An introduction to the Rhynie chert

Russell J Garwood[1,2] [iD], Heather Oliver[3] and Alan R T Spencer[2,4] [iD]

[1]School of Earth and Environmental Science, University of Manchester, Manchester, UK; [2]Earth Sciences Department, Natural History Museum, London, UK; [3]Sharples School, Hill Cot Road, Astley Bridge, Bolton, UK and [4]Department of Earth Sciences and Engineering, Imperial College London, London, UK

Abstract

The terrestrialization of life has profoundly affected the biosphere, geosphere and atmosphere, and the *Geological Magazine* has published key works charting the development of our understanding of this process. Integral to this understanding – and featuring in one of the *Geological Magazine* publications – is the Devonian Rhynie chert Konservat-Lagerstätte located in Aberdeenshire, Scotland. Here we provide a review of the work on this important early terrestrial deposit to date. We begin by highlighting contributions of note in the *Geological Magazine* improving understanding of terrestrialization and Palaeozoic terrestrial ecosystems. We then introduce the Rhynie chert. The review highlights its geological setting: the Caledonian context of the Rhynie Basin and its nature at the time of deposition of the cherts which host its famous fossils. There follows an introduction to the development of the half-graben in which the cherts and host sediments were deposited, the palaeoenvironment this represented and the taphonomy of the fossils themselves. We subsequently provide an overview of the mineralization and geochemistry of the deposit, and then the fossils found within the Rhynie chert. These include: six plant genera, which continue to provide significant insights into the evolution of life on land; a range of different fungi, with recent work starting to probe plant–fungus interactions; lichens, amoebae and a range of unicellular eukaryotes and prokaryotes (algae and cyanobacteria); and finally a range of both aquatic and terrestrial arthropods. Through continued study coupled with methodological advances, Rhynie fossils will continue to provide unique insights into early life on land.

1. Introduction

Terrestrialization – the colonization of land by living organisms – was a major event in the history of life, with profound implications for the chemistry (Kenrick *et al.* 2012) and sedimentology (Davies & Gibling, 2010) of our planet, and of course, for the history of life (Labandeira, 2005) and macro-evolutionary patterns (Deline *et al.* 2018). The adaptation of life to continental environments is a topic of active research, but is one with a significant history, in which the *Geological Magazine* has played an important role. Indeed, this publication has charted our knowledge of terrestrialization and early complex land ecosystems from its infancy, and continues to provide regular new insights in this arena today. As such, a contribution on early terrestrial ecosystems is a fitting topic for this special issue. There have been multiple recent reviews and other significant works on terrestrialization (Vecoli *et al.* 2010; Garwood & Edgecombe, 2011; Kenrick *et al.* 2012; Selden, 2012; Dunlop *et al.* 2013; Rota-Stabelli *et al.* 2013; Lozano-Fernandez *et al.* 2016) which provide a comprehensive overview of the topic. Instead of duplicating these, here we focus on a singular Lagerstätte, the Rhynie chert. This early Devonian (407 Ma) site provides key insights into the origins of life on land, and the *Geological Magazine* published one of the first papers with insights into its terrestrial arthropod fauna (Hirst & Maulik, 1926). It is also a century since the first description of fossils from the site (Edwards *et al.* 2018). This anniversary has recently been celebrated with a special issue providing a range of new insights into Rhynie fossils (Edwards *et al.* 2018). Given the depth of research into the site from this, earlier special issues (Trewin & Rice, 2004) and myriad stand-alone works, there is scope for a review article introducing the geology of the Rhynie chert, and its fauna and flora. Here we provide such a review: we first highlight the historical contributions in the *Geological Magazine* to our knowledge of early terrestrial ecosystems, and study of the Rhynie chert. We then introduce the geology of the Rhynie chert Lagerstätte, summarizing the work to date, before providing an overview of the flora and fauna of the site. Our aim is to provide a synthesis of the research to date to form a context and framework for further exploration of the literature, rather than an exhaustive account of all published studies: for the fossils especially, a comprehensive review is beyond the scope of this paper.

2. *Geological Magazine* and terrestrialization

Geological Magazine has a history of significant contributions towards our knowledge of terrestrialization, most notably that of animals. A significant factor in this was the body of work

(and influence) of Henry Woodward, editor of the publication from 1865 to 1918 (Geological Magazine, 1921). Whilst the focus of Woodward's work was Crustacea (Woodward, 1868, 1870; Jones & Woodward, 1899), his contributions also encompassed (what we now recognize to be) chelicerate phylogeny (Woodward, 1913a), the origins of life (Woodward, 1874) and the then recently discovered *Iguanodon* (Woodward, 1885). Another significant aspect, especially of his later work, and the subject of a large number of papers in the *Geological Magazine*, was Palaeozoic terrestrial arthropods. These papers included: an overview of terrestrial deposits throughout the Phanerozoic (Woodward, 1871c); and myriad insights into Carboniferous myriapods (Woodward, 1871a, 1873, 1887a), arachnids (Woodward, 1872, 1873) and insects (Woodward, 1887b, c, 1906) including an early report of a juvenile insect (Woodward, 1913b), albeit misidentified as a branchiopod (Rolfe, 1967). A key paper reported one of the first and best preserved trigonotarbid arachnids (Woodward, 1871b) which has gone on to be the focus of further studies (Pocock, 1902; Garwood *et al.* 2009; Dunlop & Garwood, 2014). This in turn attracted other workers in this area. Examples include: further works on Carboniferous arachnids (Pocock, 1903a, b; Gill, 1911); reports of Carboniferous deposit near Colne with both arachnid and myriapod fossils (Bolton, 1905); documentation of Carboniferous myriapods from the Sparth Bottoms deposit (Baldwin, 1911; Jackson *et al.* 1919) and elsewhere (Brade, 1928); an overview of Palaeozoic insects (Brongniart, 1885), and a note on the similarities between European and American fossils in this group (Scudder, 1876); arachnids, myriapods and enigmatic, probably terrestrial, arthropods from the Tyne Coalfield (Gill, 1924) that have also resulted in further study (Dunlop, 1998; Garwood & Sutton, 2012; Jones *et al.* 2014); and Palaeozoic plant taphonomy (Kindle, 1913) and palaeobotanical discoveries (Arber, 1907, 1912, 1913). These papers represent a significant body of work on terrestrial fossils at a time when the study of Palaeozoic land ecosystems was fragmented.

In the decades since these contributions, *Geological Magazine* has continued to publish a range of works on early land ecosystems and related topics. Examples include: Palaeozoic palaeobotanical papers such Silurian macroscopic plants (Edwards & Rogerson, 1979), Silurian–Devonian biostratigraphy within the Anglo-Welsh Basin (Wellman *et al.* 1998), British coal measures flora (Cleal, 1986), and Devonian lycopsids in Argentina (Cingolani *et al.* 2002), China (Xu & Wang, 2008) and Colombia (Berry *et al.* 2000); palynology studies with implications for the timing of terrestrialization in multiple groups (Marshall, 1991) and Silurian biostratigraphy (Gray *et al.* 1992); Ordovician traces potentially recording terrestrial animals (Johnson *et al.* 1994) and Early Devonian traces recording myriapods or relatives (Smith *et al.* 2003); Palaeozoic terrestrial arthropods including arachnids (Dunlop & Horrocks, 1997) and insects (Jarzembowski & Schneider, 2007); a new arthropod fauna from the Westhoughton open-cast coal pit (Anderson *et al.* 1999); and topics in Palaeozoic correlation (Rickards, 2000; Cocks *et al.* 2010).

The *Geological Magazine* was home to descriptions of some of the first animals reported from Rhynie. The earliest Rhynie arthropods were described by Hirst (1923) who documented specimens now thought to represent two arachnid orders: mites and trigonotarbids, preserved in exceptional detail. A follow-up paper was published three years later in the *Geological Magazine* by Hirst & Maulik (1926) who provided further descriptions. In particular, this contribution highlights some exceptionally preserved trigonotarbids of the genus *Palaeocharinus*, including details of the lateral eyes of these extinct

arachnids, the first reports of taxa now known to represent the enigmatic euthycarcinoid arthropods, and the first hexapods known from the site. The latter, in particular, are of note, being the oldest record of Hexapoda in the fossil record (Dunlop & Garwood, 2018). *Rhyniella praecursor*, a springtail (collembolan hexapod), has been the subject of significant research since its first publication (Tillyard, 1928; Scourfield, 1940; Whalley & Jarzembowski, 1981; Greenslade & Whalley, 1986), whilst what has since been named as *Rhyniognatha hirsti* potentially represents the earliest winged insect (Engel & Grimaldi, 2004; but see also Haug & Haug, 2017). As such, this paper was a significant milestone in the study of early terrestrial arthropods, and a fitting basis for the current review.

