WETLAND MEGABIAS: ECOLOGICAL AND ECOPHYSIOLOGICAL FILTERING DOMINATES THE FOSSIL RECORD OF HOT SPRING FLORAS

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Abstract: Siliceous hot spring deposits form at Earth’s surface above terrestrial hydrothermal systems, which create low-sulphidation epithermal mineral deposits deeper in the crust. Eruption of hot spring waters and precipitation of opal-A create sinter apron complexes and areas of geothermally influenced wetland. These provide habitat for higher plants that may be preserved in situ, by encrustation of their surfaces and permineralization of tissues, creating T₀ plant assemblages. In this study, we review the fossil record of hot spring floras from subfossil examples forming in active hot spring areas, via fossil examples from the Cenozoic, Mesozoic and Palaeozoic to the oldest known hot spring flora, the Lower Devonian Rhynie chert. We demonstrate that the well-known megabias towards wetland plant preservation extends to hot spring floras. We highlight that the record of hot spring floras is dominated by plants preserved in situ by permineralization on geothermally influenced wetlands. Angiosperms (members of the Cyperaceae and Restionaceae) dominate Cenozoic floras. Equisetum and gleicheniaceous ferns colonized Mesozoic (Jurassic) geothermal wetlands and sphenophytes and herbaceous lycophytes late Palaeozoic examples. Evidence of the partitioning of wetland hydrophytic and dryland mesophytic communities, a feature of active geothermal areas, is provided by well-preserved and well-exposed fossil sinter apron complexes, which record flooding of dryland environments by thermal waters and decline of local forest ecosystems. Such observations from the fossil record back-up hypotheses based on active hot springs and vegetation that suggest removal of taphonomic filtering in hot spring environments is accompanied by an increase in ecological and ecophysiological filtering. To this end we also demonstrate that in the hot spring environment, the wetland bias extends beyond broad ecology. We show that ecosystems preserved from the Cenozoic to the Mesozoic provide clear evidence that the dominant plants preserved in situ by hot spring activity are also halophytic, tolerant of high pH and high concentrations of heavy metals. By extension, we hypothesize that this is also the case in Palaeozoic hot spring settings and extended to the early land plant flora of the Rhynie chert.

Key words: silicification, taphonomy, geothermal wetland, epithermal Au–Ag, fossil, ecosystem.

In general, plant fossils are preserved only where sediments accumulate. In the vast majority of cases, this is in a wet environment where water transports and deposits sediment. Plant preservation potential in surface environments is negatively affected by oxidation at the surface and in the subsurface vadose zone, but increases dramatically in the presence of surface water bodies, high water tables or with rapid burial to below the vadose zone (Gastaldo and Demko 2011). These positive taphonomic circumstances are met more frequently in humid climatic environments than in arid or semi-arid environments and where sedimentation rates are high. As a consequence, wetland floras preserved in basinal environments during humid climatic intervals dominate much of the plant fossil record. This megabias is exemplified by the well-known and widespread Late Palaeozoic clubmoss (lycophyte)-dominated coal-swamp floras, which formed in wet humid climates in lowland coastal plain environments. These contrast with relatively less well-known coeval conifer, cordaitalean, pteridosperm, fern floras associated with dryland environments within the same lowland setting and with floras of time periods between coal formation with more seasonally dry climate, evaporation dominated surface environments and lower water tables (DiMichele et al. 2010; Falcon-Lang et al. 2011).

“T₀” is a term used to describe fossil vegetation, which was preserved in essentially the same spatial conformation as in life and that has undergone little or no taphonomic filtering following plant death. Geologically instantaneous events, such as rapid flooding or burial, are required for the formation of T₀ assemblages. Settings and contexts that are especially favourable for their origin include
volcanic ashfalls, drowning of coastal plains by rapid relative sea-level rise and, at smaller scales, rapid sedimentation associated with fluvial environments such as channel bars, crevasse splays and distributary lobes (DiMichele and Falcon-Lang 2011). DiMichele and Falcon-Lang (2011), having reviewed the Pennsylvanian record of such assemblages, noted that the vast majority of Palaeozoic T0 assemblages were formed in wetland settings at, or close to, sea level, whereas drylands and uplands are poorly represented. Such autochthonous plant assemblages may preserve vegetation in situ on its growth substrate allowing unique insights into plant palaeoecology. For example, T0 assemblages can provide evidence for whole-plant reconstructions and estimates of plant density, canopy height, productivity, plant hydraulics, cohort dynamics, spatial heterogeneity, ecological gradients, tree-sediment interactions and animal-plant interactions (DiMichele and Falcon-Lang 2011).

The observation that the plant fossil record has a broad bias to wetland preservation and that wetland settings host many of the most informative T0 fossil floras suggests that our knowledge of plant evolution, palaeoecology and hence reconstructions of ancient vegetation is skewed towards inhabitants of such environments (DiMichele et al. 2010; DiMichele and Falcon-Lang 2011; Falcon-Lang et al. 2011). The wetland versus dryland preservation bias and bias towards wetland T0 assemblages occur at global, regional and local (deposit) scale, and in this study, we consider the preservation potential of plants and the ecological signal provided by fossils in a set of unique T0 environments, viz. those associated with terrestrial silica-depositing hot springs. This less widespread and less common, although equally important, set of T0 environments or assemblages has a fossil record extending from active thermal areas at the present day to the early land plant flora of the Lower Devonian, Rhynie chert, and possibly beyond to microbial communities of the Precambrian (Walter 1996).

The Rhynie chert (Lower Devonian of Aberdeenshire, UK) is arguably the finest example of such an assemblage. At Rhynie, the discharge of silica-rich geothermal fluids from hot spring vents created siliceous chemical sedimentary rocks (sinter) as opaline silica (opal-A) precipitated from the hot spring water that flowed away from vents into areas of plant growth. Sinter deposition entombed a diverse early land plant flora, including the earliest well-documented plant of lycophyte affinity (Asteroxylon), rhyniophytes (e.g. Rhynia) and those of less certain relationships (e.g. Horneophyton, Aglaophyton). At Rhynie, plants with an erect in-life habit were preserved in great numbers, anatomically in three dimensions and to the cellular level, as the silica-laden hot spring waters permeated plant structures and cells (Channing and Edwards 2009a and references therein). The Rhynie assemblage provides our best insight into early terrestrial ecosystems. It underpins many inferences of the palaeoecophysiology of the plants and of their taxonomic affinities, plus the broader evolutionary patterns in basal tracheophytes (Channing and Edwards 2009a). As with other T0 environments, the Rhynie chert also captures other elements of the local ecosystem including the earliest body-fossil evidence of certain groups of insects, continental aquatic crustaceans, arachnids, algae, lichens and fungi. Interactions between the various elements of the biota, including early evidence of parasitism (chytrid fungi on aquatic algae), mutualism (mycorrhizal fungi within plants), symbioses (lichen), herbivory (mite coprolites), saprotrophism (chytrid fungi), detritivory (collembolans, myriapod coprolites) and predation (trigonotarbid arachnids and centipedes), provide a snapshot picture of a relatively complex and, in many respects, modern looking trophic web (Habgood et al. 2004; Channing and Edwards 2009a and references therein).

In earlier papers (Channing 2003; Channing and Edwards 2004, 2009a, b), we have hypothesized that, based on plant silicification and sinter accretion rates, plant numbers and density, aerial extent and longevity of conditions conducive to plant preservation, the most important environment for in situ permineralization-type plant preservation associated with hot spring settings is geothermally influenced wetland. Latterly (Channing and Edwards 2009a), we have synthesized information on the palaeoenvironments recorded in the Rhynie chert, plus anatomical and autecological data from the preserved plants and compared these features with active analogue environments and flora at Yellowstone. We concluded that many of the Rhynie plants colonized wetlands at the low-temperature fringes of the hot spring system and were versatile, but physiologically highly specialized, capable of withstanding osmotic and chemical stresses in a dynamic environment, and were probably out-competed by mesophytic vegetation elsewhere.

Here, we review the fossil record of hot spring floras from the intervening c. 400-million-year period. We augment the limited published accounts of hot spring floras with new, although admittedly often initial, observations and plant identifications and include information from mineral exploration industry grey literature and unpublished works of further research targets. We summarize the dominant ecology of plants preserved in the hot spring record. The plant fossils we describe are overwhelmingly those adapted to wetland settings, with lesser evidence of dryland groups, further suggesting the influence of the broad-scale wetland megabias in hot spring floras. Finally, we discuss physicochemical aspects of hot spring environments and ecophysiological features common to the dominant plant groups preserved through time by comparison with extant close relatives.
HOT SPRING DEPOSITS AND T₀ CONDITIONS

Silica-depositing hot springs (Fig. 1A) are the surface expression of terrestrial hydrothermal systems. They occur where meteoric water descends into the subsurface, becomes heated by magma or cooling plutons, equilibrates chemically with silicic rocks through which it is flowing and then, as it is hot and buoyant, ascends to the Earth’s surface.

The primary feature of a T₀ plant assemblage, in situ preservation of plant communities, occurs in the hot spring environment because ascending water within the hydrothermal system is rich in dissolved silica. Eruption of water from a spring vent is accompanied by cooling (from c. 100°C towards ambient temperatures), which forces dissolved silica to become supersaturated. Hence, as water flows into surface environments, amorphous silica (opal-A) precipitates. This forms siliceous chemical rocks, which create sinter mounds and aprons around vents (Fig. 1A). In addition, as water flows into areas of microbe and plant growth, opal-A deposition can entomb the local ecosystem in situ.

A second feature of T₀ plant assemblages, rapid preservation, occurs in the hot spring environment because opal-A precipitation and sinter deposition occur almost instantaneously on eruption. Two modes of preservation are discernible in active settings and in the fossil record. The first, preservation of morphology as external moulds, occurs extremely rapidly because opal-A precipitates readily on solid surfaces of materials immersed even temporarily in geothermal fluid. Plant surfaces (and microbial communities living on them) may be rapidly encrusted by this mechanism over periods of days to weeks, and in active hot spring basins, it is relatively easy to find examples of still-living plants with areas of stems/branches enveloped in sinter coatings.

The quality of plant preservation in the hot spring environment may go beyond the level of capture seen in most clastic and volcaniclastic settings (where compaction or impression preservation of nonwoody tissues and organs dominates) because anatomical preservation by silica permineralization is the second major preservation mode in hot spring settings. The classic example of this comes from blocks of Rhynie chert that contain dense, in situ stands of Lower Devonian land plants such as *Rhynia* or *Aglaophyton* with near-perfect preservation of the plants’ parenchymatous anatomy (Trewin 1996). Taphonomic experiments in active hot spring pools and sinter aprons at Yellowstone (Channing and Edwards 2004) show that permineralization of small stems of the sedge *Eleocharis* occurs on the scale of months, with complete permineralization being achieved within 11 months.

Preservation observed in the hot spring fossil record ranges from large, decay-resistant organs such as lignin-rich tree trunks and branches, to small herbaceous plants comprising relatively decay-prone parenchymatous tissues, to delicate plant gametophytes, and fungal, algal or bacterial structures. This means that, in combination, silica encrustation and permineralization by hot spring fluids are capable of capturing near-intact, taphonomically unfiltered hot spring ecosystems.

The removal of taphonomic filtering in hot spring settings allows a pair of important and related observations. Firstly, if a plant group occurred in a hot spring subenvironment where other plants are preserved, evidence of that plant group should also be present. Conversely, absence of a plant group from a subenvironment is a real, rather than taphonomic, absence and more likely a result of ecological partitioning. We will develop this idea further below by reviewing plant preservation environments of active hot springs and the fossil record of hot spring floras.

