sinter apron pools, run-off streams, geothermal wetlands and even geothermally influenced stretches of local river systems (e.g. the Firehole and Gibbon Rivers of Yellowstone) often record metal concentrations highly elevated above regional norms (e.g. [66]).

At the periphery of sinter apron margins, waters cool sufficiently (to below *ca* 40–45°C) to allow colonization of apron pools, run-off streams and geothermally influenced wetlands by higher plants (figure 1*c*–*f*) and aquatic fauna [3,4,51]. Silica remains supersaturated such that it can nucleate on plant and animal surfaces encrusting immersed organs in opaline silica promoting moldic preservation. More importantly in the context of Rhynie where organs, tissues and cells of the plants are preserved by silica infilling (permineralization), dissolved silica in the form of monosilicic acid ($Si(OH)_4$) can permeate plant structure and precipitate to form opal-A colloids that 'fix' plant materials by creating a robust inter- and intracellular mineral deposit [2,3].

Apron progradation into dryland environments (figure 1*d*) is accompanied by flooding of 'normal' terrestrial surfaces and infiltration of subsurface sediments. This leads to death of elements of the ecosystem unable to tolerate submersion of their roots and/or the physico-chemical stresses highlighted above (e.g. [51]). Stress responses, such as wilting, may be visible in immersed mesophytic plants, but are difficult to detect in the Rhynie chert. Silicification of local soils and sediments (creating silicified palaeosols) and preservation of basal plant stems and root horizons by silicification are common features of these areas. Protracted flooding leads to the establishment of geothermal wetland conditions (figure 1*d*) and eventually progradation of the apron-proper across the former area of dryland [51,67].

(d) Dryland and freshwater settings within thermal areas

Between periods of hot-spring eruption and on areas of the sinter apron between pools and channels, dryland environments are present. These environments create challenges for plant colonization. Sinter is a relatively hard, monomineralic chemical sedimentary rock. Rooting is an issue for plants on the rocky apron surface. Exposed sinter also tends to lack sufficient humus for higher plants because organic material incorporated during its formation such as microbial mat is susceptible to rapid decay on subaerial exposure. Sinter is also extremely porous and therefore tends to be well drained. This means that modern dry-aprons tend to be arid, nutrient-poor and poorly vegetated to barren (e.g. [4,51]). Elevated ground temperatures also cause colonization problems for plants. Heated ground with root temperatures in excess of 45°C prevents most higher plants surviving leading to moss zones with recorded soil temperatures of around 65°C (e.g. [68,69]). The lack of vegetation in apron environments means that aprons have relatively low diversity invertebrate faunas.

In active geothermal areas, 'normal' regional mesophytic vegetation grows in close proximity, even immediately adjacent to, geothermally influenced environments (figure 1*a*,*c*,*d*). Fallen and transported plant organs (e.g. leaves, needles, cones and pollen/spores) from these dryland mesophytes can become incorporated into accreting sinter and evidence of transport and decay are generally evident (e.g. [3,4]).

Disruption of the plumbing of hot springs and geysers (vent abandonment) and long periods of geothermal activity dormancy (plus the presence of other natural surface depressions) can allow cool water aquatic habitats to develop in thermal areas. Those dominated by freshwater input (e.g. rainfall or flooding of local river systems) can support 'normal' freshwater aquatic ecosystems within the geothermal environment (e.g. [70]).

(e) Taphonomic features

In addition to physico-chemical and ecological partitioning of the geothermal environment, taphonomic partitioning is at play. This leads to potential preservation biases. If the aquatic environment is too hot, organic compounds of organisms tend to be 'boiled away' and cellular permineralization is prevented. Replacement of the sites of cell walls and tissues by silica ensues instead. Dry areas of the environment and those infrequently flooded by geothermal waters have very low sinter accretion rates and therefore little opportunity for encrustation and permineralization of organisms to occur. Here, oxidation and decay outpace preservation.