3. The Rhynie chert: overview

The Devonian Rhynie chert is a Konservat-Lagerstätte (a deposit renowned for its exceptional preservation of fossilized organisms) located in Aberdeenshire, Scotland, preserving an important early terrestrial ecosystem, including plant, fungi, bacteria and arthropod fossils (Fig. 1). The cherts (siliceous rocks) in which the fossils are found are present as lenses within sandstone and mudstone alluvial plain laid down in an intermontane basin, and are related to localized hot-spring activity. The exact age of the cherts is uncertain: spores within the shales indicate that they date from the middle Pragian to lower Emsian stages of the Lower Devonian (Wellman, 2006). Radiometric dates are in broad agreement with this, placing the Rhynie chert as either 407.6 ± 2.2 Ma or 411.5 ± 1.3 Ma (initially reported in Mark *et al.* (2011) and Parry *et al.* (2011); modified and further discussed in Mark *et al.* (2013) and Parry *et al.* (2013) respectively). The site was discovered in 1912 by William Mackie, a local physician with an interest in geology, who unearthed the first chert blocks in local fields and stone walls. Trenching followed, and a classic five-part work by Kidston & Lang (1917, 1920a, b, 1921a, b) was the start of a century's study on the site to date. Edwards *et al.* (2018) provide a history of study of the Rhynie chert.

The fossils from Rhynie present a unique insight into life on land during the Devonian. Rhynie is valuable not just because of the exceptional preservation, but also because the terrestrialization of plants and arthropods occurred in the early Palaeozoic (Kenrick *et al.* 2012). It therefore provides an insight into these ecosystems fairly early in their history. Fossils are preserved in permineralized silica from sinter deposits surrounding hydrothermal vents. This amorphous silica derives from water saturated in silica from hot springs, which has, over time, altered to cryptocrystalline chert. In the process of doing so, it has three-dimensionally preserved a wide range of organisms living in this environment and potentially surrounding areas (Rice *et al.* 1995). The preservation of terrestrial hydrothermal deposits is rare, making Rhynie an important geological site for studying fossil epithermal environments as well as its wider palaeontological importance (Fayers & Trewin, 2003).

4. Geological setting

The Rhynie chert is located within the 21 km by 3 km Rhynie outlier of the Old Red Sandstone (Trewin & Rice, 1992; Rice *et al.* 1995). The Rhynie Cherts Unit (RCU) is hosted by the Dryden Flags Formation (Figs 1, 2; Rice *et al.* 2002; Rice & Ashcroft, 2003; Fayers & Trewin, 2004).

The chert was deposited within the Devonian (Lower Old Red Sandstone) Rhynie Basin. This narrow basin is north–south oriented, is faulted to the west, and the margins at the northern
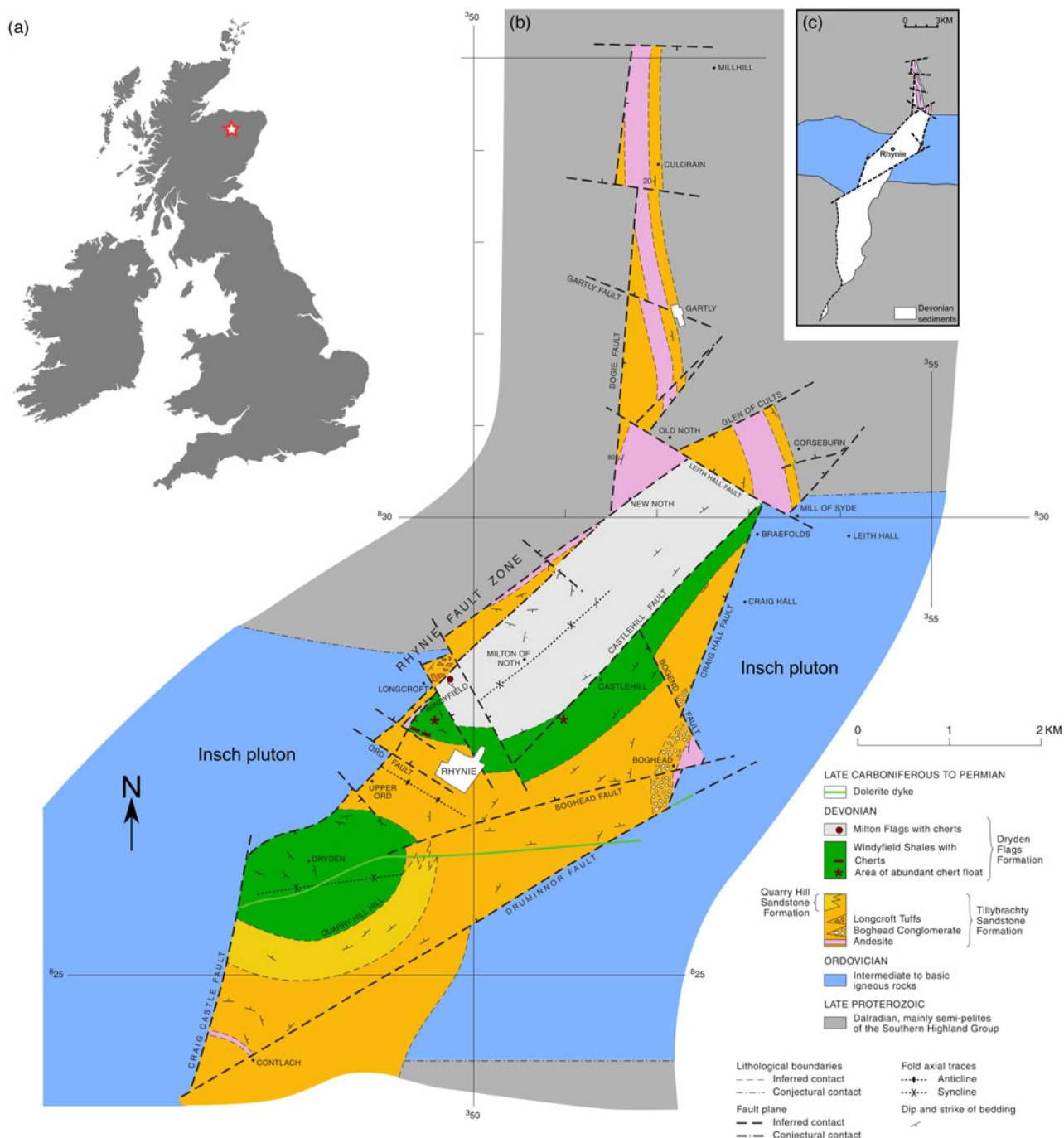
Fig. 1. (Colour online) The geological setting of the Rhynie cherts. (a) The location of Rhynie on a UK map. (b) A detailed map showing the northern half of the Rhynie Basin where the cherts are located. (c) An overview map of the basin as a whole showing its southern extent. After Rice & Ashcroft (2003).

end of the basin are primarily fault-controlled, with evidence of strike-slip movement (Rice & Ashcroft, 2003), whilst towards the southern end of the basin the sediments are unconformable with the basin at the eastern margin (Fig. 1). In this region, and across the basin as a whole, the prevailing dip of the sediments is to the west, between 15 and 35°, although this is disrupted by open folding in the area (Rice et al. 2002). As such, the basin is a half-graben. The basement lithology is the Ordovician Boganclogh intrusion (Busrewil et al. 1973), which primarily comprises quartz–biotite–norite (an orthopyroxene-dominated

gabbro) with minor serpentinite. This is intruded into the upper Proterozoic Dalradian metaturbidites of the Southern Highland Group. Associated with a major sinuous regional faulting at the west (the Rhynie Fault Zone, or RFZ) is a remnant hot-spring system (Trewin & Rice, 1992; Rice et al. 1995, 2002). The RFZ extends for 1.5 km and is 400 m wide in places (Rice et al. 1995). It dips eastward at 35°, and is offset by cross-faults down-throwing to the north (Rice & Ashcroft, 2003).