PLANT COMMUNITIES AND TAPHONOMY OF HOT SPRING SUBENVIRONMENTS

There is an inescapable requirement for the preservation of an organism by silification within a hot spring setting; the microbe, plant or animal has to be immersed in silica-rich geothermal water for either mouldic- or permineralization-style preservation to progress. This means that the presence of an organism in an ancient hot spring sinter indicates that it was within a wet environment during the course of preservation at least. The observation that rates of both mouldic- and permineralization-type preservation occur on the scale of months, rather than days or weeks, suggests that immersion has to be relatively protracted. In addition, for three-dimensional preservation of collapse-prone cells and tissues such as parenchyma, extended periods of drying must be prevented (Channing and Edwards 2004, 2009b). Silification of an organism does not occur in isolation and chemical precipitation of opal-A is also ongoing, and as distinctive sinter macro- and microfabrics form in different subenvironments of a hot spring complex (discussed below), its fossil occurs within a matrix recording the palaeoenvironmental conditions of the site of preservation.

Observations of active thermal areas reveal three main routes for plant material to be incorporated into sinter deposits. Allochthonous and potentially para-autochthonous plant organs shed from local vegetation (either within the hot spring complex or beyond the margins) and transported into an environment of silification include twigs and branches, angiosperm leaves, conifer
needles as well as reproductive structures such as cones, seeds and pollen. These may occur within any area of the hot spring system. Preservation state is variable and related to subenvironment. On aprons where drying and oxidation prevail, in general, preservation is confined to external moulds and permineralization of degraded and collapsed organs, whilst in lower temperature and more frequently wet settings, anatomical preservation may be
observed. The context of preservation environment for such material is provided by matrix chert macro- and microfabrics.

Autochthonous preservation of ‘normal’ dryland and wetland vegetation occurs by progradation of apron and peripheral geothermal wetland margins into areas formerly unaffected by geothermal fluids. This process creates a distinctive sedimentary sequence that is visible in the fossil record. Typically, bases of vertical sections comprise clastic sediments that show evidence of flooding by thermal waters in the form of partial to pervasive silicification. Some contain fragments of sinter apron material indicating off-apron fluid flow. Palaeosols may be associated with these horizons and contain well-preserved root horizons, and top surfaces may preserve in situ sapling and tree stumps. Initial sinter horizons may preserve degraded plant litter and better-preserved fallen trunks, branches and shed foliar and reproductive organs from the recently drowned vegetation. Given prolonged flooding of the environment, geothermal wetland conditions develop, giving rise to the third route to preservation, fossilization of plants actually colonizing cooler areas of geothermal discharge. Typically, in this environment, small herbaceous plants replace arborescent forms and species diversity declines. In situ permineralization of plants with intact roots/rhizomes and upright stems is common. Sustained input of thermal waters normally sees the encroachment of sinter apron environments into the geothermal wetland and many fossil flooding sequences are capped by laminated cherts with evidence of low- to mid-temperature sinter aprons with microbial silicification fabrics.

Hot spring subenvironments

Hot spring sinter aprons (Fig. 1A–B) form around point sources of thermal up-flow (vents), and silica deposition is dominantly controlled by rapid, cooling-driven supersaturation of dissolved silica. As a consequence, most precipitation occurs close to vents producing vent mounds and lower angle apron deposits. Areas proximal to vents aggrade more rapidly than distal, giving sinter deposits a convex lenticular morphology, and proximal regions of the outflow complex tend to be elevated relative to apron margins, geothermal wetlands and surrounding clastic environments.

At the deposit scale, limits to the habitability of hot spring subenvironments for various plant groups and facies-dependent taphonomic conditions produce a broadly concentric (but sometimes mosaic-like) range of variability in the quantity and quality of palaeobotanical content of active and fossil sinters. Broadly, high temperature or topographically high and dry regions close to vents offer poor habitat to higher plants (Fig. 1A), whilst distal, lower-temperature, less steep areas of apron with shallow water pools and low-lying apron margin wetlands (Fig. 1B) offer progressively more habitable geothermally influenced environments. In active hot spring areas of Yellowstone, a suite of hot spring subenvironments provides habitats for communities of higher plants (those most important with respect to potential preservation are discussed in detail by Channing and Edwards (2009a) and highlighted below).

Vent pools. Vent water temperatures, which approach boiling point in many examples, exclude all eukaryotic organisms, and fluids are habitat only for archaea and extremophile bacteria (Brock 1994). The vast majority of vent pools observed in active settings contain plant fragments from local vegetation but lack in situ plant communities. Cooler vent pools may form habitats for communities of aquatic and semi-aquatic plants and such a setting has been suggested for some plant preservation within the Rhynie/Windyfield cherts (Trewin et al. 2003).

Sinter aprons. Apron complexes may reach many hundreds of metres in diameter (Fig. 1B), and thicknesses in excess of 10 m are not uncommon (Walter et al. 1996). Depending on eruption style and frequency, apron morphology may develop various surface subenvironments,
most of which are dominated by bacteria. Where apron surfaces have a shallow dip and where sheet-flow eruptions are common, sets of shallow apron terraces (from a few millimetres to tens of centimetres high) form (Walter et al. 1996). Water, in this area of the apron (Fig. 1A), cools to temperatures which allow colonization by mat-forming bacterial communities (Cady and Farmer 1996; Walter et al. 1996). Silification of mats forms distinctive internal lamination and or bedding within developing sinter deposits which, because different microbial communities and bacterial growth habits occur at different temperatures and hydrodynamic settings, may be environment specific (Walter et al. 1996; Jones et al. 1998). Where filamentous microbes are entrained in the flowing water in apron environments, they become silicified to create distinctive streamer fabrics that are indicators of local flow direction (White et al. 1989). When these become silicified, they form strongly laminated sinter deposits, which are commonly preserved in the rock record and have distinctive microfabrics that aid their recognition.

Dry areas of sinter aprons offer a poor substrate for higher plant growth (Channing and Edwards 2009a, b). They are essentially a hard, but relatively porous, monomineralic rock that proves difficult for roots to penetrate (Channing 2001). As the only organic matter present in these areas comprises low volumes of microbial material, they have poor water retention properties and low nutrient availability (Channing and Edwards 2009a). In Yellowstone, colonization of abandoned areas of aprons is a slow process, bryophytes and lichens are early colonizers and alkali- and salinity-tolerant bunch grasses are not uncommon (Channing and Edwards 2009a, fig. 2d). Aprons generally remain essentially barren on the scale of decades rather than years with trees eventually becoming established on old, weathered and eroded apron surfaces (Jones and Renault 2003). Plant taphonomic potential is low on frequently dry apron areas because sinter accretion, plant encrustation and permineralization rates are too slow and commonly outpaced by oxidation and microbial decay (Channing and Edwards 2009a, b).

Wet areas of sinter aprons may also be hostile environments for higher plant growth and high water temperatures in areas proximal to vents prevent colonization (Channing and Edwards 2009a). However, where water temperatures drop below c. 40°C, higher plants can colonize apron settings, and in Yellowstone (Fig. 1A–B), two wetland species *Triglochin maritimum* (seaside arrow grass) and *Eleocharis rostellata* (beaked spikerush) form a sparse low-diversity vegetation (Channing and Edwards 2009a, fig. 1d, e). Plant preservation is controlled in this setting by frequency of flooding by thermal waters, flow rates and water depth. Deep, cool apron pools may have relatively high preservation potential but shallow areas of flow have much lower potential.

**Geothermal wetlands.** At the periphery of sinter aprons (Fig. 1B), where water temperatures drop below c. 35–40°C, extensive tracts of thermally influenced wetland develop (Channing and Edwards 2009a, fig. 1d). These provide habitat for large numbers of emergent aquatic plants, typically in Yellowstone *Triglochin maritimum* and *Eleocharis rostellata*. Relative to apron surfaces, plant numbers and density are high; however, species diversity remains low (Channing and Edwards 2009a, b). High initial plant numbers and constant immersion of plants during life and immediately following death mean that geothermal wetlands are sites of widespread *in situ* preservation. In Yellowstone, they are by far the most important environment for *in situ*, permineralization-style preservation (Channing and Edwards 2009a, b).

**Mesic environments.** Sharp boundaries (Fig. 1A–B) between mesic (forested and grassland) and stressed (aquatic and/or geothermally influenced) vegetation types are evident around hot spring areas (Channing and Edwards 2009a). At Yellowstone, *Pinus contorta* (lodgepole pine) forest surrounding geothermal areas is adapted to growth on low-nutrient, monomineralic soils derived from weathering of volcanic rocks. The species is a colonizer of abandoned sinter aprons. However, it is intolerant of high root temperatures and flooding and is commonly killed in geothermal areas by both processes (Fig. 1B; Channing and Edwards 2009a, fig. 2a–c). The progradation of sinter aprons and geothermally influenced wetlands across mesic environments causes drowning of broad areas of lodgepole forest and meadows (parkland). When inundation of forest areas occurs, drowned trees may remain standing (Fig. 1B) and bases of trunks and root systems may become silicified by permeating silica. However, geothermal wetland environments quickly develop between stumps (Channing and Edwards 2009a, fig. 2c).

The biosedimentary features created by silification of microbial and higher plant communities create environmentally diagnostic sinter microfabrics. Identification of such features in fossil hot spring deposits allows interpretation of palaeoenvironments and by linking lateral and vertical facies changes, reconstruction of physical (e.g. temperature) and chemical (e.g. pH, salinity) gradients or changes over time. Excellent examples of publications illustrating the concepts of hot spring facies interpretation and palaeoenvironmental reconstruction, which underpin the observation and interpretation of plant preservation and environment of growth that follow, include those from the Cenozoic (Campbell et al. 2001, 2003; Hampton 2002; Himman and Walter 2005; Lynne et al. 2005, 2008; Ertel 2009; Lynne 2012), Mesozoic (Guido and Campbell 2009, 2011, 2012; Guido et al. 2010; Channing et al. 2011) and Palaeozoic (Walter et al. 1996, 1998).
Postdepositional processes

In clastic T0 environments, increasing accommodation space is viewed as a prerequisite for rapid burial and increased preservation potential. In the hot spring setting, rapid burial may have an opposite taphonomic effect as geothermal gradients in thermal areas may be extremely steep leading to removal of organic structures by overpressured water in the form of steam and/or superheated liquid. Ground temperatures at Yellowstone may exceed 70°C (Channing and Edwards 2009a), and down-hole temperatures observed within sinter horizons encountered at the top of research drill-holes have been observed at 80–90°C at 10–11 m below the surface (Bargar and Beeson 1981; Guidry and Chafetz 2003).

Loss of biological information has been observed in cores drilled in Yellowstone geothermal basins where even woody plant materials buried only a few metres below the current surface are preserved as external moulds or ‘ghosts’ of plants with few organic anatomical tissues persisting (Guidry and Chafetz 2003). Additionally in the shallow subsurface, secondary opaline silica plus other minerals including calcite, iron and magnesium oxides, zeolites and clay minerals may be deposited filling former porosity and overprinting primary textures. The effect of overprinting on fidelity of preservation and ease of plant identification is variable.

Most silica deposited by hot springs at the surface is in the form of hydrated X-ray amorphous opal-A (Herdianita et al. 2000). It converts over timescales of tens of thousands of years to progressively more crystaline forms via opal-C, opal-CT to chalcedony, quartz (Herdianita et al. 2000). This transformation process may destroy plant tissues or obliterate features required for plant identification. Sinter deposits preserved from within this maturation window are often opaque, and whilst containing evidence of plants, anatomical details are hard to discern (Fig. 2A).

Finally, the lenticular nature of sinter deposits, with thickly developed apron cores and thinner apron and geothermal wetland margins, biases preservation during erosion towards the resistant apron cores. Numerous sinter deposits we have investigated retain well-preserved, although generally, plant-poor aprons, the marginal geothermal wetland environment having been largely destroyed and only present as blocks preserved on deflation surfaces or in drift.