Areas that are conducive to preservation by silica permineralization therefore need to be frequently inundated with silica supersaturated geothermal water at temperatures below around 45°C (e.g. [53]). Two environments in Yellowstone most frequently meet these requirements, cooler wet regions of sinter aprons (low-temperature apron pools (figure 1*c*) and low-temperature regions of run-off streams (figure 1*e*)) and geothermally influenced wetlands [4]. Wet areas of sinter aprons with water temperatures close to 45°C can preserve large areas of microbial mats with distinctive fabrics discussed below. However, it is in areas of apron/wetland with water temperature below 45°C, where higher plants join the list of colonizing organisms and where geothermally influenced living biomass is greatest, that present the aerially most extensive sites of exceptional, permineralization-style preservation. Here, because geothermal waters are permanently present and water temperatures are near ambient, preservation potential is extremely high and preservation quality is at its greatest. It is in this setting that vast numbers of higher plants can be preserved *in situ* with vertically orientated aerial organs [3,4,51].

Taphonomy experiments conducted in vent pools and wet sinter apron surfaces [2] and in geothermal wetlands [3] indicate that permineralization of higher plants requires months rather than days to occur and that the notion of 'instantaneous' permineralization under conditions pertinent to most hot-spring settings is unrealistic (e.g. [2,3] cf. [71,72]). For this reason, wetland plants and aquatic elements of the fauna are by far the most likely to be preserved in geothermal environments. Observations of hot-spring deposits ranging in age from the Late Devonian to present day where ecology of both hot-spring floras and 'normal' floras are known with some certainty illustrate that the wetland megabias evident in the broader fossil record also applies to hot-spring ecosystems [4]. In hot-spring environments such as geothermal wetlands, where preservation potential can be exceptionally high, taphonomic bias is accompanied by an ecological bias. This extends beyond a bias to aquatic, emergent-aquatic and flooding tolerant plants because of the physical and chemical properties of hot-spring waters [4,73,74].

3. Comparisons of extant environments and ecosystems with those recorded at Rhynie

Most research activity associated with the Rhynie chert has focused on the entombed ecosystem and therefore there has been a collection bias towards fossiliferous chert material. However, float blocks, trench material and drill-core samples record a number of chert lithologies which reveal the existence of vent-pools and sinter aprons (figure 2*a*), the higher temperature environments formed in proximal areas of hot-spring or geyser discharge, plus the lower temperature geothermally influenced environments represented by plant-rich cherts (figure 2*b*,*c*).

(a) Sinter fabrics and fossils as evidence of geothermal sub-environments present at Rhynie

The siliceous sinter rocks formed by hot-spring and geyser activity can be diagnostic of the environment and sub-environments in which they were created. Studies of Rhynie's modern hot-spring analogues, e.g. at Yellowstone National Park, Wyoming, USA (e.g. [3,4,38,51,53,63,70,75]) and the Taupo Volcanic Zone, New Zealand (e.g. [40,54,55,76]), plus younger fossil hot-spring deposits (e.g. [67,77–82]) reveal that the physical and chemical conditions (water temperature and availability) plus pH, salinity and phytotoxic dissolved elements associated with life in and around hot springs, lead to marked partitioning of the local ecosystem. Because