A silicified breccia, along with slivers of basement and fault gouge, is present along much of this contact (Rice et al. 2002).
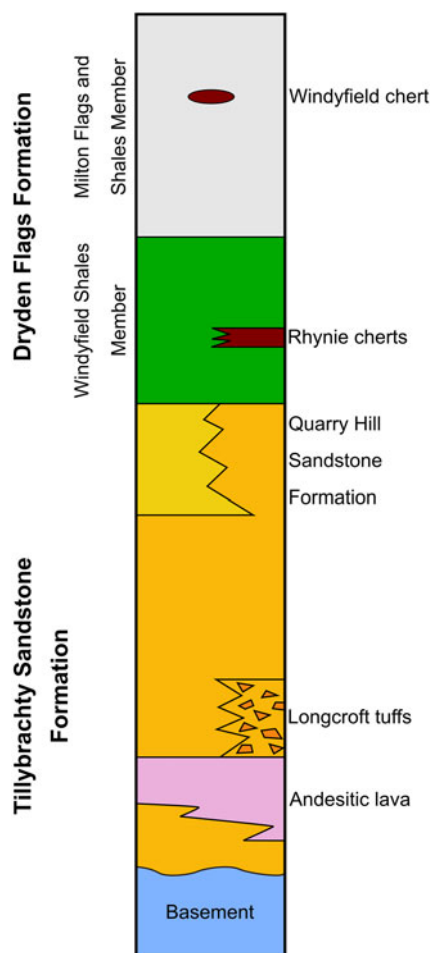
Fig. 2. (Colour online) Generalized stratigraphic column for the Rhynie Basin, focusing on the northern half (after Rice & Ashcroft, 2003; Parry et al. 2011).

Fault-bounded slivers of Devonian sedimentary rocks and andesite occur within the RFZ, adjacent to the RCU (Mark et al. 2011), which show similarities to rocks stratigraphically below the chert-bearing succession, exposed at the eastern extent of the basin (Rice et al. 2002). These blocks are hydrothermally altered, with two primary alteration facies: K-feldspar–quartz–illite, and illite/smectite–quartz–K-feldspar–chlorite–calcite (Baron et al. 2003). The andesitic blocks host the former facies, which contains high levels of As and Au (100 ppb; Rice et al. 1995; Rice et al. 2002; Mark et al. 2011). The blocks are crossed by a number of quartz–K-feldspar veins, mostly oriented N–S to NE–SW, and dipping eastward at 35°, aligned with the RFZ, thus suggesting that the veins are related to fracturing during the development of the Rhynie Basin (Mark et al. 2011).

The lowest sediment in the Rhynie Basin stratigraphy is a sandstone formation. Based on cores, Rice et al. (2002) suggested that this White Sandstones Unit may correlate with the Quarry Hill Sandstone, the uppermost unit of the Tillybrachty Sandstone Formation (Fig. 2; Rice & Ashcroft, 2003). Fossils are found within the RCU. This is within the dark, muddy sandstones and laminated shales, which form the Windyfield Shales Member of the Dryden Flags Formation (Rice & Ashcroft, 2003).

The Rhynie fossils are found within a single discrete, 35 m thick sedimentary package – the RCU –– that Rice & Ashcroft (2003) report as occurring towards the base of the Windyfield Shales Member,

whereas Rice et al. (2002) suggest it separates the Upper from the Lower shales within this member (Fig. 2). The Windyfield Shales Member comprises over 50 chert beds, with interbedded shales, carbonaceous sandstones and locally abundant tuffaceous debris (Rice et al. 2002). The unit is continuous for 80 m down dip and 90 m along strike, although individual chert beds are not continuous over distances greater than 20 m and show rapid lateral variation (often over less than 1 m; Trewin & Wilson, 2004). The uneven nature of the cherts, which were originally deposited as sinters resulting from hot-spring activity, may result from regular flooding of a northward-flowing axial river (Trewin, 1994, 1996). This would have deposited the interbedded sands and muds, and potentially precluded sinter deposition periodically through dilution reducing the silica content of hot-spring water (Trewin & Wilson, 2004). Retreating flood waters could have further exacerbated an uneven topography by allowing erosion of the sandy deposits. The chert beds preserve evidence of both subaqueous and subaerial environments. Chert 'pods' of less than 1 m lateral extent, and exhibiting a 'clotted' texture, were deposited subaerially, with various plant tissues, arthropods and spores preserved amongst the bacterially mediated clots (Trewin et al. 2003). The silica may also be directly precipitated onto the cuticle of plant surfaces as an amorphous bacterial coating, similar in composition and appearance to the clotted texture. Subaqueous environments are represented by filamentous chert meshworks. These most commonly form: laminated sheets between plant stems, which provided support to the plants; irregular meshworks with clots, growing within an organic mush; and straight filaments crossing voids created by gas bubbles or left after the decay of plant stems (Trewin et al. 2003). The clasts within some chert breccias located at the basin margin are coated with many layers of chert to form a ball breccia. This texture resembles geyserite, found at or near the surface of hot-spring systems (Rice et al. 1995).

Overlying the Windyfield Shales is the Milton Flags and Shales Member which contains the Windyfield chert (Fig. 2) – another important lithified wetland ecosystem. This is stratigraphically younger than the other cherts (including the Rhynie chert), but not significantly so. It is laterally separated from the Rhynie chert by a distance of c. 700 m and a fault running NW–SE, and preserves subtly different environmental conditions (Fayers & Trewin, 2004).

5. Development of the Rhynie Basin

The Caledonian Orogeny provides the geological context for the Rhynie outlier, having created the dominant metamorphic assemblages and structures in the upper Proterozoic Dalradian metaturbidites that form the basement of the outlier at its northern and southern extents. The Caledonian Orogeny initiated in the Early Ordovician with the microcontinent Avalonia separating from northern Gondwana. Crust beneath the Iapetus Ocean was subducted beneath Avalonia which drifted northwards towards a more northerly continent, Laurentia. The key event in the Rhynie area pre-dated the collision of Avalonia with this continent: the c. 475–460 Ma Grampian event resulted from convergence between a shallow-water carbonate shelf (the Laurentian margin; Lambert & McKerrow, 1976; Strachan et al. 2003) and a volcanic arc (Dewey & Shackleton, 1984; Draut et al. 2009; Strachan, 2012). The arc–Laurentia collision resulted in the overthrusting of an exotic ophiolite nappe, and deformation plus associated Barrovian metamorphism of the Moine and Dalradian Supergroups (Dewey & Shackleton, 1984; Strachan et al. 2003). The Rhynie outlier is a part of the resulting Grampian terrane (Stephenson, 2000). Associated with the Grampian Event was widespread intrusion of gabbroic and granitic rocks into the
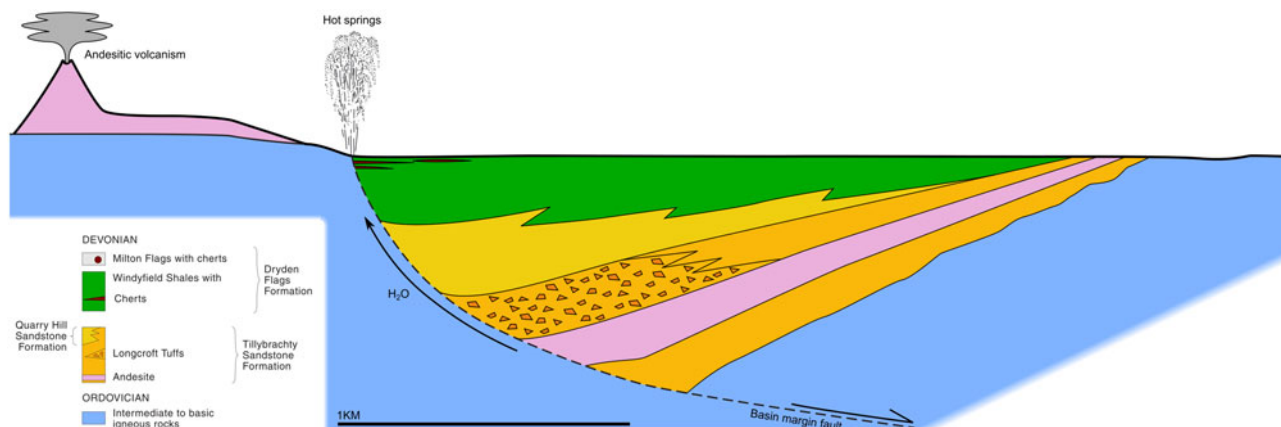
Fig. 3. (Colour online) A schematic cross section of the Rhynie basin during hot-spring activity, and the deposition of the Dryden Flags Formation.

Dalradian metasediments. In Aberdeenshire, the tholeiitic Newer Gabbros were intruded at *c.* 470 Ma, coincident with the peak of regional metamorphism, and overprinted the regional Barrovian zones with sillimanite contact metamorphism (Droop & Charnley, 1985; Stephenson, 2000). Many plutons in Aberdeenshire follow the tholeiitic differentiation trend, as crystals within the chamber settle and form cumulate layers (Strachan et al. 2003). Two of these intrusions possess faulted contacts with the Rhynie outlier, thus comprising the igneous portions of the basement. To the east lies the largest of the Aberdeenshire intrusions, the Insch Pluton, a 43 km long and 8 km wide intrusion of the 'Younger Gabbros' (Clarke & Wadsworth, 1970; Lambert & McKerrow, 1976; Stephenson, 2000). The westerly extension of the Insch Pluton, found to the west of the Rhynie Basin, is the Boganclogh Mass. By the Late Silurian, the Iapetus Ocean had closed, and Laurussia had formed through the collisions of Avalonia, Laurentia and a third continent, Baltica (Stephenson, 2000), which collided with Laurentia in the *c.* 435–420 Ma Scandian event (Kinny et al. 2003; Strachan et al. 2003). Whilst this event caused widespread ductile thrusting and folding of the Moine Supergroup and development of the Moine Thrust Zone, the Grampian terrane was located away from the main collision and did not undergo significant deformation.