THE FOSSIL RECORD OF HOT SPRING FLORAS

A worldwide hunt for epithermal and hot spring Au/Ag/ Hg mineral deposits and geothermal energy resources has led to a dramatic expansion of the number of verified fossil hot spring deposits and hot spring ecosystems. Geothermal energy exploration uses the presence of relatively young fossil sinters as guides for potentially concealed high-temperature geothermal systems, and mineral exploration uses the presence of sinters as a guide to potentially economic breccia and/or vein mineralization in the shallow subsurface. As both resources are most easily identified in regions of active or geologically recent volcanism, the world’s tectonically active plate margins have been a focus for major exploration activity, but increasingly palaeo-orogenic belts are coming under scrutiny from mineral exploration companies. Further examples of hot spring deposits have reached the academic literature as the result of astrobiological and Precambrian research aimed at unravelling the formation and subsequent long-term preservation of microbial fossils and their biofabrics. Reviews including information on the geographical and temporal distribution of hot spring deposits include: Nelson (1988); Walter (1996); Nakanishi et al. (2003); and Sillitoe and Hedenquist (2003).

Mineral exploration activity has led to the creation of ever more complex ore-deposit models, which aid deposit discovery and recognition. From these it can be seen that sinter deposits occur almost exclusively associated with a class of epithermal deposit know as low-sulphidation deposits. These are created by deeply circulating meteoric fluids as opposed to high-temperature magmatic fluid and, at depth in the hydrothermal system, have an alkali- and chloride-rich water chemistry rather than an acid- and sulphate-rich character (Panteleyev 1996b). Waters flowing from sinter-depositing hot springs above these systems have a high dissolved silica content and also relatively high sodium and chloride content and carry a suite of heavy metals and metalloids (Channing and Edwards 2004, 2009a, b and references therein). As we discuss later, this has a profound effect on vegetation that is growing around active springs and also on vegetation preserved in the fossil record.

CENOZOIC HOT SPRING FLORAS

Tectonically and volcanically active regions and Cenozoic volcanic provinces host the majority of the world’s known epithermal gold and silver deposits and represent vast geothermal energy resources. As sinter deposits are the surface expression of subsurface geothermal circulation and potential mineralization and hence a target in exploration for these resources, reports of fossil hot spring deposits are relatively frequent in Cenozoic (particularly Neogene) strata. Most important amongst the major Cenozoic epithermal provinces are those of the ‘Ring of Fire’ that encircles the Pacific Ocean, which are associated
with extensional areas of island and continental margin arcs and back-arc basins. Further examples are associated with continental rifts and extensional continental margins (Sillitoe and Hedengquist 2003) and hot spot volcanism (Saunders et al. 2008).

Mining and geothermal energy company grey literature (e.g. technical reports, investor presentations and corporate websites) from these areas abound with references to surficial sinter deposits and, as the presence of plant fossils is a major criterion for sinter identification confirming deposition at the surface, in many instances makes reference to preserved plants and plant moulds. Description of plant material present in the vast majority of these deposits extends only as far as terms for plant organs (branches, roots, stems, leaves) or broad identifications of plant groups such as sedges, reeds or rushes. As few palaeontological investigations have yet been conducted, these floras (Table 1) represent an untapped palaeobotanical resource.

These younger hot spring deposits are very instructive; fossil plants present are for the most part from extant species and genera allowing robust comparisons of ecological and ecophysiological characteristics and habitat preferences with living analogues. The deposits also provide clear evidence of what habitats and typical plant ecologies are favourable to preservation and incorporation into the rock and fossil record.

Western USA

By far the most well-characterized and extensively explored geothermal province in the world, the Western USA, hosts active to Eocene-aged hot spring deposits associated with the Coast Ranges of California, extensional rift settings (e.g. Nevada Rift, Oregon-Idaho Graben) and the volcanism of the Yellowstone hot spot.

To date, plant descriptions related to most sinter deposits are rudimentary, often limited to the fact that plants are present or indicating broad affinity (e.g. reeds or rushes). Examples of these deposits include recently active geothermal systems with Holocene to Pliocene-aged fossil sinter deposits, for example Roosevelt Hot Springs, Colorado, Holocene (Lynne et al. 2005), Beowawe, Nevada, Holocene–Pleistocene (Rimstidt and Cole 1983) and Steamboat, Nevada, Pleistocene–Holocene (Lynne et al. 2008), Rainbow Rock, Imperial County, California, Pleistocene (Pigniolo 1995). Miocene examples include Buckhorn Mine, Nevada (Plahuta 1987); Baxter Project, Nevada (Kizis 2006); Cordero Project, Nevada (Carew 2006); Hycroft Deposit, Nevada (Harris 2011); Jabo Prospect, Nevada (Keith et al. 1987); Bodie Bluff, California (Herrera et al. 1993); Red Butte, Oregon (Zimmerman and Larson 1994); and Summitville, Colorado (Gray and Coolbaugh 1994).

Older sinter deposits from the Western USA include examples from the Oligocene associated with the Crooked River caldera, Oregon (McCloughry et al. 2009). In the same region, the richly fossiliferous Eocene Clarno chert, which contains angiosperms plus aquatic ferns and horsetails, is suggested to have originated from hot spring activity around a lake environment (Arnold and Daugherty 1963; Brown 1975). In the Republic Graben, Washington, Eocene epithermal gold vein systems and surficial sinter deposits are associated with marginal lacustrine environments that contain abundant and well-preserved plants (Gaylord et al. 2001). Examples of sinter deposits containing fossil floras for which plant identifications have been provided include Holocene to Miocene examples from Yellowstone, Nevada and California.

Yellowstone National Park, Wyoming. Holocene – Late Pleistocene. In Yellowstone, sinter apron complexes and geothermally influenced wetlands are revealed by downcutting of the Gibbon River at Elk Park (Channing 2001; Channing and Edwards 2009a). The sedimentary succession at the locality shows a typical prograding hot spring apron sequence. The base comprises silicified sandstones with meshworks of unidentified silicified rootlets. Wetland conditions are marked by two distinct lithological/plant associations. Dark organic-rich beds with a massive opaline matrix contain extensive root horizons, which may represent geothermal water flooding of a pre-existing wetland. Identified roots, rhizomes, tubers and basal

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**FIG. 2.** Plants preserved in Holocene, Pleistocene and Pliocene hot spring deposits. A. Pleistocene hot spring sinter from Ohakuri, Taupo Volcanic Zone, NZ (NMW 2009.43G.1). Sinter is partially transformed from opal-A to more ordered phases (opal-C/Ct) and appears opaque white. Plant anatomy is poorly discernible. Scale bar represents 1 mm. B–C, wetland root horizons, Holocene–Late Pleistocene, Yellowstone National Park, Wyoming, USA. B, basal stems (with distinctive triangular cross section) and rhizomes/tubers of the cyperaceous genus Scirpus (NMW 2001.29G.29). Scale bar represents 1 mm. C, geothermally influenced wetland sinter containing abundant stems of Eleocharis rostellata with distinctive lacunae visible in transverse sections (NMW 2001.29G.25). Scale bar represents 1 mm. D, base of early Holocene apron sinter horizon at Potts Basin, Yellowstone with numerous rosettes formed by silica encrustation of in situ but wilted stems and leaves of bunch grasses. Scale bar represents 10 cm. E, conifer needle litter horizon preserved in sinter apron sinter at Potts Basin. Scale bar represents 10 mm. F, anatomically preserved stems of Eleocharis sp. preserved within geothermally influenced wetland environment at the Pliocene McGinness Hills hot spring deposit, Nevada (NMW 2009.43G.2). Scale bar represents 1 mm. NMW, National Museum of Wales, Cardiff, UK.
stems within the deposit belong to the Cyperaceae genera *Scirpus* (Fig. 2B) and *Eleocharis* (Fig. 2C). Stabilization of geothermal wetland conditions is marked by lighter-coloured sinter dominated by *in situ* clumps of *Eleocharis* basal stems surrounded by microbial mat fabrics. Top surfaces of these beds have a thick litter of randomly oriented *Eleocharis* stem fragments. Sinter apron encroachment on the wetland environment is evidenced by laminated sinter with well-preserved microbial mat fabrics.

Elsewhere in Yellowstone, examples of fossil vegetation of sinter apron surface environments are preserved. Holocene sinter deposits on the shore of Yellowstone Lake at Potts Basin contain rosette-like structures (Fig. 2D) created by *in situ* silica encrustation of wilted stems and leaves of alkali and salinity-tolerant ‘bunch grasses’ (e.g. *Puccinellia nuttalliana*). In the same area, lenses of well-preserved conifer needles represent para-autochthonous material transported into shallow pools on the apron surface (Fig. 2E).

Older hot spring deposits identified in Yellowstone include a Middle to Upper Pleistocene sinter apron core complex at Artists Point (Hinman and Walter 2005) and areas of scattered laminated sinter boulders and cobbles in the Norris Geyser Basin/Elk Park area (White *et al.* 1988; Channing 2001). These deposits, which contain abundant evidence of microbial fabrics, exemplify the low volume of plant material incorporated into sinter apron environments because they have yielded only rare unidentifiable higher plant specimens with poor straw-like preservation that lacks cellular replication (Powell 1994).

Beyond Yellowstone, members of the Cyperaceae dominate the flora at two other Holocene – Late Pleistocene hot spring deposits. Erwin and Schorn (1996) reported cyperaceous species in Holocene hot spring deposits associated with the volcanic vent lake at Soda Lake, Nevada. At Clearlake, California Taylor *et al.* (2006) reported rhizomes and basal stems of a *Cyperus*-like species within wetland sediments that also contained algal filaments and diatoms.

**Nevada, Miocene–Pliocene.** The oldest thoroughly investigated hot spring deposit in the region with identified plants occurs at the McGinness Hills, Nevada (Ertel 2009). This Pliocene-aged hot spring system is largely intact and is well-exposed. The locality preserves a sinter apron core complex that is up to 24 m thick and approximately 500 m in diameter. The sinter apron provides evidence of multiple vents and coalesced apron deposits exhibiting microbial fabrics, which represent a typical down-apron zonation of progressively cooler subenvironments. Sinter-chip breccias and geothermal wetlands located at the periphery of the deposit are the only two subenvironments from which plants have been reported. Only sparse plant fragments occur in the sinter-chip breccias. In contrast, abundant and often well-preserved plants are preserved in the adjacent geothermal wetland setting. Ertel (2009) provided the general description ‘marsh vegetation consisting of reeds, grasses and roots’ and identified some roots and woody stems as belonging to dicots. The ‘reeds’ at the deposit occur as small match-stick-like fragments of aerial stems that form litter on bedding top surfaces, a feature that is directly comparable with active and subfossil wetland surfaces at Yellowstone. Vertical sections through the deposit reveal *in situ* vertical bunches of stems that radiate from a common origin. Our observations of the wetland vegetation reveal the presence of monocot roots and rhizomes and that the dominant plant present in both subenvironments is a species of *Eleocharis* (Fig. 2F), the most commonly preserved plant in active and subfossil deposits of Yellowstone.

Roots and basal stems are preserved in stacked root-mat horizons within massive dark-brown to black chert that occurs in float blocks at the margins of an *in situ* sinter apron core complex at the Miocene Hasbrouck Mountain epithermal deposit at Tonopha, Nevada (Gra-

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**Table 1.** Age and geographical distribution of Cenozoic fossil hot spring sinter deposits.

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Compiled from mining and geothermal energy company grey literature plus Sillitoe and Hedenquist (2003), Nelson (1988), and Nakanishi *et al.* (2003).