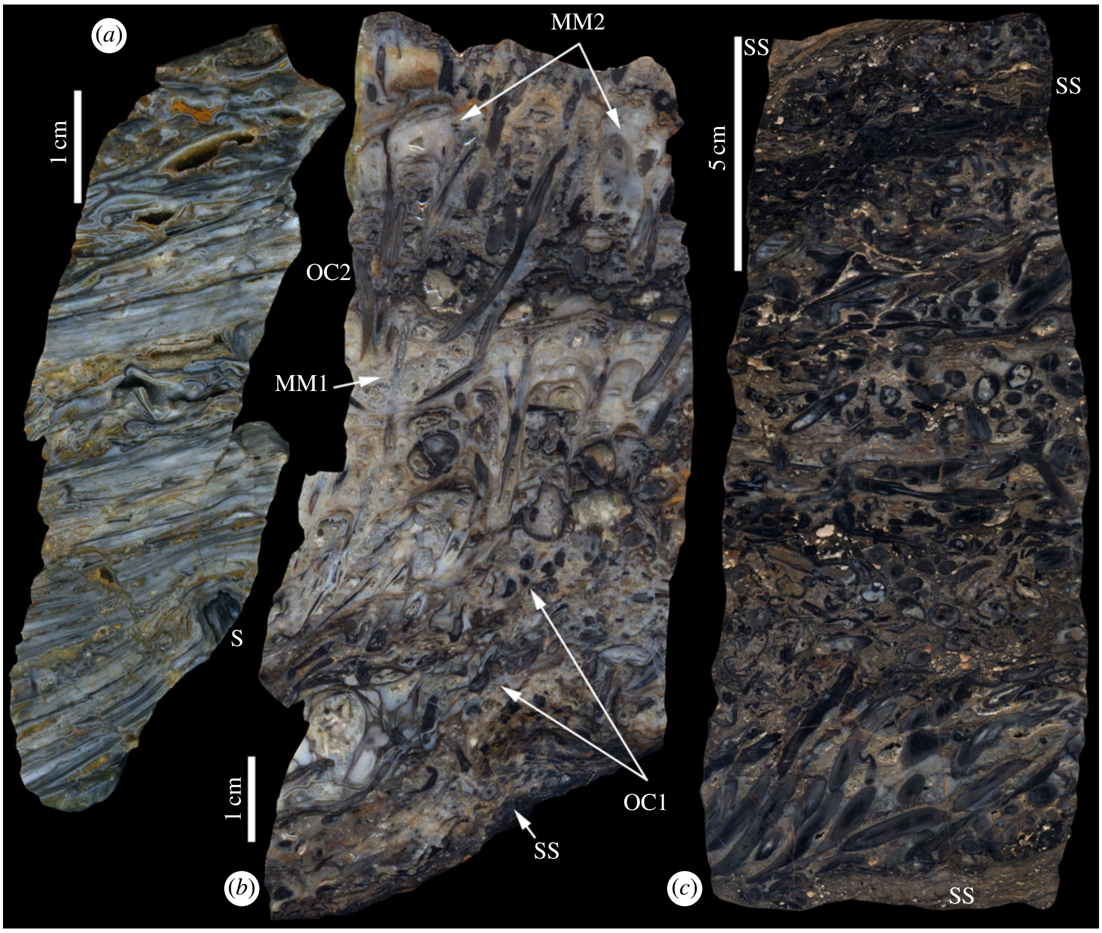

Figure 2. Rhynie chert macro-textures. (*a*) Strongly laminated chert with amygdaloidal cavities and curvy/wavy bedding formed by silicification of microbial mats in a mid-temperature apron environment. A single unidentifiable plant axis (S) creates a doming of the overlying sinter laminae. (*b*) Plant-rich chert lens from an apron pool setting with *in situ* erect stems of *Rhynia* that traverse alternations in matrix chert fabric. Dark organic rich horizon at base comprises a thin silicified siltstone with carbonaceous laminae (SS) and cuticle and spore-rich chert with partially permineralized prostrate axes (OC1). Vertical axes above are surrounded by a silicified microbial meshwork and wavy mat laminae (MM1). Several vertical axes traverse a second horizon with prostrate axes and organic-rich chert matrix (OC2) extending into another microbial meshwork and mat horizon (MM2). (*c*) Distal apron, geothermal wetland chert block with silicified carbonaceous siltstone horizons (SS) at base and top indicating river flooding. Intervening chert horizon has multiple alternations between dark massive to mottled organic rich chert with prostrate axes and lighter chert with less organic content and microbial meshwork between vertically orientated axes.

hot-spring sinters form as elements of the local ecosystem are immersed by spring waters they contain distinctive fossil assemblages and biosedimentological fabrics that ‘fingerprint’ the various hot-spring subenvironments.

(b) Vent pools—geyserite

In high temperature vent-pools and in apron settings immediately adjacent to vents, eukaryotes are all but excluded and only hyperthermophilic and thermophilic archaea and bacteria are able to survive. The environment thus has low biomass and chemical precipitation of opal-A dominates sinter deposition. Opal-A precipitates as colloids directly from the water column creating gel-like sediments (e.g. [38,53,83]). Geyserite is a term used to describe sinter created in the high temperature (*ca* 75–100°C) environments within or immediately surrounding a geyser or hot-spring vent pool. It forms as surging, splashing or spraying vent waters alternately wet surfaces and cool/evaporate to cause opal-A precipitation. The rock is typically internally laminated with successive laminae that build up to form distinctive knobby, botryoidal, columnar or wavy stratiform morphologies similar in appearance to stromatolites (e.g. [83]). Geyserite is extremely rare in the rock record, in part due to the limited extent of vent pools and increased likelihood of post deposition erosion of vent mounds, which commonly sit above active faults. A single block of geyserite with a botryoidal surface morphology is reported from the Windyfield locality at Rhynie (e.g. [26]).