The Rhynie Basin formed in the Early Devonian, at *c.* 25° S, on the SE margin of Laurussia (Wellman, 2018). In excess of 200 m of sediments and limited extrusive volcanics accumulated within a rapidly subsiding basin located within the Caledonian orogenic belt. Within this intermontane basin was a northward-flowing river, subject to regular flooding, resulting in fluvial and overbank deposits. The Rhynie Basin represents a half-graben with a low-angle listric fault zone at the western margin and a bounding unconformity to the east (Rice et al. 2002). This could have resulted from regional extension, or alternatively as a pull-apart basin above a releasing bend or stepover within a strike-slip fault zone (Rice & Ashcroft, 2003; Parry et al. 2011). The maximum depth at the centre of the basin is 600 ± 50 m (Rice et al. 1995).

The hot springs, the source of the silica that formed the Rhynie chert, represent the late stages of andesitic volcanism. Their location was controlled by the intersection of the RFZ with the northern contact of the Boganclogh Mass (Parry et al. 2011) (Fig. 3). This fault system became the main conduit for the hydrothermal fluids of the hot-spring system (Rice et al. 2002). The magma (basaltic-andesite) providing the heat for the spring system likely formed due to decompression melting of the upper mantle as

a result of the Early Devonian formation of the Rhynie Basin (Parry et al. 2011): pull-apart basins, particularly those formed during transtension, produce deep conduits for mantle-derived magmas (Tosdal & Richards, 2001). A plausible source of the fluids for the hydrothermal activity was surface-derived meteoric waters, with evidence for some limited fluids derived from a magmatic source (Rice et al. 1995; Baron et al. 2003; Channing, 2018).

6. Palaeoenvironment of the Rhynie chert

The Tillybrachty Sandstone Formation was deposited during regional extension and initiation of the basin. The clastic sediments were dominantly locally derived conglomerates and sandstones (Rice et al. 2002), with many clasts originating from the basement rocks of the Boganclogh Mass. The sediments are moderate to poorly sorted, and lack cross bedding or evidence of well-developed channels. Rare caliche nodules are present and indicative of a sub-aerial semi-arid environment, and a poorly developed soil profile (Trewin & Rice, 1992). The sedimentological evidence points towards rapid and sporadic deposition, with the sandstones and conglomerates deposited by a small alluvial fan (Rice et al. 1995) up to 1 km wide. Sandstones with floating pebbles may be evidence of deposition by non-channelized flash floods, whereas rare cross-bedded facies preserve evidence of poorly channelized flows (Trewin & Rice, 1992).

Above the locally derived sandstones and conglomerates lies a discrete andesitic lava flow. The flow is up to 20 m thick and is traceable along strike for 350 m. Wherever the lava is exposed, it is overlain by sediments containing volcanic clasts not observed below the lava (Trewin & Rice, 1992). The source of this lava was likely volcanic centres at the margins of the basin, with lava production controlled by movement on major faults (Rice et al. 1995; Rice et al. 2002). Above the lava, tuffaceous beds are common and decrease up stratigraphy (Trewin & Rice, 1992).

Deposition of the Quarry Hills Formation, and later Dryden Flags Formation, occurred whilst the tuffs were erupted (Rice et al. 2002). The Quarry Hills Formation consists of fine-grained sandstones and shales, with laminations and beds centimetres to millimetres thick (Trewin & Rice, 1992), deposited by a fluvial system running along the basin axis (Rice et al. 2002). These beds contain varying quantities of volcanic debris, with highly vesicular volcanic clasts occurring as distinct, oversized grains within the sandstone. Only a few beds consist entirely of tuffaceous material.
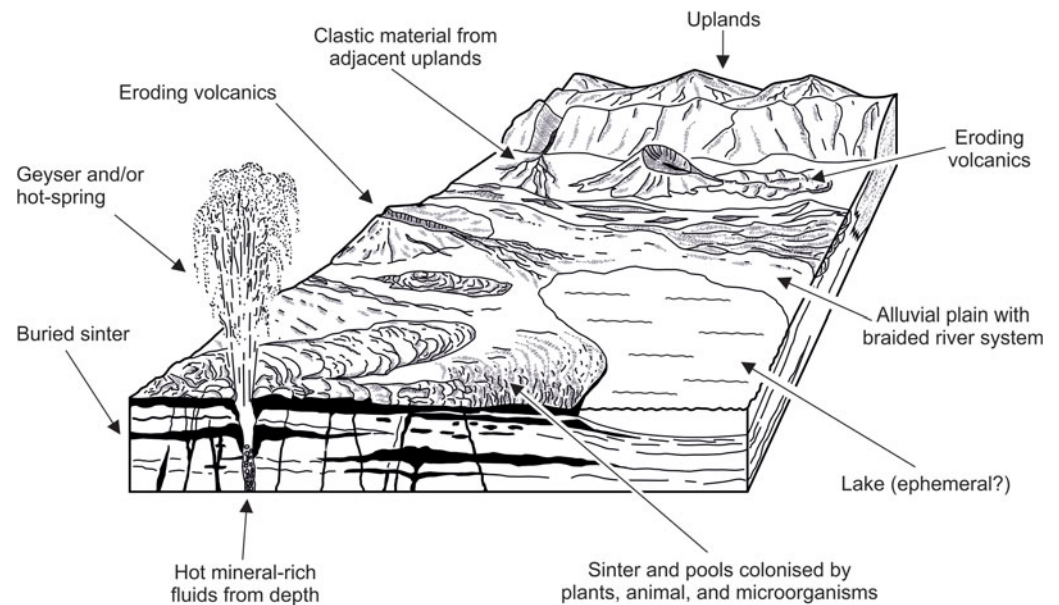
Fig. 4. (Colour online) Palaeoenvironmental reconstruction of the Rhynie chert locality. Adapted from Trewin (1994) and Preston & Genge (2010).

Some tuffaceous beds show normal grading and evidence of airfall deposition, though most are parallel and ripple-laminated from water transport after erosion from nearby tuff cones (Trewin & Rice, 1992).

The muddy sandstones of the Dryden Flags Formation were deposited by ephemeral lakes on an alluvial plain (Fig. 4). It is possible that the sediments were deposited on the floodplains of the Quarry Hills Formation (Rice *et al.* 2002). Hot-spring activity occurred late in the basin development during the deposition of this formation. Hydrothermal fluids migrated along the basin margin fault zone from a source below and to the southeast of the basin, heavily altering lithologies in the hanging wall. The deposition of the cherts within the lacustrine shales and sandstones indicates that sinter deposition interrupted the usual alluvial plain depositional processes (Rice *et al.* 2002) by disrupting drainage networks as silica was deposited (Trewin & Wilson, 2004) and forming small pools (Fig. 4; Powell *et al.* 2000). Desiccation cracks in the shales indicate periods of subaerial exposure of the mudflats, possibly due to seasonal variation in sediment supply (Trewin & Rice, 1992; Rice *et al.* 1995, 2002). Periodic flooding of the alluvial plain would likely cause breaks in the colonization of bacteria and deposit the sandstones and shales between cherts. Laminated cherts are evidence of deposition in sinter terraces (Powell *et al.* 2000), and a loose chert block has been found with a texture characteristic of deposition in the splash zone around a hydrothermal spring (Trewin, 1994). There is further evidence for the presence of runoff streams, wet sinter aprons with cyanobacteria colonies, and wetland areas related to hot-spring outwash (Channing & Edwards, 2009*b*). Plants are thought to have primarily colonized the sandy substrate at the edge of the lakes (Trewin & Rice, 1992), though they would also colonize bare sinter (Fig. 4; Powell *et al.* 2000).

Plant axes have been found up to 15 cm in length, with growth support provided by bacterial mats (Trewin *et al.* 2003). Freshwater-filled hollows and pools would also house plants, as well as arthropods such as *Palaeonitella* and *Lepidocaris* (Powell *et al.* 2000; Rice *et al.* 2002). A modern analogue for the Rhynie chert depositional environment is Yellowstone National Park, USA, suggesting preservation of plants at temperatures ≤ 45°C in brackish water with a neutral to alkali pH (6.5–9.1 at Yellowstone) and containing silica at or above the saturation point (Channing & Edwards, 2009*a*, *b*).