*, sinter deposits reported; P, plant fossils reported; ?, not verified.
ney 1987). Roots (Fig. 3A) have anatomy (large cortical air spaces traversed by small vascular strands) that are similar to *Scirpus* roots preserved in Holocene environments of Yellowstone. The top surfaces (wetland sediment surfaces) of some float blocks preserve fragments of small decorticated tree or shrub branches.

Iceland

Jones and Renaut (2007) and Jones et al. (2007) investigated the stratigraphy and chronology of Holocene siliceous sinters associated with the active Geysir hot spring in Haukadalur, Iceland. In contrast to most other hot spring deposits in the literature, plant material preserved within the deposit is dominated by leaf litter created by shed leaves of shrubby dicots, most notably *Betula* (Fig. 3B). Preservation of leaf anatomy is extremely common and extends to preservation of parenchymatous cells of the palisade layer and spongy mesophyll, indicating rapid silicification despite transport to the site of preservation. The genus is still present within the active hot spring area and occurs as low-growing, shallow-rooting plants that are present within the sinter-forming environment where thermal run-off channels traverse and cut into areas of remnant peaty soils.

*In situ* plants occur in a widespread wetland horizon that occurs on the hillside above the current area of hot spring activity. These slopes were considered by Jones et al. (2007) to be the site of vents responsible for the formation of the oldest sinter horizons in the Geysir sinter apron deposit. Here, basaltic basement is overlain by silicified tephras/volcaniclastics with upper horizons containing sinter chips and *Betula* roots. Stratigraphically above these, wetland sinter contains upright axes of *Equisetum* that grow through surfaces covered with horizontal *Betula* twigs and leaf mats (Fig. 3C). An eroded vent mound within the outcrop of geothermal wetland sinter appears to represent the point source of geothermal fluids. Additional fossil species recorded include abundant bryophytes (Fig. 3D), unidentified grasses, stems and leaves of *Carex* and the dicot *Plantago maritima*. The latter species is a common component of the present flora of the area and one of the many salt tolerant species that lives in areas of thermal run-off. Other species present in active Icelandic sinter deposition areas include *Triglochin palustris*, *Agrostis stolonifera*, *Carex nigra* and *Carex maritima*, species that often occur as part of Boreal salt-marsh communities.

New Zealand

The North Island of New Zealand, like the Western USA, is a site of active geothermal activity with an extensive record of low-sulphidation epithermal mineralization and fossil hot spring deposits, which extends back to the Holocene. Fossil plants occur associated with most reported hot spring deposits including the Holocene (8.5 ka) Mangatete sinter (Brathwaite 2003), Late Pleistocene (c. 15–40 ka) Umakuri (Campbell et al. 2001), Tahunaatara (Campbell et al. 2003), Ohakuri (Henneberger and Browne 1988) sinters and older (60–140 ka) Otamakokore and Whirinaki (Holland, 2000; Rodgers et al. 2004) sinters within the active Taupo Volcanic Zone. In the Northland region, plants are reported from Late Pleistocene (c. 40 ka) sinters at Omapere (Herdianita et al. 2000; Pastars, 2000) and Pliocene (3–4 Ma) sinters at Whenuaroa (Hampton 2002). Sinters of Pliocene to Miocene age occur associated with the Coromandel Volcanic Arc in the Hauraki goldfield, Coromandel Peninsula. Examples occur at Waitaia near Kuaotunu (Edbrooke 2001), Broken Hills, Ohui, Onemana and Ascot Mine (Brathwaite and Christie 2000).

Taupo Volcanic Zone, Pleistocene. The most thoroughly investigated Late Pleistocene hot spring sinters occur at Tahunaatara (Campbell et al. 2003) and Umakuri (Campbell et al. 2001). At both localities, sinter apron and associated geothermal wetland and clastic sediments are revealed in cliff sections allowing detailed observations of stratigraphy and palaeoenvironments.

The Tahunaatara sinter (14–20 ka) is a well-preserved but partially eroded hot spring deposit with preserved mid to distal areas of a sinter apron complex, peripheral geothermally influenced wetland and intercalated ashfall and fluvial deposits (Campbell et al. 2003). Geothermal wetland settings of the deposit are dominated by anatomically preserved stems of a member of the Restionaceae, *Apodasmia (Leptocarpus) similis* (Fig. 3E). The plant occurs in great numbers in monospecific stands preserved in growth position and surrounded by a litter of fallen aerial stems. Up to 50 per cent of rock volume in wetland horizons is plant material. The same species occurs in, and growing through, intercalated tuffaceous siltstone lenses. Less common wetland plants include an unidentified member of the Cyperaceae (Fig. 3F) preserved as leaves and seeds. Wetland sediments dominate the Tahunaatara sequence, and the stacked plant horizons are repeatedly colonized by the same species.

Laminated/bedded low-temperature apron sinter within the deposit contains much less plant material (up to about 10 per cent of rock volume). Infrequent *in situ* plants are preserved as clusters of basal stems and mouldic preservation of scattered plant material lying on bedding dominates. Coarser silicified clastic and volcaniclastic sediments at the locality, in contrast to peripheral apron and wetland horizons, contain more diverse plant types and organs. Preserved material is dominated by
woody organs, such as twigs and branches, and isolated small leaves. Occasional leafy shoots exhibit good preservation of lignified tissues but lack preservation of parenchyma. Less frequent monocots within the detrital horizons include compressed stems of *Apodasmia*. Plants preserved in life position are less common than in wetland horizons.

The Umukuri sinter has a minimum age of 27 ka and is considered to preserve vegetation of either the last interglacial oxygen isotope stage III, 20–30 ka (Campbell *et al*. 2001) or oxygen isotope stage V between 80 and 120 ka (Rodgers *et al*. 2004). As at Tahunaatara, the hot spring subfacies preserved at Umukuri represent mid- to low-temperature sinter apron and slope areas, and distal geothermally influenced wetland. Thinly laminated and palisade apron sinter fabrics and plant-rich sinters dominate. Campbell *et al*. (2001) considered that the thinly laminated microfacies at Umukuri formed from silicification of filamentous bacterial mats at low temperatures (c. 35°C) under sheet-flow conditions. Palisade fabrics also formed at similarly low temperatures although under different hydrodynamic conditions. Closely spaced, lateral and vertical intercalation of various microfacies in outcrop implies changing local flow and temperature conditions.

At Umukuri, most facies contain some plant matter although evidence for *in situ* preservation is less frequent than at Tahunaatara. Most plants are preserved as external moulds formed around plant fragments that were lying on bedding surfaces. Campbell *et al*. (2001) compared the plant-rich microfacies at Umukuri to active environments at the nearby Orakei Korako thermal area, where they observed low-density areas of living rushes being actively silicified along moist, outflow-channel interfluves and found plant moulds formed in sinter. Anatomically preserved plant organs at Umukuri are dominated by roots or rhizomes of wetland monocots with large air spaces and stem fragments of *Apodasmia* (Fig. 4A; Campbell *et al*. 2001, fig. 13). Less frequent larger plant moulds formed around woody twigs and branches and poorly preserved small dicot leaves appear to represent material transported into the apron/wetland environment.

A third Late Pleistocene (c. 40 ka) hot spring deposit at Lake Omapere, Northland, is exposed sufficiently to view apron complex and wetland facies in plan view (Pastars 2000; Rodgers *et al*. 2004). The sinter apron environments preserved all contain fabrics typical of low-temperature (<35°C) depositional hot spring environments. Massive to diffusely bedded, vitreous, black plant-rich sinter, comparable with that at Tahunaatara, occurs in marginal areas of the deposit and below apron sinter in cores. Peat horizons intercepted in cores indicate apron development adjacent to a lacustrine environment. Plants preserved *in situ* are dominated by reeds with tissue organization comparable with *Apodasmia* preserved elsewhere (Herdianita *et al*. 2000, fig. 3h). Less frequently preserved plants include unidentified grasses and leaves and the basal stems of *Cordyline australis* (Rodgers *et al*. 2004).

All three Late Pleistocene deposits are dominated by a low-diversity wetland plant assemblage. *Apodasmia similis*, the most commonly preserved species, is endemic to New Zealand and occurs most commonly at present in coastal settings such as estuaries, salt marshes, dunes and sandy flats and hollows. The species also occasionally grows inland in gumland scrub, along lake margins, fringing peat bogs or, as in the fossil record, surrounding hot springs.

**Northland, Pliocene.** The Puhipuhi geothermal field, Northland hosts Pliocene (3–4 Ma) fossiliferous sinter deposits. Hampton (2002) investigated the stratigraphy and microfabrics of sinters at Mt Mitchell and Plumduff and reconstructed palaeoenvironments within two discrete apron complexes. Recorded hot spring subenvironments range from near-vent apron with columnar stromatolites (T > 70°C), to medium-temperature apron with conical (tufted) and shrubby microfabrics (c. 40–60°C) to lower-temperature apron with palisade fabrics. Plant-rich, low-temperature facies were found to be concentrated around the distal margins of the aprons although small

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**Fig. 3.** Plants preserved in Holocene, Pleistocene and Miocene hot spring deposits. A, root/rhizome of unidentified wetland plant from the Miocene Hashbrouck Mountain hot spring deposit, Nevada (NMW 2009.43G.3). Cortical regions of the organ have large air spaces traversed by root traces. Scale bar represents 1 mm. B, anatomically preserved *Betula* leaf from dense leaf litter within a Holocene sinter apron deposit preserved below the active apron of Geyser hot spring, Haukadalur, Iceland (NMW 2009.43G.4). Scale bar represents 10 mm. C, Three transverse sections of *Equisetum* stem (fractured at, or adjacent to, stem nodes) and a collapsed, bedding-parallel stem fragment viewed on the underside of wetland sinter block from fossil vent complex adjacent to the Haukadalur geothermal area (NMW 2009.43G.5). Scale bar represents 5 mm. D, bryophyte material from Holocene sinter, Iceland (NMW 2009.43G.6). Scale bar represents 1 mm. E, several transverse sections of *Apodasmia* stem in wetland sinter matrix from the Late Pleistocene, Tahunaatara sinter, TVZ, New Zealand (NMW 2009.43G.7). The epidermal regions of the stems have distinctive dark radial cells (pillar cells) that line areas of parenchyma cells. Stem centres have variably preserved parenchymatous pith. Scale bar represents 1 mm. F, leaves of an unidentified member of the Cyperaceae from Tahunaatara (NMW 2009.43G.8). Scale bar represents 1 mm. NMW, National Museum of Wales, Cardiff, UK.
pockets of silicified plants occurred across many of the lower-temperature apron surfaces. Most plant organs are preserved as moulds and casts considered to represent fallen and transported branches and twigs and in situ reeds. Vertical sections through the base of the Mt Mitchell apron record lateral facies changes from high-temperature settings in eastern outcrops (columnar structures) to low-temperature in the west (abundant silicified reeds). At the site of reed silicification, overlying sinter horizons indicate progrediation of the sinter apron over the wetland setting and a progressive reduction in plant numbers. At Plumduff, distal areas of the apron complex record the flow of silica-rich water down apron slope into marshy ground on the edge of a lake, where reeds and other small plants became silicified. Within both wetland areas, stem casts and moulds are preserved in multiple layers as randomly organized litter and upright stems set in an indurated black to grey quartz matrix. Generic identifications of species present have not been made; however, the tissue organization of better-preserved stems illustrated by Hampton (2002, fig. 5.1) appear to confirm the presence of abundant wetland monosots.