(c) Sinter aprons

As vent waters flow out into the surrounding environment further silica precipitation forms sinter mounds, terraces and aprons via lateral and vertical accretion. Here, water temperature can drop sufficiently for bacterial and cyanobacterial mats to form. Once again, laminated internal fabrics dominate sinter. Initially, these are finely laminated as in vent pools, however, the change in mat forming organisms and increase in biomass alters sinter internal fabrics sufficiently that mid- and low-temperature apron sinters in the rock record can generally be differentiated from those formed in proximal high temperature settings (e.g. [53,67,77–81]).

Mid-temperature apron sinter has wavy-laminated internal fabrics, often with conspicuous bedding parallel lenticular voids (‘bubble mats’) that formed as photosynthesizing cyanobacterial mats living in waters between 65 and

45°C with trapped pockets of gasses became silicified (e.g. [67,79–81]). In mid to low temperature apron settings mat thickness increases and laminated fabrics give way to thicker bedded fabrics. Low temperature sinter environments (less than 45°C) are typified by filamentous palisade fabrics, horizons characterized by dense assemblages of filamentous microbes oriented perpendicular to silica lamination direction. The fabric results from silicification of *Calothrix*-type cyanobacteria (e.g. [53]).

At Rhynie, in contrast with most other fossil hot-spring deposits thus far discovered (e.g. [67,77–81]), laminated/bedded apron sinter is poorly represented and to date thick sinter terrace deposits (which in active and other fossil hot spring areas may reach up to 10 m in thickness and several hundred metres diameter) have not been intersected by drilling [45]. One trench (Lyon's Trench 8A) at Rhynie, which is potentially the trench located closest to the Rhynie Fault Zone (see [84, fig. 7]) contained 'chert with only scanty plant remains' but does contain chert blocks with typical mid-temperature apron fabrics (figure 2*a*). The Windyfield chert also contains evidence of apron environments although, again, these form only a minor sub-environment (e.g. [26]). Fayers & Trewin [26] interpreted stacked parallel laminated cherts with microbial laminae that lacked *in situ* plants to represent stromatolitic sinter apron deposits, which formed as silica precipitated from periodic laminar flows of vent fluid. They considered the environment to have water temperatures below 59°C based on the presence of filamentous photosynthetic bacteria and probable cyanobacteria displaying phototactic orientations. Run-off streams containing brecciated laminated sinter clasts and flowing across sinter surfaces have been identified at Windyfield but, again, these are uncommon at Rhynie ([26] cf. [43]). Trewin and Fayers [26] estimate that the plant-rich cherts of the Rhynie deposit formed some 200 m from vent sources to the west associated with the basin margin fault zone. The intervening ground, given the volume of silica deposited to create the large numbers of chert beds should hold evidence of significant apron deposits. It may be that faulting and erosion have removed the apron material. Collection bias could also be at play, as Lyon's 8A trench was closed when plant-rich cherts were found to be scarce [84].

(d) Geothermal wetlands

The distal areas of sinter aprons and geothermally influenced wetlands at the periphery of apron complexes where water temperature is close to ambient are characterized by diffusely bedded and mottled sinter that contains abundant higher plants and evidence of aquatic micro- and macro-flora and fauna (e.g. [3,4,67,73]). Chlorophyte algae, including filamentous forms, become more common as cyanobacteria numbers decline (e.g. [3,85]). Observations of unconsolidated wetland sediment from Yellowstone reveal the presence of fragments of variably silicified plant tissue and pollen/spores. Other organisms include (but are not limited to) aquatic crustaceans, amoeboid protists, silica scaled heliozoans and chrysophytes, dinoflagellates, nematodes, diatoms, and coccoid, rod-shaped and filamentous microbes. The microbiota is contained in a sediment dominated by colloidal-dimension opal-A particles (microspheres), many of which are aggregated around organic material or in the form of floc-like particles [75,85]. Drying of the wetland surface causes suspended flocs to collapse and a sinter-like crust forms above unconsolidated layers of the sediment [3,75]. Flow of geothermal water across the wetland surface creates sinter horizons that alternate with wetland horizons.