7. Taphonomy

The exceptional preservation of the Rhynie chert fossils makes them particularly valuable as a record of the early land biota. For example, the plant fossils preserve cellular details in three dimensions (Hetherington & Dolan, 2018*a*, *b*; Strullu-Derrien *et al.* 2018). The most exceptional preservation is indicative of extremely rapid silicification (Trewin *et al.* 2003), as supported by preserved fine structures in the soft tissues (book lungs) of a trigonotarbid arachnid (Claridge & Lyon, 1961), spores in the process of germination (Lyon, 1957) and the release of sperm from a plant gametophyte (Remy *et al.* 1993). Such fossils are an exception in the deposit, and it is likely most of the sinters accumulated at a rate similar to that of modern-day hot spring systems (Trewin *et al.* 2003): for example, modern sinters at Yellowstone National Park accumulate at 1–5 cms per year (Channing, 2018). As a result, fossils from the Rhynie chert are found in varying states of decay, even within a single bed (Powell *et al.* 2000). Because both decaying leaf litter and *in situ* plants are found within the Rhynie chert, a single silicification event might record a transect through a full community of living plants and leaf litter above a primitive soil (Powell *et al.* 2000). Similarly, arthropod preservation varies from complete individuals with cuticular structures such as setae/trichobothria still attached and internal anatomy preserved (Garwood & Dunlop, 2014) through to moults and cuticular fragments. The main factors dictating the quality of preservation are the degree of silicification, and the amount of decay and disarticulation that occurred prior to silicification. Decay resulted from fungi (Trewin, 1996), and also probably bacteria, as saprotrophs have been reported (Powell *et al.* 2000). In general, fossils occur in cooler areas of the hot-spring system.

Taphonomic processes in Rhynie are best understood in the macroflora, which is outlined first herein, followed by the fauna. Living plants were not always completely silicified, in which case decay occurred after partial preservation. Because the outer cortex and xylem strands are more resistant to decay than the centre, hollow fragments of plant material are commonly found partially filled with sediment (Trewin, 1996). The best-preserved plants were flooded with hot-spring waters whilst still in life position growing on the sandy substrate (Powell *et al.* 2000). Silicification progressed from the outside of the stem inwards, typically beginning with the

coating of plant material by amorphous silica from the hot-spring waters. Individual plant cells were progressively filled or the contents replaced by silica, continuing until the stem was completely silicified (Trewin, 1996). After burial, this amorphous silica is converted to chert, preserving the plant structure (Powell *et al.* 2000). Preservation through silica deposited directly onto the stem is most common, but some plants were only preserved after bacterial colonization of exposed surfaces (Trewin *et al.* 2003). Bacterial mats growing between plants may also have assisted in the silicification of plants in life position (Trewin *et al.* 2003).

Silicification of plants occurred in three main settings: after episodic surface flooding; from violent geyser eruptions; or from more sedate overflows from pools that form sinter terraces that disrupt and alter the direction of water flow. This flooding may also carry uprooted plants: plant axes have been found with a preferred orientation posited to be caused by the flow (Trewin, 1996) having been deposited as allochthonous material in sinter beds (Powell *et al.* 2000). Additionally plants likely colonized vents abandoned due to changes in distribution channels, which were subsequently flooded (Trewin, 1996). Silicification may also have occurred on the banks of hot-spring pools, where temperatures were cool enough to sustain plant growth on the banks. Around these pools, plants would take up siliceous water, increasing preservation potential (Powell *et al.* 2000). Silicification due to subsurface permeation also occurred (Trewin, 1996).

Arthropods in the Rhynie chert are preserved as complete animals and moults, or as disarticulated whole or fragmented elements (Anderson & Trewin, 2003). The *in situ* arthropods are often extremely well preserved, with some showing setae, fine cuticular structures such as slit sense organs, gut contents (euthycarcinoids, myriapods) or respiratory organs (trigonotarbids; Dunlop & Garwood, 2018). Fragmentary remains represent allochthonous debris, and are associated with spores, plant fragments and occasional clastic grains. In part through comparison to the Windyfield cherts, the best-preserved arthropods were thought to be inhabitants of small, ephemeral freshwater pools within the hot-spring system, and were likely preserved when hot siliceous fluids percolated through the cool pools. The siliceous water then cooled and the silica precipitated, coated and permineralized organisms and their remains. As the aquatic organisms (such as Lepidocaris, a crustacean) already inhabited these freshwater pools, they were more likely to be preserved than terrestrial organisms that must fall into the pool before silicification (Anderson & Trewin, 2003). The entrapment of arthropods may have been helped by the presence of mulm, an organic-rich product of decay found at the base of freshwater pools (Anderson *et al.* 2003). In areas where the siliceous fluids flowed as thin sheets over subaerial sinters, arthropod preservation is poorer and disintegration of the cuticle is more likely. This may be due to drying and brittle fracturing from exposure during times of low fluid flow (Anderson & Trewin, 2003). Arthropod remains are typically found in two distinct chert textures: sections with dense accumulations of plant material from flooding of *in situ* plant growth or plant litter; or sections of clear chert matrix with rare plant material, mulm clots, coprolites and charophyte axes deposited in shallow, cool-water pools (Anderson *et al.* 2003).

8. Mineralization and geochemistry

A 150 m wide zone of intense hydrothermal alteration occurs at the Rhynie Basin margin in the RFZ, demonstrating this was the key pathway migrating fluids. These were dominated by neutral to weakly alkaline heated meteoric water, rising from depth along the fault zone (Baron *et al.* 2003). Alteration primarily affects the sedimentary rocks, and a range of alteration textures is present: chert breccia with irregular and tabular cavities from dissolution of barite and/or calcite; sandstone breccia with chert cement; locally silicified and chert-veined sandstone; and green, massive, silicified and weakly pyritized chert breccia (Rice & Trewin, 1988; Rice *et al.* 1995). The lavas are chert veined, with the intensity of alteration decreasing with depth, and with distance from the basin margin. Near the surface and adjacent to the fault zone is a high-temperature K-feldspar–quartz–illite facies (formed at 250–350 °C), the most heavily altered, followed by a laterally adjacent medium-temperature layered illite/smectite–quartz–K-feldspar–chlorite–calcite facies (formed at 150–200 °C) and a low-temperature layered illite/smectite–chlorite–calcite facies (formed at 100–150 °C). These have been juxtaposed through faulting (Baron *et al.* 2003).

The finest-grained sediments (shales, thin sandstones and tuffaceous sandstones) are most heavily altered when next to chert beds. They have an alteration assemblage of calcite, haematite and chlorite/illite clays. Throughout the alteration zone, the rocks also contain disseminated fine-grained pyrite (Rice & Trewin, 1988; Rice *et al.* 1995). The salinity and temperature of the hydrothermal fluids responsible for the basin margin mineralization and alteration have been determined through fluid inclusion microthermometry. The fluids had low salinity and ranged from 91°C to 360°C: comparable with other heated meteoric fluids from both ancient and modern hot-spring systems. Minor input of high-temperature hydrothermal fluids from magmatism also aided mineralization within the fault zone. Alteration, mineralization and cementation elsewhere in the basin resulted from low-temperature and low- to high-salinity fluids characteristic of basinal brines (Baron *et al.* 2003).

The highly altered rocks in the feeder zone for the hot-spring system are notable for high levels of heavy metals, particularly As, Au and Sb (Rice & Trewin, 1988). Concentrations of As and Au are correlated (Rice *et al.* 1995): much gold is housed within arsenian pyrite (Mark *et al.* 2011). Gold is also found in intensely altered (K-feldspar) and silicified lava, especially where brecciated (Rice *et al.* 1995) and rarely as micron-scale particles on the surfaces of quartz and K-feldspar crystals (Rice *et al.* 1995; Mark *et al.* 2011). The likely source of this gold is the andesitic magmatism occurring at Rhynie (Baron *et al.* 2003; Mark *et al.* 2011).

Oxygen isotope analysis of the Rhynie chert lends further credence to a hot-spring source for the cherts. Trewin (1994) reports $\delta^{18}O$ varying in a sample between +13.1‰ and +16.5‰, values that are comparable to both fossil and recent sinters (Ewers, 1991) but differ from values typical of marine cherts (+31‰ to +37‰; Levitan *et al.* 1975). Assuming a Devonian meteoric water source, the $\delta^{18}O$ value suggests the temperature of sinter deposition is 90–120 °C (Rice *et al.* 1995). This assumes pristine meteoric water: given it is known the water interacted with the sediments at Rhynie, this is best considered a minimum value, and the true temperature of precipitation was likely higher (Rice *et al.* 1995).