**Coromandel Peninsula, Pliocene–Miocene.** Miocene sinters occur associated with two epithermal mineralization events at c. 16.3–10.8 and 6.9–6.0 Ma on the Coromandel Peninsula (Mauk et al. 2011). Most fossiliferous sinter deposits are highly dissected and preserved as in situ erosional remnants or boulder fields. Some plant-rich cherts (e.g. those in the Waihi area) occur only as clasts in hydrothermal explosion breccias or transported river cobbles.

Perhaps the most intact hot spring deposit occurs at Waitaia where sinter occurs as seven discontinuous boulder strewn fields, distributed over an area of 4.5 × 1.5 km. Sinter fabrics representative of low- to moderate-temperature sinter apron and plant-rich marsh facies can be distinguished in the area (Rodgers et al. 2004). In places the sinter apron deposits are interbedded with swamp deposits and where in situ dissected sinter masses occur at Black Jack Hill, Kuaotunu, Rowland and Sibson (1998) described plant-rich deposits at the base of sinter apron deposits as containing ‘edges’.

A similar series of sinter outcrops and boulder fields occurs at Kohuamuri Stream, south of Whitianga (Harvey 1981). Apron sinter present in the boulder field of the deposit contains abundant transported leaves and twigs. Tissue preservation at the deposit is extremely poor, and most plant material is preserved as external moulds infilled with a later generation of clear quartz (Fig. 4B). Some leaves (Fig. 4C) appear comparable to small, linear parallel (elliptical)-shaped leaves of *Podocarpus* with constricted leaf bases and a strong mid-rib illustrated by Pole (1992) from the Miocene of New Zealand. The poor-quality preservation of samples and matrix chert fabrics suggest preservation of allochthonous plant material on apron surfaces.

Plant-rich chert cobbles discovered by amateur collectors in the Waihi area contain abundant roots and basal stems of wetland monocots with a distinctive central stele and large cortical air canals defined by thin radial strands of parenchyma. Further examples of plant-rich sinters of Pliocene to Miocene age are reported from Broken Hills (Handley and Campbell 2011), Ascot Mine, Mackaytown (Edbrooke 2001) and Waitekauri valley in the Waihi area (Simpson and Mauk 2011). Species identifications have not been made for any of these occurrences.

**Japan**

Hot spring sinter deposits of Japan range in age from active to Miocene (Nelson 1988; Nakanishi et al. 2003). To date, only two reports of preserved plant material have been published. A Holocene sinter deposit (Ozaki 1972) associated with the Hakone caldera in Kanagawa Prefecture preserves a diverse (39 species) leaf, seed and cone-scale flora, which records local coniferous (Abies) and broadleaf woodland vegetation. A single species of *Carex* is reported. Belhadi et al. (2002) illustrated a dicot

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**FIG. 4.** A, poorly preserved stem of *Apodasmia* from apron sinter environment of the Pleistocene, Umukuri hot spring deposit, TVZ, New Zealand (NMW 2009.43G.9). Little organic material remains within the stem. Anatomy is only visible due to voids once occupied by cell walls remaining free of later phases of infilling opal-A. Scale bar represents 0.5 mm. B, external moulds of small *Podocarpus* leaves from the Miocene, Kohuamuri Stream sinter deposits, Coromandel, New Zealand. All organic structures have been lost from within the moulds and a later phase of quartz fills the open space (NMW 2009.43G.10). Scale bar represents 1 mm. C, a *Podocarpus* leaf external mould revealed by fracturing along a sinter lamina (NMW 2009.43G.11). Shrunken remnants of the leaf that created the mould remain. Scale bar represents 1 mm. D, transverse section of anatomically preserved *Equisetum thermale* stem from geothermally influenced wetland of the Jurassic San Agustin hot spring deposit, Santa Cruz, Argentina (Accession MPM-PB 2029). Scale bar represents 0.5 mm. E, gleicheniacous fern stipe (oblique TS) from geothermal wetland, San Agustin (Accession MPM-PB 2029). Regions of cortex with thin-walled parenchyma cells forming an open aerenchyma are heavily degraded. Scale bar represents 1 mm. F, in situ stump of conifer preserved in geothermal wetland sinter formed during flooding of dryland environment at San Agustin. Scale bar represents 10 mm. NMW, National Museum of Wales, Cardiff, UK; MPM, Museo Padre Jesus Molina, Rio Gallegos City, Santa Cruz Province, Argentina.
leaf within Pliocene sinter, which caps epithermal vein deposits in the Hoshino area, Hohi volcanic zone, Fukuoka Prefecture.

Africa

Detailed accounts of fossil Holocene to Pleistocene hot spring deposits of the East African Rift system are scant. The complexities of the lakeshore/spring complex palaeo-environments, typical of active examples, coupled with a mix of cool-, warm- and hot spring-fed environments, plus potential chert formation via routes other than deposition from hot springs (e.g. magadiite formation) make interpretations of fossil examples difficult (Owen et al. 2004, 2008). Notwithstanding these caveats, Holocene to Pleistocene (7 ka to c. 500 ka) sinter deposits are reported from volcanic centres of the northern Kenya Rift Valley (Sturchio et al. 1993; Darling and Spiro 2007) and Pleistocene sequences of the Afar Rift (Moussa et al. 2012). A single fossiliferous hot spring deposit of Pleistocene age is reported from the Stratex International owned Megenta Project, Afar Depression (Hall 2012), which contains in situ stands of ‘reeds’.

A species of Equisetum is reported from Holocene–Pleistocene hot spring sinter deposits located close to extinct volcanic craters, near Ambohidratrimo, Madagascar (Baron 1889).

China

The Lincang superlarge germanium deposit contains siliceous hydrothermal sedimentary structures interpreted (rather controversially) as sinter, which are interbedded with Neogene lignites. The presumed sinter contains abundant but as yet unidentified permineralized plants (Qi et al. 2004). Three fossil sinters of Pleistocene age (the oldest dated at 380 ka) occur in the Tengchong (Rehai) area and are reported to contain abundant casts of plant stems, roots and leaves (Meixiang and Wei 1987).

Central and South America

Cenozoic sinter deposits are reported from along the length of the Central and South American Pacific Margin. Examples from mining company grey literature include Monte Cristo, Mexico (Paramount Gold and Silver); Ludavina, Mexico (Cardero Resource); Cerro Blanco, Guatemala (Goldcorp); Camporo, Honduras (First Point Minerals); Santa Rosa, Panama (Greenstone Resources); Ganarin, Ecuador (Nortec Minerals); Cacapaqui, Peru (Alturas Minerals); Puchuldiza, Chile (Southern Legacy Minerals); and Valle del Cura, Argentina (Malbex). Reports of plant fossils from these regions are at present limited to a report of fossil ‘reed casts’ from the El Gallardo sinters associated with the Pliocene El Dorado epithermal gold district, El Salvador (Richer et al. 2009).

PRE-CENOZOIC RECORDS OF HOT SPRING FLORAS

Whilst many of the world’s orogenic belts have evidence for the former presence of hot spring activity in the form of epithermal mineralization, only a handful of epithermal provinces retain evidence of surficial sinters. Estimates of the number of epithermal deposits created during the Phanerozoic suggest that about 83 per cent have been removed completely by erosion leaving approximately 63 000 deposits to be discovered (Kesler and Wilkinson 2009). Hot spring environments as surficial deposits associated with fault-related settings within tectonically and volcanically active terranes are even more susceptible to erosion and removal from the rock record (Gray et al. 1997). This problem of long-term preservation is highlighted by the scarcity of pre-Cenozoic examples of sinter deposits.

Exploration activity in the Mesozoic magmatic-arc and back-arc environments of the American Cordillera and Western Pacific and Palaeozoic and Mesozoic regions of the Tethyan-Himalayan and Ural–Mongolian tectonic belts has discovered increasing numbers of deposits preserving near surface vein systems and hydrothermal breccias. At present, sinter deposits are represented within most geological periods (Table 2). Hot spring deposits that lack information on the presence of plants include Cretaceous cherts presumed to have formed in the hot spring environment from the American Cordillera of Alaska (Bundtzen and Miller 1997) and La Rioja, Argentina (Fiorelli et al. 2011); Jurassic examples preserved in the Solenker epithermal district of south-east Mongolia (Xanadu Mines Ltd 2011) and Silurian examples of the Botwood Basin, Newfoundland (Wardle 2007).

Mesozoic hot spring floras

Mesozoic hot spring floras are recorded from just two palaeogeothermal provinces (Table 2).

China. The Sipingsang epithermal gold deposit, Heilongjiang Province, NE China, occurs in the Late Jurassic–Early Cretaceous Wandashan Fold Belt part of the circum-Pacific tectonic belt. The sinter deposit occurs above an Upper Jurassic rhyolite. Mineralization has been dated as Upper Cretaceous, c. 87 Ma (Huang et al. 2011).
The deposit comprises silica-cemented breccias and gravels overlain by a 3 to 15 m thick sequence of laminated chert. The bulk of the in situ cherts appear to represent sinter apron environments, although blocks of organic-rich chert with a mottled to massive matrix suggestive of geothermal wetland settings also occur. To date, identifications of plants are limited to fragments associated with apron surfaces and appear to be disseminules of adjacent forest vegetation. Identification is hampered by a high degree of tissue loss, with most plant organs being preserved as silica encrusted tubes with poorly preserved anatomy. Transverse sections of many tubes are reminiscent of conifer needles. Only the most recalcitrant organic compounds remain intact; fungal structures, spores and pollen (including bisaccate forms) and wood fragments are relatively common.

*Argentina.* The Jurassic strata of the Deseado Massif, Santa Cruz Province, Argentina, host the largest concentration of epithermal systems with preserved hot spring deposits in the world, after the Cenozoic of the Western USA. In this region, Late Jurassic volcanism, extension and a high thermal gradient in a back-arc setting produced hydrothermal mineralization including epithermal deposits and their surface expression, hot spring deposits (Guido and Campbell 2011). To date, about 25 examples of silica sinter and carbonate (travertine) hot spring systems have either peripheral terrestrial or lacustrine clastic depositional environments (Guido et al. 2010). Features of plant colonization and preservation visible in active and Cenozoic hot spring complexes are readily discernible at San Agustín. Apron complexes, which constitute the most extensive features at the deposit, provide abundant evidence of microbial communities in mid- to low-temperature sinter apron settings but lack identifiable plants.

Plant preservation within the apron environment is limited to silica-rimmed low terraces on the outermost sinter apron, which encosed localized supra-apron geothermal ponds (10–20 cm deep, 5–10 m diameter). These provided habitat for dense monospecific carpets of the sphenophyte *Equisetum thermale* (Channing et al. 2011). Geothermal wetlands forming beyond the apron are dominated by the same species (Fig. 4D) and less common gleicheniaceous ferns with clear adaptations to wetland conditions as indicated by well-developed aerenchyma.
(Fig. 4E). Other plant organs within the wetland deposits include infrequent transported branches, leafy shoots and seed scales of conifers from nearby forested environments.

Vertical sections through the larger sinter apron deposits reveal typical apron development sequences comparable with Cenozoic examples. Bases of sections have silicified clastic or volcanoclastic sediments and palaeosols with silicified roots and sometimes small sinter fragments. Basal cherts contain in situ conifer stumps (Fig. 4F) and rotted fallen trunks in a mottled matrix containing conifer branches, leafy shoots, cones and cone scales. Successive chert horizons contain the typical geothermal wetland species. The top of the sequence is capped by cherts preserving evidence of low- to mid-temperature apron environments with lenticular higher-temperature fabrics indicating outflow channels.

In other outcrops, thermal discharge entering lacustrine environments via shore-line stands of shrubby conifers and their seedlings is evident. Here, abundant Classopolis pollen indicates the presence of members of the Cheirolepidiaceae, which have been considered to be xerophytic, drought-tolerant and thermophilic and are commonly (although not exclusively) associated with oligohaline to saline environments (Alvin 1982; Mendes et al. 2010). Plant remains within the lake shoreline facies are enveloped by dense, ‘felted’ microbial linings, suggesting wet, marshy conditions during preservation (Guido et al. 2010).