Higher plants in the wetlands are typically plants that are emergent aquatics that inhabit shallow water and/or saturated soils (figure 1*c–f*). At Yellowstone the most common geothermal wetland plant, beaked spikerush, *Eleocharis rostellata* (Cyperaceae), colonizes wetland surfaces by clonal growth via stolons (figure 1*c*) and vegetatively via rhizome fragments forming widespread, near monospecific stands. The species can grow on sinter aprons in water temperatures in excess of 40°C. In lower temperature regions of the geothermal wetlands, large areas of the substrate are occupied by monotypic stands of the plant. Here, they withstand high pH (often in excess of pH 9) and elevated salinity (1.5 parts per thousand, oligohaline-brackish), plus metals and metalloids in solution that would be at phytotoxic concentrations for most other plants. The plant is a silicon accumulator in life, biomineralizing opal-A to create phytoliths that are associated with epidermal, parenchymatous and sclerenchymatous cells [2–4,51]. It is a widespread species across North America, and normally grows in environments with high alkalinity and elevated salt levels such as coastal marshes, tidally influenced brackish marshes, alkaline fens and, in upland areas of the Rockies and High Plains, associated with salt lake margins and saline seeps and meadows. The plant thus appears to be pre-adapted to the stresses of geothermal wetlands by life in more widespread stressed environments ([4,51], and see discussion of pre-adaptation of the Rhynie plants in Wellman [20]). In favourable growth conditions, the plant can grow to 1.2 m tall, however, geothermal wetland populations exhibit stunted growth and those plants most frequently inundated by thermal water seldom exceed 15–20 cm. The geothermal wetland environment is sufficiently hostile that dryland mesophyte plant communities are excluded [4,51].

At Rhynie, plant-rich cherts (figure 2*b*,*c*) dominate the available float block collections, trenched sections and drill cores (e.g. [45]). Sedimentological features of these cherts plus intervening clastic sediments have allowed detailed interpretation of the palaeoenvironments of plant growth and preservation (e.g. [12,26,43,45,86–89]).

The broader environment comprised a river system with sandy levee banks within a floodplain. Breaches of levees during flood events led to the accumulation of crevasse splay sediments and deposition of overbank deposits of shale, silt and sand. This created a number of freshwater influenced shallow-water habitats (small lakes, ponds, muddy pools and small lake deltas), which were ephemeral in nature and subject to evaporation and drying, evidenced by desiccation cracks. During drying episodes, these aquatic environments would have developed into emergent to terrestrial habitats that were colonized by the Rhynie plants and terrestrial arthropods such as trigonotarbid spiders (e.g. [26,43,45]). Vegetation growing beside these waterbodies in 'normal environments' was incorporated into the accumulating sediments where they are occasionally preserved as identifiable compression fossils and as unidentifiable organic material in carbonaceous sandstones, siltstones and shales. Several features of the clastic sediments suggest relatively frequent (sub-decadal) river flood frequency, a high local water-table and/or dominance of waterlogged, wetland conditions. These include a lack of evidence of terrestrial paleosol formation (e.g. vertisols and calcretes) that are present in the basin fill sedimentary sequence above and below the chert bearing unit; the reduced nature of the sedimentary sequence and the absence of red-beds that would signify drying and oxidizing conditions; the common presence of early diagenetic framboidal pyrite (sometimes observed to be replacing plant material) and preserved (but compacted and degraded) organic matter in the subsurface (e.g. [51]). Flooding of surface sediments and/or a high local geothermal water-table is evidenced by silica-cemented equivalents of the clastic lithologies above and nodular chert nucleated on organic material in sandstone units (e.g. [26,43,45]). A combination of flooding by the local river system and geothermal system prevented development of climax terrestrial plant communities and the development of soil profiles between sedimentation events (e.g. [44,45]). These observations suggest a relatively wet general setting for the Rhynie Basin during the period of geothermal activity beyond the preservation environments represented by the cherts-proper [51].