Some geochemical analysis of Rhynie fossils has also been conducted. Preston & Genge (2010) used Fourier transform infrared (FTIR) spectroscopy and gas chromatography – mass spectrometry (GC-MS) to study the preserved plant matter to identify preserved biomolecules in the cherts, including alkanes, posited to result from degradation of fatty acids and other biological molecules within the organisms (Preston & Genge, 2010). Boyce *et al.* (2002) demonstrate, using Scanning Transmission

X-ray Microscopy (TEM) and X-ray absorption near-edge spectroscopy (XANES), zonation that reflects the deposition of lignin and structural polysaccharides within a stem lycopod (*Asteroxylon mackiei*) from Rhynie. This team has also mapped spores and tracheids using an electron microprobe (Boyce *et al.* 2001).

9. Biota of the Rhynie chert

The Rhynie chert flora is more diverse than its fauna, and is most famous for its land plants, but the biota also comprises numerous fungi and bacteria, algae, an amoeboid protist and a lichen. Rhynie is particularly important because it is a whole ecosystem, and thus interactions are preserved. These have been studied between fungi, bacteria, plants and animals, and have been a focus of work in recent years. Many interactions have yet to be fully interpreted (Taylor *et al.* 2003).

9.a. Flora

The terrestrial tracheophyte plant component of the Rhynie chert biota, first described in the five-part monograph by Kidston & Lang (1917, 1920*a*, *b*, 1921*a*, *b*), comprises six monospecific sporophyte (spore-bearing phase) genera: *Aglaophyton majus* (Figs 5b, 6c; following Edwards et al. (2018) we correct spelling of the specific epithet of *Aglaophyton* from 'major' to 'majus' in accordance with article 23.5 of the ICN Shenzhen Code), *Asteroxylon mackiei* (Fig. 5e, 6b), *Horneophyton lignieri* (Fig. 5d), *Nothia aphylla* (Fig. 5a), *Rhynia gwynne-vaughanii* (Figs 5b, 6a) and *Trichopherophyton teuchansii*. At least two of the six species are placed within an extinct group, the rhyniophytes, one amongst the early lycopods, and one within the extinct zosterophyllophytes. In addition, a seventh Rhynie Basin species not included herein, *Ventarura lyonii*, has been described from the nearby Windyfield chert. Within the chert there are also four associated monospecific gametophyte (the sexual reproductive phase) genera: *Remyophyton delicatum* (Fig. 5h, i), *Lyonophyton rhyniensis* (Fig. 5j, 6d), *Langiphyton mackiei* (Fig. 5f) and *Kidstonophyton discoides* (Figs 5g, 6e).

All sporophytes were diminutive in size (<50 cm), but due to their ground-creeping horizontal axes, formed wide area colonies, with many of these plants displaying primitive rooting structures in the form of hair-like rhizomes along these axes (Fig. 5a–e). Recent work by Hetherington & Dolan (2018b) has shown that *A. mackiei* possessed rooting organs lacking root caps – a defining feature of all modern vascular plant roots – but that they did possess a unique self-renewing root meristem with a continuous epidermis. This transition rooting organ shows that roots evolved in a stepwise fashion, and is consistent with the hypothesis that roots evolved multiple times within terrestrial plants (Kenrick & Strullu-Derrien, 2014). All Rhynie chert plant taxa are superficially similar in morphology, being leafless with dichotomizing axes, with the exception of *A. mackiei* which bares veinless leaf-like outgrowths (Fig. 5e) (Kidston & Lang, 1921*b*). Their arial axes consist of a relatively small proportion of vascular pathways, with the bulk composition made up of parenchymous tissue. The most common plant found in the chert, *A. majus*, has dichotomizing axes terminated by spindle-shaped sporangia (Fig. 5c) (Kidston & Lang, 1921*b*). Similar, but smaller in stature, *R. gwynne-vaughanii* is defined by more extensive branching, vascular tissue with recognizable tracheids, and small axial projections (Fig. 5b) (Kidston & Lang, 1917). *Horneophyton lignieri* is *c.* 20 cm high and

characterized by bulbous rhizomes and a unique branching sporangium; each lobe consists of a central axis of sterile tissue, analogous to the sporangia of modern hornworts (Fig. 5d) (Kidston & Lang, 1920*a*; Barghoorn & Darrah, 1938). *N. aphylla* (Fig. 5a) has been described as having aerial stems which were covered with oval 'emergences' formed by cell expansion (not by cell multiplication as seen in zosterophylls and trimerophytes), each bearing a single stoma (El-Saadawy & Lacey, 1979). *T. teuchansii* is the first zosterophyll to be described from fragmentary remains in the Rhynie chert. As such it is not as well understood, but did possess laterally attached valved sporangia, spinous hairs and exarch xylem (Lyon & Edwards, 1991). For further discussion and additional references of Rhynie chert sporophytes see Kerp (2018) and Mills *et al.* (2018).

Of the gametophytes, *L. rhyniensis* was the first with anatomical preservation to be described from the Rhynie chert (Remy & Remy, 1980*a*, *b*). *R. delicatum* (Fig. 5h, i), *L. rhyniensis* (Figs 5j, 6d) and *L. mackiei* (Fig. 5f) are the archegoniate- and antheridia-bearing gametophytes of *R. gwynne-vaughanii*, *A. majus* and *H. lignieri* respectively. In contrast, only the antheridia-bearing axis, *K. discoides* (Figs 5g, 6e), is known for *N. aphylla*. These gametophytes were small free-growing non-thalloid plants, with a vegetavative body plan resembling that of the sporophytes, with archegonia or antheridia near or at the apex terminal. For more details and references of Rhynie chert gametophytes see Kerp (2018).

How typical this collection of macroplants really was remains debated: some authors suggest that these plant communities were highly adapted to hot-spring environments and therefore do not represent regional flora (e.g. Scott, 1923, 1924; Channing & Edwards, 2009*a*, *b*). It is possible, however, these plant communities may have been pre-adapted to increased pH and salinity levels from habitation in more commonly found environments (e.g. salt-marshes, saline seeps and coastal estuaries; Channing, 2018). Furthermore, whilst geothermal wetlands do constitute a unique environment, it is likely that they include habitats (and thus potentially biotas) more typical of the surrounding hinterland, and are thus distinguished by varied extremes of environment and rapid change between these on small spatial scales. However, comparison with modern systems suggests that the Rhynie taxa may not be representative of coeval regional floras and at best contain a subset of the whole flora (Channing, 2018). Spore assemblages have been recovered from the cherts since the late 1960s (e.g. Richardson, 1967), but it was not until the mid-1990s and 2000s that significant palynological work was undertaken on borehole samples (Rice *et al.* 1995; Wellman, 2004, 2006). Recent quantitative comparative studies of the *in situ* and dispersed palynological record preserved in Rhynie chert (e.g. Fig. 6f, g), its intermontane basin and surrounding floodplains suggests that only a small proportion of these plants were inhabiting the hot-spring environment (Wellman, 2018); the surrounding basin has a relatively high diversity of flora compared to the hot springs. Comparison of spore assemblages from the Rhynie basin with the coeval lowland floodplain deposits indicates the basin itself is a rarefied environment, with significantly lower diversity reported, but with some unique elements. Some plants (*H. lignieri*, *R. gywnne-vaughanii* and *A. majus*) are shown to be highly versatile, inhabiting both the hot-spring and basinal environments; moreover some (e.g. *H. lignieri*) were palaeogeographically widespread (Wellman, 2018).