Nonsilicified lacustrine deposits associated with the San Agustín hot spring complex (Zamuner et al. 2011) contain plants from seven genera (14 morphospecies) including the corystosperm Pachypteris, four species of the bennettitelean genus Dictyeaunites, three forms of araucarian seeds and Pagiophyllum/Brachyphyllum foliage. Lycopsids (Isoetes) and stems of Equisetum comparable with E. thermale are also present. Whilst species and morphogenetic patterns of basal cherts related to initial flooding of terrestrial settings are comparable in diversity with these sediments, the diversity relative to demonstrable geothermal wetland species is high. It appears here, as in active environments, that the onset of geothermal wetland conditions is marked by a reduction in ‘dryland’ species. These are replaced by species with obvious anatomical, and by analogy with extant species, physiological adaptations to oligohaline wetland conditions (Channing et al. 2011).

At the La Claudia exploration project, a broad suite of hot spring environments is preserved including both travertine and sinter aprons. Plants have not been identified in the apron settings of the deposit, and geothermal wetlands are poorly represented. Root horizons (Fig. 5A) dominate plant-rich cherts and these contain abundant evidence of shrubby conifers (leafy shoots and small branches) and much less frequent evidence of Equisetum and gleicheniaceous ferns.

The La Bajada and Cañadón Nahuel deposits (Guido and Campbell 2011) have not been fully investigated sedimentologically or palaeontologically, but initial observations indicate at both sites a mixed flora comparable with those preserved during initial flooding of terrestrial settings at San Agustín. In situ permineralized stumps and well-preserved roots occur in variably silicified volcanoclastics at the base of sections along with thickets of well-preserved osmundaceous ferns. In situ conifer stumps, sapling stems and osmundaceous ferns also occur in basal chert horizons (Fig. 5B) in association with large decorticated sections of conifer trunks and fallen branches. Smaller fragments of conifer leafy shoots, branches, cones and seed scales, which are well-preserved, occur in the extremely plant-rich chert above. The wetland genera Equisetum and gleicheniaceous ferns present at San Agustín occur within the same horizon and in life position within the massive, but generally plant-poor, chert that caps chert beds.

Lenticular chert lenses at the Laguna Flecha Negra deposit (Channing et al. 2007) similarly contain large volumes of variably preserved wood fragments, in situ roots, rootlets and young stems of conifers plus shed conifer shoots with scale leaves of Brachyphyllum and Pagiophyllum morphology, cycadophyte (cycad or bennettitelean)
leaves and conifer cones and seeds (Channing et al. 2007). Intercalated sandstones within the chert beds of this locality appear to indicate frequent disruption of sinter formation in an alluvial depositional environment.

**Palaeozoic hot spring floras**

Palaeozoic hot spring floras have been recorded from only three palaeogeothermal provinces (Table 2).

**Massif Central, France.** The Massif Central is well known for Carboniferous and Permian floras preserved in cherts (Galtier 2008). The majority of cherts are considered to be related to early preservation of plant materials in lacustrine, fluvial or swamp settings by silica derived from dissolution of intercalated volcanic and volcanioclastic horizons (Rex 1986; Matysova et al. 2010). Many plant-rich cherts from the region occur as isolated float blocks or as clasts within tuffs or conglomerates and suffer a lack of spatial context. An exception to this is provided by the Meillers ‘quartzite’ of the Autun Basin, which, based on geochemical, structural and textural evidence, has been re-interpreted as a hot spring sinter formed c. 295 Ma in the early Permian (Marcoux et al. 2004). Detailed sedimentological and palaeoenvironmental investigations of the deposit required to identify hot spring subenvironments have yet to be conducted. However, the stratigraphy of the deposit, which shows intercalations of laminated ‘sinter facies’ and clastic sediments within a general sequence that progresses from mottled, diffusely bedded cherts to laminated cherts with vuggy bedding-parallel porosity and ‘pillar and stall’ microbial mat fabrics (Marcoux et al. 2004), appears to show an apron complex prograding over peripheral wetland environments. Palaeontological data from the deposit are limited. Marcoux et al. (2004) reported Psaromius, ‘fructiform spikes’ and silicified ostracods in the upper sinter horizon of the deposit. Freytet et al. (2000) recorded various algal, cyanobacterial and stromatolitic fabrics and pollen, silicified woods, possible Cordaites leaves, vertical traces, which may be stems in their living position and possible moulds of roots. Hand specimens with matrix fabrics comparable with low-temperature sinter apron and wetland environments reveal abundant plant material (pers. obs.). Initial observations suggest the dominance of the sphenophyte Sphenophyllum in these environments (Fig. 5C).

Elsewhere in the Massif Central, suspected hot spring deposits with epithermal geochemical signatures (anomalous levels of As, Au, Ag and Sb) are reported from the Upper Carboniferous at St-Priest-en-Jarez near St-Etienne and hydrothermally silicified fluvial conglomerates and sandstones at Lugeac (Copard et al. 2002). The St-Priest deposit contains freshwater algae and stromatolitic horizons (Freytet et al. 2000).

**Drummond Basin, Queensland, Australia.** The Drummond Basin, Queensland represents a major north–south trending back-arc extensional system located at the inboard margin of the northern New England Orogen. It contains an early rift infill sequence comprising Upper Devonian to Lower Carboniferous volcanic, volcanioclastic and sedimentary rocks (Henderson et al. 1998).

Numerous epithermal deposits with proven or probable associated hot spring sinter deposits occur within the Basin (e.g. Bimurra (Wood et al. 1990; Ewers 1991), Durrah Creek (White et al. 1989; Ewers 1991) and Pajingo (AC pers. obs.)). The best-preserved and exposed hot spring complexes located at Woobegong (near Conway Station north of Mount Coolon) and Verbena (south-east of Mount Coolon) respectively occur within the Bimurra and Silver Hills Volcanics. New SHRIMP U–Pb zircon ages indicate deposition of these units in the latest Devonian (Famennian) at around 360 Ma (Cross et al. 2008). Latest radiometric dates for mineralization with associated sinters and silicified lacustrine sediments at Twin Hills Mine (Uysal et al. 2011) suggested a mineralization age of $313 \pm 6$ Ma placing this deposit in the latest Carboniferous.

The geology, geochemistry, sedimentology and palaeontological of the Conway and Verbena sinters have been studied in great detail (Cunneen and Sillitoe 1989; White et al. 1989; Ewers 1991, Walter et al. 1996, 1998). Walter et al. (1996) recorded 13 different microfacies in field investigations of the two deposits and classified these groups into four main facies associations, which broadly reflect down-apron temperature and topographical gradients. Very high-temperature microfacies ($>73^\circ$C) occur in vent zones and comprise geyserite and vent wall and pool deposits. High- ($60–73^\circ$C) to mid-temperature ($35–59^\circ$C) microfacies represent proximal to distal areas of run-off channels and supra-apron terrace pools and ponds. Down-slope and down the temperature gradient ($35^\circ$C to ambient) towards the periphery of the apron complex, low-temperature terrace-slope, terrace-pool and marsh environments occur (Walter et al. 1996, 1998).

Plant preservation within apron environments at the deposits is dominated by silica sinter encrustation of lycopsid stems and their external moulds are preserved lying on the bedding planes of thin-beded cherts. Walter et al. (1996, 1998) considered that these plants were growing on interfluvos between run-off streams on the apron. In other areas of the apron complexes, lenses and tabular beds of chert contain stems with orientations that vary from horizontal to vertical. Commonly, stems occur within thick encrusting concentric sheaths of chert.
containing evidence of filamentous microbial fossils. Many of the vugs within this microfacies have circular cross sections and were interpreted as moulds of lycophyte stems and roots (rhizoliths). Walter et al. (1996, 1998) considered these deposits to be analogous to environments in active spring systems where bushes and trees in growth position are engulphed by newly formed ponds and become encrusted with opaline silica. Walter et al. (1998) described three vegetative axis morphotypes from the Drummond basin sinters and a single strobilus. Two of the axes types and the strobilus represent herbaceous lycophytes and the third axis a possible sphenophyte.

In our field investigations of the Drummond Basin sinter deposits, we specifically focused on plant-rich microfacies. At Wobegong, in addition to the microfacies described by Walter et al. (1996, 1998), we found horizons of grey to red-brown massive to mottled or diffusely laminated/bedded chert characterized by a matrix rich in microporolites. These microporolite-rich sediments are recorded at San Agustin in geothermal wetlands and at Rhynie. At all three deposits, in addition to exceptionally preserved higher plants, algae and aquatic invertebrates occur. At Conway, anatomically preserved examples of the lycophyte described by Walter et al. (1998) occur in monotypic, stacked horizons above ‘root horizons’ that are also enclosed within microporolite-rich chert. Field relationships and anatomical features of the lycophyte, most notably the substantial air spaces within stems (Fig. 5D–E), are consistent with life in wetland conditions. This single species appears to dominate the full spectrum of geothermally influenced environments represented by the Conway and Verbena sinters.

As at San Agustin, local clastic and volcaniclastic environments contain evidence of plants beyond the limit of thermal activity. Tuffs adjacent to the Conway locality contain large (10–20 cm diameter) arborescent lycopsid stems. Fluvial sediments of the Bimmura Formation at Conway Station (approximately 2 km from the apron complex) contain a diverse compression flora comprising, herbaceous, plus arborescent, lycophytes (stigmalian roots, stems, branches, cones and dispersed sporophylls), sphenophyte stems and fragments of pteridosperm foliage. No examples of the arborescent groups have been discovered in geothermally influenced environments of the Upper Devonian Drummond Basin sinters suggesting partitioning of the local flora.

The Upper Carboniferous Twin Hills sinter deposit (Uysal et al. 2011) comprises broad areas of laminated sinter within lacustrine sediments some of which are silicified. Plants preserved at the deposit occur in massive chert that appears laminated due to bedding parallel collapsed and partially permineralized plant material. Collapsed arborescent lycophyte stems and/or branches up to 70 mm in diameter cover top surfaces of these chert outcrops. Three-dimensionally preserved plant organs in the bed include fragments of possible coraitaleans or ferns and unidentified leaves preserved as silica-infilled external moulds (Fig. 5F).


Unlike the majority of hot spring deposits described above, the Rhynie chert system does not crop out and occurs only as float or where intersected by trenching and research boreholes (Powell, 1994; Powell et al. 2000). Drill core recovered from the deposit intersected 45 in situ chert beds, most of which contained permineralized plants, although a few were barren (Powell 1994). In situ plants occurred in 29 of the 45 chert horizons (Powell et al. 2000 reporting Rhynie drill-core 19C) and in situ rhizomes with aerial axes were recorded for Rhynia, Aglaophyton, Horneophyton and Asteroscyton. Only Nothia and Trichopherophyton were not found as in situ rhizomes, and the least common permineralized Rhynie plant, Ventarura, was not recorded at all. Compared with the majority of younger hot spring floras, species diversity at Rhynie is relatively high, comprising seven species of sporophytes, four of which also have identified gametophytes. We suspect this is an observation bias, as in reality, four species (Rhynia, Aglaophyton, Horneophyton and Asteroscyton) might be considered to dominate the flora.