The environment of deposition for plant-rich cherts at Rhynie is hypothesized to be the distal (low-temperature) margin of a low-angled, low-relief hot-spring outwash apron where sinter was being deposited and conditions were often marshy [26,44,45]. Sub-environments that were plant and animal habitats identified at Rhynie based on sedimentary fabrics include shallow, low-temperature pools on the sinter apron surface (e.g. [90], figure 2*b*), which were habitat for filamentous microbes and also the site of growth of *Remyophyton delicatum* the gametophyte of *Rhynia*. Wet sinter apron surfaces were also colonized by *Horneophyton lignieri* (e.g. [43]) and *Rhynia* (e.g. [90]). Other small pools on the apron surface formed in depressions with metre-scale diameters and estimated depths of *ca* 15 cm (figure 2*c*). These create lenticular chert beds that at Rhynie and Windyfield often contain an aquatic biota, including the charophyte algae *Palaeonitella* plus aquatic crustaceans and chytrid fungi (e.g. [26,44,45]). Rhynie plants preserved *in situ* in such pools include *Horneophyton*, *Aglaophyton* and *Rhynia* (e.g. [26,43,45,51]). A relatively frequent association of draped microbial laminae surrounding *in situ*, well-preserved plant axes in these chert beds (figure 2*b*) provides evidence of shallow standing geothermal water among growing plants prior to silicification [45]. In these depressions, chert lens formation and plant permineralization clearly indicates the presence of silica-rich alkali-chloride geothermal fluids at least over the scale of several months to a year as this timescale is required for plant silicification by permineralization (e.g. [2,3]). This observation does not conflict with often cited examples of instantaneous 'preservation' (cf. permineralization) recorded at Rhynie such as clouds of sperm cells being ejected into a silica gel sediment (e.g. [45]). As plant-rich cherts are those most frequently recovered from the Rhynie deposit and they make up the majority of chert horizons within cored sections (e.g. [26,43–45]) distal, low-temperature apron to geothermally influenced wetland environments appear to have dominated the Rhynie geothermal landscape.

A very close lateral and topographic proximity between fluvial and lacustrine clastic sedimentary environments and plant-rich sinter forming geothermal environments is evident in Rhynie sections (e.g. [26,43–45]). Composite chert beds, a common occurrence within cores/trenches, comprise alternations between plant-bearing chert and thin clastic horizons (often silicified). These indicate sinter apron development being halted temporarily by incursions of river water, presumably leading to dilution of dissolved silica to concentrations below saturation (e.g. [44]). The environment was, therefore, close to and, for much of the time, below both the local 'freshwater' and geothermal water table.

4. Were the Rhynie plants specialized?

The plants of geothermally influenced wetlands are usually outcompeted by mesophytic plants in normal dryland terrestrial environments. Strong ecosystem partitioning and the requirement for alkali-chloride, silica-rich geothermal waters for sinter formation and organism encrustation and permineralization mean that there is a very clear bias towards the preservation of wetland plants (and other elements of geothermal ecosystems) evident in active analogue environments for the Rhynie chert [3,4,51]. A relatively extensive record of fossil hot-spring deposits with preserved ecosystems spanning the Holocene to Late Devonian confirm this to be a long-standing taphonomic bias. Sedimentological and biotic associations recorded at Rhynie that indicate wetland conditions and growth and preservation of Rhynie plants such as *Horneophyton*, *Aglaophyton* and *Rhynia*, suggest that this bias extends back to the embryophyte-dominated hot-spring ecosystem of Rhynie [4].

The geochemistry of low-sulfidation epithermal systems and their associated alkali-chloride hot springs mean that this wetland bias also creates an ecophysiological bias in the fossil record. Again, this is evident in active thermal areas and the Holocene to Late Devonian fossil record. Broadly, fossil hot-spring floras are dominated by genera tolerant of elevated salinity, high pH and stresses related to dissolved phytotoxic elements including heavy- and transition-metals and metalloids [4,51].

The stresses associated with life in geothermally influenced wetlands are sufficient to prevent mesophytic plants of adjacent 'normal' terrestrial habitats colonizing environments conducive to eventual exceptional preservation via silica permineralization. This means that hot-spring floras generally exhibit low diversity. However, plant endemism and hot-spring specialization are not a feature evident in active and fossil hot-spring floras. Instead, they are dominated by plants pre-adapted to life in hot-spring environments via life in more widespread, but chemically and physically stressed, environments such as saline and alkaline seeps, salt marshes and on metal and metalloid stressed substrates [4].

An implication arising from these observations is that hot-spring floras are not representative of coeval regional floras and at best contain a subset of the whole flora. This is probably true of the Rhynie flora, which, for a hot spring flora, is relatively diverse containing seven species of sporophytes [4,51,20], but no examples of typical plants of coeval Old Red Sandstone assemblages.

Data accessibility. This article has no additional data.

Competing interests. I declare I have no competing interests.

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