This brief overview introduces the Rhynie flora. This is an active research area, and Rhynie plant fossils are providing key new insights into the evolution of plants: their life cycle (Kenrick, 2018), physiology (Hetherington & Dolan, 2018*a*; Kerp, 2018;
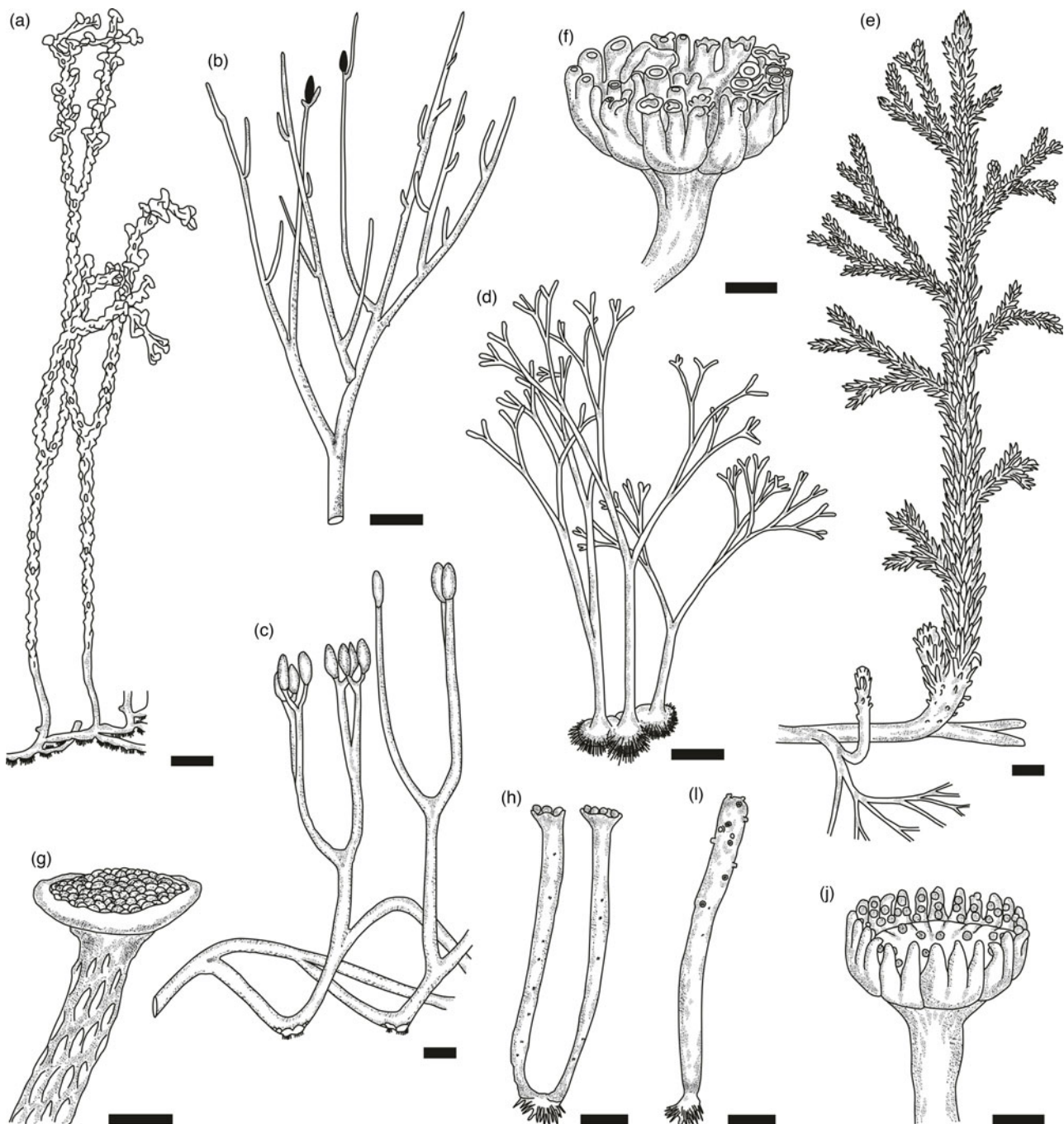
Fig. 5. Reconstructions of Rhynie chert sporophytes and gametophytes. Sporophytes (a–e): (a) *Nothia aphylla*. Scale bar 10 mm. (b) *Rhynia gwynne-vaughanii*. Scale bar 5 mm. (c) *Aglaophyton majus*. Scale bar 10 mm. (d) *Horneophyton lignieri*. Scale bar 5 mm. (e) *Asteroxylon mackiei*. Scale bar 10 mm. Note: *Trichopherophyton teuchansii*: due to its fragmentary nature, no reconstruction is presented here. Gametophytes (f–j): (f) *Langiophyton mackiei*. Scale bar 2 mm. (g) *Kidstonophyton discoides*. Scale bar 2 mm. (h) *Remyophyton delicatum* – male. Scale bar 2 mm. (i) *R. delicatum* – female. Scale bar 2 mm. (j) *Lyonophyton rhyniensis*. Scale bar 2 mm. Figures redrawn and modified from: (a) Kerp *et al.* (2001); (b) Edwards (1980); (c) Edwards (1986); (d) Eggert (1974); (e) Kidston & Lang (1921*b*); (f, g, j) Remy *et al.* (1993); (h, i) Kerp *et al.* (2003).

Raven, 2018), development (Kofuji *et al.* 2018) and interactions (Krings *et al.* 2018).

9.b. Fungi

Many of the macroplants are thought to be associated with fungi in an endomycorrhizal (also known as arbuscular mycorrhizal) symbiosis, which has been successfully demonstrated for *A. majus* (Taylor *et al.* 1995*a*), *R. gwynne-vaughanii* (Karatygin *et al.* 2006), *N. aphylla* (Krings *et al.* 2007*b*, *c*) and *H. lignieri*

(Strullu-Derrien *et al.* 2014). In modern ecosystems, these fungi are known to help define ecological niches, determine plant community composition, play a role in plant nutrition and soil fertility and contribute to soil weathering. The endomycorrhizal fungi found colonizing *A. majus*, *R. gwynne-vaughanii* and *N. aphylla* are of the genus *Glomites* (Glomeromycota). One species of *Glomites* that colonizes *R. gwynne-vaughanii*, *Glomites sporocarpoides*, displays clear pathogenicity in addition to symbiotic features: mycelium actively colonize plant axes, causing necrotic zones. Here fungal sporocarps (fruiting bodies) grow. The modern
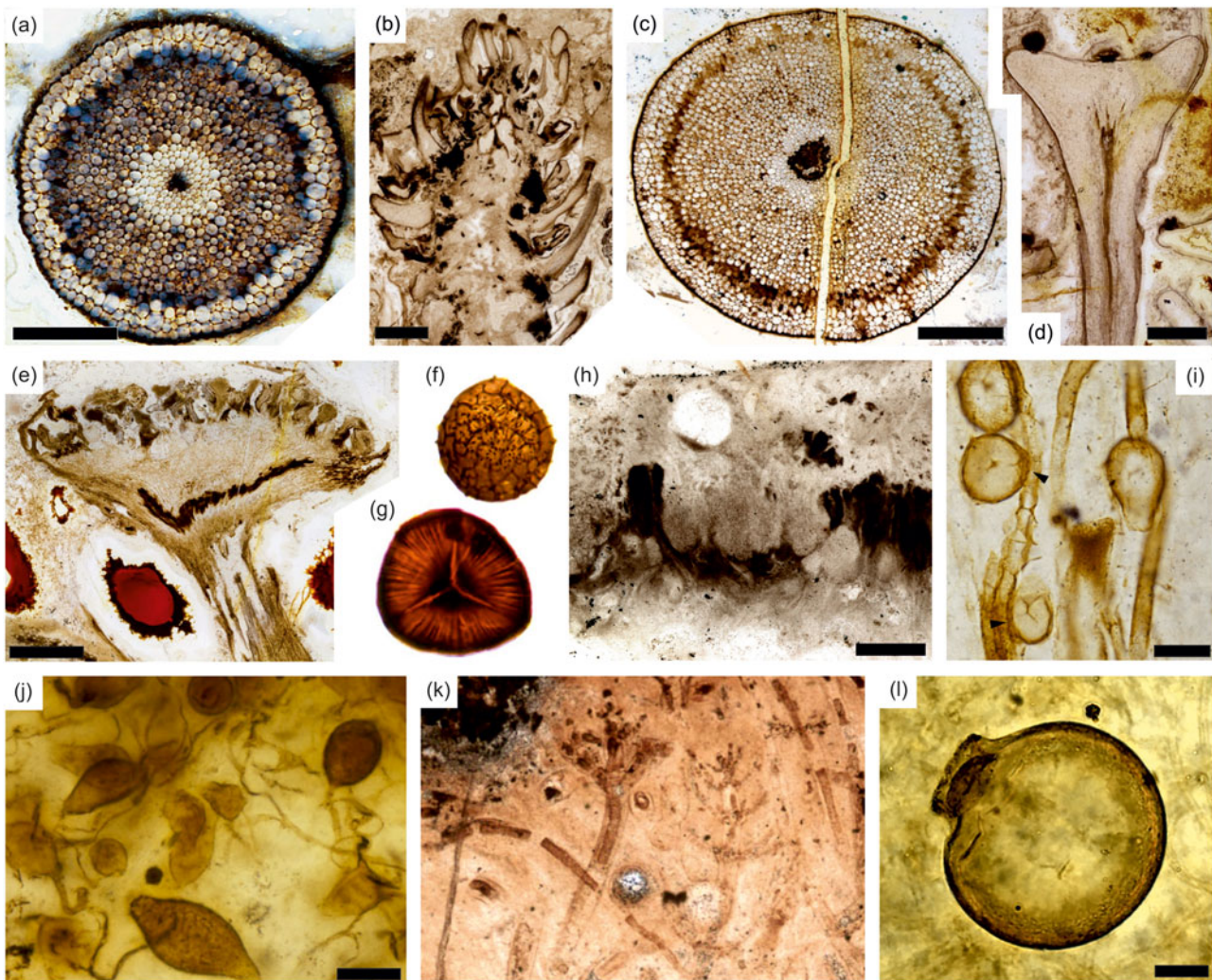
Fig. 6. (Colour online) Exemplars of the Rhynie chert biota. (a) Cross-section of *Rhynia gwynne-vaughanii*. Scale bar 500 μm. (b) Longitudinal section of *Asteroxylon mackiei*. Scale bar 2.5 mm. (c) Cross-section of *Aglaophyton majus*. Scale bar 1 mm. (d) Cross-section of gametophyte *Lyonophyton rhyniense*. Scale bar 1 mm. (e) Cross-section of gametophyte *Kidstonophyton discoides*. Scale bar 1 mm. (f) Common dispersed spore *Dictyotriletes kerpii*. (g) Common dispersed spore *Emphanisporites edwardsiae*. (h) Thallus of lichen *Winfrenatia reticulata*. Scale bar 500 μm. (i) Reproductive structures of the fungi *Palaeozoosporites renaultii*. Scale bar 38 μm. (j) Hyphae and fungal swellings of *Retesporangicus lyonii*. Scale bar 30 μm. (k) Branch of freshwater algae *Palaeonitella cranii*. (l) Testate amoebae *Palaeoleptochlamys hassii*. Scale bar 12 μm. Photographs reproduced with permission from: (a–e) Kerp (2018). All copyright H Kerp; (f, g) Wellman (2018); (h) Copyright H Kerp; (i) Strullu-Derrien *et al.* (2015); (j) Strullu-Derrien *et al.* (2018); (k) Copyright H Kerp; (l) Strullu-Derrien *et al.* (2019). Notes: see Wellman (2018) for scales of (f, g); Taylor *et al.* (2003) for more information on (h); and Kelman *et al.* (2003) for more information on the algal specimens seen in (k).