Mega-fossil floras from coeval, but geographically separate, clastic settings are not dramatically more diverse than the chert flora, containing eleven species (Channing and Edwards 2009a, table 4). However, when viewed relative to the dispersed spore assemblage of the broader Rhynie drainage basin (which yields over 40 distinctive dispersed spore types) and the total dispersed spore diversity of coeval sedimentary sequences (over 100 distinctive spore types), the chert flora is depauperate (Wellman 2006). Wellman (2004, 2006) considered that the plants preserved within the hot spring cherts were the only elements of the regional flora that were capable of survival in the hot springs environment and that other elements of the regional flora simply could not tolerate this inhospitable environment. Comparisons of coeval macrofossil floras from more ‘normal’ sedimentary environments, which are dominated by groups of trimerophytes and zosterophylls that are not recorded within the chert, appear
to provide further evidence of this ecological partitioning and exclusion of plants that might be considered typical Lower Devonian mesophytes from hot spring influenced settings (Channing and Edwards 2009a).

Wellman (2004, 2006) also considered the possibility of endemism and hot spring specialization of the Rhynie chert plants in relation to the dispersed spore record of the Rhynie drainage basin and broader geographical areas of the Old Red Sandstone continent. He observed that the distinctive spores of the Rhynie chert plants *Horneophyton lignieri* (*Emphanisporites cf. decoratus*), *Aglaophyton major* (*Retusotriletes* sp. A; Wellman, 2004) and *Rhynia gwynne-vaughanii* (*Apiculiretusispora plicata*) are palaeoecologically widespread and abundant elements of coeval dispersed spore assemblages. This suggests that the parent plants inhabited more normal environments throughout the remainder of the Rhynie drainage basin and were also common and widespread components of the regional flora (Wellman 2004). As the plants were not confined to hot spring environments, Wellman (2004, 2006) considered that it was likely that the three plants were pre-adapted to survive in hostile conditions rather than being highly adapted plants specialized for survival only in geothermally influenced environments. The true distribution of the remaining four chert plants, unfortunately, is masked due to the relatively simple morphology of their spores (e.g. various species comparable with *Retusotriletes*). Potential habitats for pre-adaptation of the Rhynie chert plants include those identified above for more recent hot spring plant species (e.g. coastal or inland salinity-influenced environments). However, it is possible that water-stressed environments were more common and widespread during the Late Silurian to Lower Devonian as terrestrial surfaces had less well-developed soils and were more sparsely vegetated by plants of lower stature.

The Rhynie chert plants rarely appear in coeval macro-fossil assemblages. A single specimen assigned to the genus *Horneophyton* (Edwards and Richardson 2000) is recorded from the Lochkovian of the Anglo-Welsh Basin. Additionally, some species of the compression fossil, form genus *Salopella*, with fusiform sporangia terminating naked, isomotously branched axes, have been linked with *Aglaophyton* based on sporangium morphology (Edwards and Richardson 1974). Given the dispersed spore record, this absence most likely arises from taphonomic removal of the parenchymatous Rhynie plants from most clastic environments (Wellman 2004, 2006).

Sinter apron environments are not well-represented at the Rhynie deposit, whilst plant-rich cherts are extremely abundant. The interpretation of environments of plant growth and preservation at Rhynie rely fully on identification of chert matrix fabrics and associations with other enclosed elements of the biota (e.g. aquatic fungi, algae, crustaceans suggesting wetland settings and terrestrial arthropods dryland). Various palaeoenvironments have been suggested for plant growth and preservation. Many chert lenses at Rhynie overlay silicified silt or sandstone sediments or contain sediment intercalations, some of which represent silicified plant litter or soil horizons (Powell 1994, Powell et al. 2000). Plant growth associated with these horizons indicates that at least some of the plant communities that were eventually preserved by sinter accumulation and permineralization were not necessarily submerged throughout their life. Such clastic sedimentary settings that were colonized by plants and subsequently flooded by hot spring waters were favoured in early accounts of the chert. El-Saadawy (1966) considered that the Rhynie plants grew in and around ephemeral pools within a barren landscape. Trewin and Rice (1992) considered that the plants generally grew on sandy substrates or sinter surfaces and close to pools on the fluvial floodplain prior to inundation by hot spring water. Powell (1994) envisaged the cherts as fossilized subaerial sinters in the vicinity of hot spring vents, with laminated cherts typical of deposition on sinter terraces and massive and lenticular cherts containing the charophyte *Palaeoniella* and aquatic crustaceans as pond deposits. Trewin et al. (2003) and Trewin and Wilson (2004) suggested that plant preservation occurred on a low-angled hot spring outwash apron in a distal region of sinter deposition (a geothermally influenced wetland). We favour this latter interpretation and discussed the evidence for, and implications of, growth of the Rhynie plants in geothermally influenced environments in Channing and Edwards (2009a).

**ECOLOGICAL FEATURES OF FOSSIL HOT SPRING FLORAS, MEGABIAS AND ECOLOGICAL BIAS**

Observation of the Cenozoic and Mesozoic record of hot spring floras suggests that widespread wetland species, with broad specific and generic geographical ranges, are preserved rather than hot spring specialists or endemics. Mesophytic species are captured and preserved by initial flooding by geothermal waters and as transported organs. In better-preserved and exposed hot spring deposits, these ‘innocent bystanders’ can be identified with some certainty from field relationships and chert macro- and micro-fabrics.

Broadly, in hot spring settings, plant preservation environments are confined to those where plants undergo an early and protracted period of immersion in silica-rich fluid. The boundary between preservation and taphonomic loss of plants may be as sharp as the position of a stem relative to the local water table. Plants growing in
alternately wet and dry environments (e.g. sinter aprons) are rarely or poorly preserved. Plants growing in wetland environments, conversely, are commonly preserved anatomically. These two end-member taphonomic settings, again, are readily observed in subfossil and fossil deposits. Sinter apron outcrops are essentially barren having rare prostrate plant organs preserved as external moulds. Wetland outcrops contain abundant *in situ* plants that are anatomically preserved. Even in wetlands, however, plant preservation is seen to be influenced by the local water table, and basal stem preservation dominates over preservation of areas of the stem situated above the water table.

Investigations of active silica-depositing hot spring systems reveal a strong bias towards *in situ* and permineralization-style preservation of plants in geothermally influenced wetlands (Channing and Edwards 2009a, b). This bias is clearly present in Cenozoic fossil floras, as members of the wetland family Cyperaceae and, in the Southern Hemisphere, ecologically analogous members of the Restionaceae dominate plants preserved *in situ* in Holocene (e.g. Yellowstone), Pleistocene (e.g. Taupo Volcanic Zone, New Zealand) and Pliocene to Miocene (e.g. Nevada) hot spring deposits. Based on ecological evidence from closely related extant relatives and anatomical features such as aerenchyma and extensive lacunae, wetland ecology can be demonstrated for the Mesozoic *Equisetum* and gleicheniaceous fern-dominated floras of the Deseado Massif, Argentina (Channing and Edwards 2009). The same lines of evidence, plus comparison with ecological preferences of coeval vegetation found in more widespread wetland settings, support a bias to wetland species in the Palaeozoic herbaceous lycophyte dominated flora of the Drummond Basin, Australia (Walter et al. 1998).

A number of morphological and biological features characterize the fossil record we have observed. Plants are small and herbaceous with photosynthetic stems and few or reduced leaves. In Cenozoic deposits, graminoid forms with reduced leaves are typical, and microphyllous groups characterize Mesozoic and Palaeozoic deposits. Shallow rooting is common and plants use rhizomatous and/or stoloniferous growth to cover available substrates. Vegetative reproduction appears to be more common than sexual reproduction (Channing et al. 2011). These latter two features lead to broad areas of monotypic vegetation.

Despite growth in an environment with a high water table and ample water supply, where physical drought is unlikely, plants preserved in the geothermal wetland environment show a range of xeromorphic characters and anatomical adaptations that we suggest would provide high water use efficiency (Channing and Edwards 2009a). These include, as already mentioned, small size, photosynthetic stems and reduced leaves, plus in various species, well-developed cuticle (*Eleocharis*, *Apodasmia*, *Equisetum*), hypodermis (*Eleocharis*), thickened outer walls of epidermal cells (*Eleocharis*, *Equisetum*), low numbers or reduced size of stomata (*Cyperaceae*, lycophytes), stomata protected by cover cells and/or silica pilulae (*Equisetum*) and stem hairs (*Apodasmia*). A final feature links all of the plants observed as dominant geothermal wetland species at each deposit (or at least their closest extant relatives): in life, they all take up, accumulate and biomineralize silica (Hodson et al. 2005).

In combination, the observation that life, death and anatomical fossilization of wetland plants is commonplace in the record of hot spring environments and the observation of characteristics typical of high water use efficiency lead us to a final area of discussion. Is taphonomic bias replaced by ecological and ecophysiological bias throughout the 400-million-year history of hot spring ecosystems? We suggest that the major bias towards wetland ecology is amply demonstrated. The question of ecophysiological bias arises because silica precipitating hot springs have tightly constrained hydrochemistry (Brock 1971, Channing and Edwards 2009a, tables 1 and 2 and discussion therein) and during life geothermal wetland inhabitants are immersed in fluids that have high pH, brackish salinity and contain trace concentrations of phytotoxic elements including heavy metals and metalloids (e.g. arsenic (As), mercury (Hg), antimony (Sb), thallium (Tl)). They are therefore required to have tolerance mechanisms for multiple physicochemical stresses.

Tolerance of these stresses is readily demonstrated for vegetation of Cenozoic geothermal wetlands. In the case of salinity stress, species (or genera) that are recorded in Cenozoic fossil geothermal wetlands of Yellowstone, Western USA, Iceland and New Zealand including *Eleocharis* (and various other members of the Cyperaceae), *Apodasmia* and *Equisetum* may all be observed not only in active geothermal wetlands but also in more widespread (usually oligohaline) salinity-stressed environments including coastal marshes, estuaries, saline seeps and salt lakes (Channing and Edwards 2009a). Analogy with extant species of *Equisetum*, which are common members of communities associated with saline soils and oligohaline to saline wetlands (Williams 1991; Boggis 2000; Funk et al. 2004, Purdy et al. 2005; Van der Hagen et al. 2008), appears to allow inclusion of *Equisetum thermale*, which dominates Mesozoic geothermal wetlands in the Deseado Massif within this list of halophytes (Channing et al. 2011).

In a similar vein, heavy metal and metalloid tolerance is demonstrable in the Cenozoic and Mesozoic hot spring floras by either direct observation of active geothermally influenced wetlands, other natural or anthropogenic metal-stressed environments or analogy with extant close relatives. Members of the genus *Eleocharis*, for example, naturally colonize or are transplanted into wetlands associated with abandoned metal mine workings (Flores-Tavizón 2003; Ha et al. 2009a, b, 2011a, b; Lottermoser
and Ashley 2011; Sa’ad et al. 2011; Adams et al. 2012; Olmos-Márquez et al. 2012; Alarcón-Herrera et al. 2013) where, because they are accumulators or hyperaccumulators of elements such as silver (Ag), arsenic (As), cadmium (Cd), chromium (Cr), copper (Cu), iron (Fe), indium (In), manganese (Mn), nickel (Ni), lead (Pb), antimony (Sb), tin (Sn) and zinc (Zn), they are used in phytoremediation (Rai 2009; Rai et al.). Transplanted Apodasmia similis grow successfully on tidal wetland sediments affected by elevated As concentrations (Thomsen et al. 2005). Extant species of Equisetum are commonly found in environments with high concentrations of heavy metals and grow on metal-polluted soils where they tolerate high concentrations of elements including As, cobalt (Co), Cu, Hg, Zn and Sb (Siegel and Siegel 1982; Siegel et al. 1985, Barghigiani et al. 1989, Hozhina et al. 2001, Deng et al. 2004, Chang et al. 2005, Cornara et al. 2007; Mir et al. 2007; Närhi et al. 2012).

Salinity, alkalinity and metal stress tolerance of the herbaceous lycophytes of the Late Devonian Drummond Basin wetlands are less easy to justify purely on the basis of living analogues. However, living and fossil lycophytes appear to indicate a long history of tolerance of the typical stresses present in hot spring settings. The living pantropical species Lycopodiella cernua (Lycopodium cernuum), which is often reported in coastal settings (Given 1983), also occurs in geothermal areas in New Zealand (Given 1980) and New Britain (Paijmans 1973). The species is often observed in extremely close proximity to steam vents (Powell et al. 2000) and is generally associated with acidic soils (Burns and Leathwick 1995) but also occurs in semi-aquatic settings associated with apron complexes developing around alkali-chloride hot springs (Channing 2001). Lycopodium deuterodensum and L. volubile are also reported from lower temperature (c. 20°C) thermally altered and heated soils from New Zealand geothermal areas (Burns and Leathwick 1995). Various other species amongst the three extant families of lycophytes (Isoetaceae, Lycopodiaceae and Selaginellaceae) may be found in saline and alkaline settings and growing in metal-stressed habitats. Salinity tolerance is exhibited by numerous species of Isoetes. Isoetes flaccida is an obligate brackish or salt marsh species (Light et al. 2007), L. coronandina and L. riparia grow in saline coastal and estuarine environments (Swain and Kearsley, 2001; Shukla et al. 2002), and I. muelleri tolerates brackish to saline conditions in ephemeral lakes with salinities up to 4000 mg/L (Hart et al. 1991). Species of Isoetes colonize vernal pools where they are subjected to increasing salinity stress during drying phases (Keeley and Bowes 1982).

Several species of Isoetes that are components of oligotrophic lake floras tolerate high pH, examples include I. lacustris, pH 8.6–8.9 (Szmeja et al. 1997), and I. bolanderi, pH 9.1 (COSEWIC 2006). Vernal pool species (Keeley 1990; Keeley and Zedler 1998) are subjected to seasonal and diurnal fluctuations of pH. During diurnal cycles, typical predawn pH ranges from 6 to 7. This increases by two to four pH units by early afternoon (Keeley 1990). Species of Selaginella and Lycopodium are reported as accumulators (rather than hyperaccumulators) of toxic metals and metalloids including arsenic (Meharg 2003) and aluminium (Hutchinson 1943) and are common members of plant communities associated with metal-polluted environments such as mine sites where they tolerate high concentrations of As, Cd, Cu, Hg, Mn, Ni, Pb, Sn, Ti and Zn (Zhang et al. 2000; Visoottiviseth et al. 2002; Ha et al. 2009b, 2011b; Ashraf et al. 2011). Lycopodiella cernua is considered to have potential in phytoextraction for remediation of Pb, Cu, Zn, As and Sn (Ashraf et al. 2011).

The Palaeozoic to Mesozoic record of fossil lycophytes includes evidence of salinity and alkalinity stress tolerance in both arborescent and herbaceous forms. At East Kirkton, West Lothian, Scotland, Lower Carboniferous arborescent lycophytes, represented by Lepidophloios sp., Lepidophyloides sp. and stigmatic root mats (Scott et al. 1994), inhabited the wetland margins of an alkaline, hot spring–influenced lake (McGill et al. 1994). Whilst most arborescent lycophytes are interpreted to have been intolerant of salt water (DiMichele and Philips 1985), arborescent lycophytes occupying salinity-stressed near-shore and marginal marine sites are recorded as in situ Stigmaria in bioclastic carbonates of the Lower Carboniferous, Battleship Wash Formation, Arizona (Gastaldo 1986). Hartsellea, a Lower Carboniferous cormose herbaceous lycopsid, which inhabited back-barrier marshes (Gastaldo et al. 2006) is considered to have been tolerant of brackish to saline waters. Other small, cormose forms, such as Challoneria, have been interpreted as capable of living in coastal marsh-like habitats (Greb et al. 2006) as well as more normal settings. Isoetalean lycophytes such as Pleuronea from the Triassic are regarded by many authors as halophytes that grew on salt marshes in coastal or ephemeral semi-desert environments (Retallack 1975, 1997), coastal mangroves (Krasilov and Karasev 2009) and as submerged aquatic plants of oligotrophic lakes and ponds (Retallack 1997).

Analog with specific living (or fossil) plants is not applicable to the unique early land plants of the Rhynie chert, because (perhaps with the exception of the putative lycopsid, Asteroxylon) they lack credible living close relatives. However, based on the ecology of extant plants living around silica-depositing hot springs and the many examples of younger fossil floras containing stress-tolerant plants preserved by ancient hot spring activity
detailed here, it appears quite plausible to extrapolate and suggest similar tolerance back to the Early Devonian. Anatomical adaptations amongst the various Rhynie plants to reduce evapotranspiration and increase water use efficiency were reviewed by Channing and Edwards (2009a). *Rhynia* and *Aglaophyton* both possess stomata with a substomatal cavity that widens into a substomatal channel with thickening and probable cutinization of the walls of hypodermal and cortical cells adjacent to the channel. The hypodermal cells partially underpin or cradle the guard cells, which possess pronounced stomatal ledges. The deeply seated substomatal chamber is lined with parenchymatous cells, which often possess extensions such that there is an extensive intercellular space system forming a tissue that is inferred to have been the site of photosynthesis. These hypodermal and outer cortical cell adaptations are thought to have reduced transpiration as would have the very low stomatal densities (also noted in *Nothia* and *Horneophyton*). A further adaptation to reduce water loss is seen in the sunken stomata of *Asterosyphon*, which are borne only on stems with short spiny and distal leaves in the fertile zone (Edwards et al. 1998).

Intercellular space systems of various configurations are observed in *Rhynia*, *Asterosyphon* and the zosterophylls *Venturaria* and *Trichopherophyton*, although none are as well-developed as the large aereating systems of the younger plants described above. *Nothia* and *Horneophyton* have large, modified epidermal cells (‘giant cells’) that have been interpreted to have a water storage function. The aerial axes of *Nothia* are characterized by a ‘multilayered epidermis’ of thick-walled cells that may have reduced transpiration. Some axes of *Rhynia* possess rhizoids around the entire periphery of their basal regions, which may be involved in absorption of atmospheric moisture. These adaptations, putatively to reduce water loss and hence increase water use efficiency or for water storage and absorption of atmospheric water, all suggest that either water was not consistently present in the substrate (i.e. drought), or if present may not have been readily available to the higher plants. The observation that *in situ* growth, early and rapid permineralization and therefore anatomical preservation were extremely common within the Rhynie hot spring environment suggests to us that the latter situation is more likely.

**A 400-million-year record of abiotic stress amelioration by silicon?**

Silicon-mediated alleviation of abiotic stress is a relatively well-known and widely documented phenomenon amongst living plants (Ma 2004; Liang et al. 2007; Cooke and Leishman 2011) against excessive heat (Agarie et al. 1998; Linjuan et al. 1999; Wang et al. 2005), drought (Trenholm et al. 2004; Hattori et al. 2005; Eneji et al. 2008; Nolla et al. 2012), salinity (Yeo et al. 2002; Liang et al. 2003; Zhu et al. 2004; Kaya et al. 2006; Romero-Aranda et al. 2006; Xu et al. 2006; Tuna et al. 2008; Chen et al. 2010; Karmollachaab et al. 2013; Mateos-Naranjo et al. 2013) and toxic concentrations of metals and metalloids (e.g. Al (Cocker et al. 1998); Cu, Sn, Fe (Neumann and zur Nieden 2001); As (Guo et al. 2005); Mn (Liang et al. 2007); Zn, Cd (da Cunha et al. 2008); Sb (Huang et al. 2012); Pb (Li et al. 2012) and Cr (Ali et al. 2013)). To date, such studies have concentrated on agricultural species of angiosperms (rice, wheat, barley, maize, sugar cane, sorghum, cucumber, tomato) and turf grasses. However, Cooke and Leishman (2011), in a recent review of silicon amelioration of plant stress, concluded that ‘it seems inevitable that silicon will also prove to be an important element in abiotic stress alleviation in a range of taxa in natural plant communities’. Indeed, a recent study of the salt marsh monocot *Spartina densiflora* has revealed that silicon plays a significant role in salinity tolerance in this wetland halophyte (Mateos-Naranjo et al. 2013).

There are numerous suggested mechanisms by which silicon alleviates stress. Silicification of leaf and stem surfaces (biomineralization ofopal phytoliths) is considered to significantly decrease water loss by transpiration thus reducing both real drought (water deficiency) and salinity-induced physiological drought stress (Ma 2003). The key mechanisms of silicon-mediated alleviation of toxic element stresses (reviewed in Ma 2004; Liang et al. 2007; Channing and Edwards 2009a; Cooke and Leishman 2011) include (1) stimulation of antioxidant systems in plants; (2) complexation or coprecipitation of toxic metal ions with Si; (3) immobilization of toxic metal ions in the soil; (4) modification of element uptake processes; and (5) compartmentation of metal ions within plants.

Close extant relatives of the plants we find preserved in geothermal wetlands from the Cenozoic (Cyperaceae, Restionaceae, Equisetaceae), Mesozoic (Equisetaceae and ferns allied to the Gleicheniaceae) to Late Devonian (lyco-phyes) accumulate silicon in life and biomineralize to form phytoliths (Prychid et al. 2004; Briggs and Linder 2009; Mazumdar 2011) and inter- and intracellular silica bodies in tissues other than the epidermis (Prychid et al. 2004). Silicon is considered an essential element for *Equisetum* growth, whilst for other higher plants, it is considered only a beneficial element (Chen and Lewin 1969; Hoffman and Hillson 1979). In a meta-analysis of mean relative shoot Si concentration of 735 plant species (Hodson et al. 2005), members of the genera *Eleocharis* (Cyperaceae), *Equisetum* (Equisetaceae) and the lycophytes *Lycopodium* and *Selaginella* ranked as some of the highest accumulators of silicon amongst higher plants. A likely general consequence of in-life deposition of silicon is to increase plant preservation potential.
We do not believe that it is coincidence that hot spring floras both extant and fossil are dominated by silicon accumulators and that the list of stresses that silicon has been demonstrated to alleviate encompasses all of the major stresses associated with growth in hot spring wetlands. We suggest instead that a long-standing ecophysiological resolution to the stresses inherent to geothermal wetlands is provided by the silicon-rich hydrochemistry of the environment itself.

CONCLUSIONS

Hot spring habitats are strongly affected by ecosystem partitioning. The wetland plants most commonly preserved by hot spring activity appear to be outcompeted in ‘less stressed’ environments and are usually absent from contemporaneous mesophytic communities. Conversely, mesophytic plants are always excluded from geothermal wetlands, the dominant environment of plant preservation. As a result, the plant fossil record associated with silica-depositing hot spring systems is strongly biased towards wetland plants.

The dominant plants of hot spring floras from Cenozoic to Late Devonian times provide clear evidence of both anatomical and ecophysiological adaptation to life in geothermal wetlands. However, plant endemism and hot spring specialization in these unusual environments are not supported by available data. Instead, evidence supports pre-adaptation of plants 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. An implication arising from these observations is that hot spring floras are not representative of coeval regional floras as a whole.

The fossil floras of ancient hot springs preserve a long record of higher plant stress tolerance. The c. 400-million-year record of life, death and preservation in geothermally influenced wetland settings suggests the early advent of stress alleviation mechanisms for excessive heat, salinity, alkalinity and heavy metal or metalloid stress. Whilst anatomical adaptations that improve water use efficiency (e.g. small size, photosynthetic stems, reduced leaves, well-developed cuticle, modified stomata) have undoubtedly had a major role in stress reduction, silicon, an element that occurs in abundance in such hot spring settings and that is known to ameliorate multiple forms of abiotic plant stress, may have a long-standing role in ecophysiological reduction in plant stress.

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