equivalent, *Glomus*, has lost the ability to form sporocarps, suggesting that through coevolution an increasingly mutualistic relationship between the fungi and plants has developed (Karatygin *et al.* 2006). *H. lignieri* is colonized by *Palaeoendogone gwynne-vaughaniae* and *Palaeoglomus boullardii*. The former has Mucoromycotina affinities, whilst the latter has Glomeromycota affinities. Strullu-Derrien *et al.* (2014) also report a symbiotic relationship between *H. lignieri* and the fungi and suggest on this basis that the fungal associations of early land plants were more diverse than initially thought.

The majority of documented fungal interactions with the Rhynie plants have been saprotrophic. Saprophytes including chytrids (Chytridiomycota) and ascomycetes (Ascomycota), alongside bacteria, are likely responsible for the great amounts of unidentifiable degraded plant matter in the Rhynie chert. Chytrids are the most common microbial organism in the Rhynie fossils: both unicellular and multicellular chytrids were present in the chert, and had saprophytic and/or parasitic relationships with the plants.

They may have been the principal organic decomposers. Parasitic chytrids have been found associated with green macroalgae, such as *Krispiromyces discoides* on the stems of *Palaeonitella cranii* (Taylor et al. 2003). They elicit a host response in the algae: infected cells display hypertrophy, growing up to ten times larger than uninfected cells (Taylor *et al.* 1992). Nodule-like swellings on the rhizoids of *N. aphylla* may also be evidence of chytrid infection points (alternatively, these swellings may be evidence of hyperplasia, an infection response). Ascomycetes are significant saprophytic consumers in modern ecosystems. They form pathogenic, beneficial and mutualistic relationships, and many have symbiotic relationships with arthropods. However, their fossil record is poorly understood (Taylor *et al.* 2003). Parasitism in the group has been reported in Rhynie within *A. mackiei*, where the fungus *Paleopyrenomycites devonicus* has been reported in the cortex directly beneath the epidermis of the aerial stems and rhizomes (Taylor *et al.* 2003). Parasitism has also been reported in the interactions of *Palaeozoosporites renaultii*, a fungus of uncertain

affinity, and the rooting system of *A. mackiei* (Fig. 6i) (Strullu-Derrien *et al.* 2015). Mycoparasites in the Rhynie chert (fungi that obtain carbon via parasitism of other fungi) have also been reported (Hass *et al.* 1994). The recently described *Retesporangicus lyonii* is known to represent one of the earliest known fungi to produce multiple sporangia on an expanded hyphal network, and was a saprotroph within the Rhynie ecosystem (Fig. 6j; Strullu-Derrien *et al.* 2015).

9.c. Lichens

Approximately 20 % of modern fungi enter into obligate symbiotic relationships with green algae and/or cyanobacteria to form lichens. The most credible Palaeozoic lichen, *Winfrenatia reticulata*, is known from the Rhynie chert (Taylor *et al.* 1995*b*, 1997, 2003). It is a three-parted lichen, consisting of filamentous and coccoid cyanobacteria and a mycobiont (Fig. 6h). The taxonomic affinity of the fungus is uncertain, but its morphology suggests it is related to the Glomeromycota. The filamentous cyanobacterium most closely resembles *Archaeothrix contexta*, though other filamentous cyanobacteria of the order Oscillatoriales have also been described. Though there are *c.* 500 modern lichens described constituting two photobionts and one mycobiont, no modern lichen are known to contain a glomeromycete fungus. *W. reticulata* is therefore a unique symbiosis, and may instead be an unstable association between a cyanobacterial colony and a parasitic fungus (Karatygin *et al.* 2009). As such, *W. reticulata* may in fact not be a true lichen, or it may represent a plesiomorphic form (Karatygin *et al.* 2009).

9.d. Amoeba

Amoebozoa are a major eukaryotic group that is sister to the clade that includes animals and fungi. Until recently, with the discovery of *Palaeoleptochlamys hassii* in the Rhynie chert by Strullu-Derrien *et al.* (2019), the oldest widely accepted terrestrial amoebozoans from the fossil record dated from the upper Permian. *P. hassii* is described as a testate amoebozoan of the order Arcellinida, with a spheroidal-shaped test and a round apical opening defined by an internally reinforced collar (Fig. 6l). Its discovery provides the first tangible evidence of phagotrophic protists in early terrestrial environments and supports the idea that arcellinids colonized the land at the same time as early vascular plants started to transform the land surface.

9.e. Bacteria/algae

Primary producers (photoautotrophs) are vital components of modern aquatic ecosystems, producing oxygen, providing organic matter at the base of the food chain and potentially converting inert atmospheric N_2 into nitrate or ammonia (Krings *et al.* 2007*a*). Cyanobacteria were therefore undoubtedly important in the Rhynie ecosystem, but extensive study of the fossilized bacteria is challenging. This is because the morphological features required for classification of algae and cyanobacteria are extremely difficult to identify in fossils. Consequently, it is rarely possible to identify the affinities of Rhynie photoautotrophs via comparison with extant analogues with any confidence. It has, however, been possible to identify distinct groups of bacteria from their structural features (Taylor & Krings, 2015). Rhynie cyanobacteria are motile benthic or planktonic: no strictly sessile cyanobacteria have been identified in the Rhynie chert (Krings *et al.* 2007*a*). The

filamentous *Archaeothrix contexta* and *A. oscillatoriformis* (Kidston & Lang, 1921*a*) were the first Rhynie cyanophytes to be identified (Edwards & Lyon, 1983). These possess both discoid cells and heterocysts, with the broadest cells seen in *A. oscillatoriformis*. *Kidstionella fritschii*, *Langiella scourfeldii* and *Rhyniella vermiformis* were all identified by Croft & George (1959). The former two taxa are filamentous cyanobacteria assigned to the family Stigonemataceae (Cyanophyceae). Both contain multiple cells with evidence of intracellular masses, interpreted as the best-preserved residues of cellular contents witnessed in fossil cyanophytes: they provide an excellent example of naturally silicified, organelle-like artefacts (Oehler, 1977). The latter species is filamentous and heterocystous and has been assigned to the family Scytonemataceae (Taylor *et al.* 2003). *Croftlania venusata* is a filamentous colonial cyanobacteria, of the order Oscillatoriales. It is aquatic and grew on sediments and submerged decaying plant matter. *C. venusata* filaments are associated with mat formation (Krings *et al.* 2007*a*). The most recently described Rhynie cyanobacteria are: *Rhyniosarcina devonica*, which comprises densely packed cubic, spheroidal or irregular colonies of up to several hundred cells (Taylor & Krings, 2015); *Rhyniococcus uniformis* which forms plate-like colonies and bears similarities to modern *Merismopedia* (Synechococcales) (Krings & Harper, 2019); and *Ryhyniotaxillus devonicus*, which forms irregular to cuboid colonies of up to 64 gelatinously enveloped cells, the colony morphology resembles present-day *Eucapsis* (Synechococcales) and *Entophysalis* (Chroococcales), as well as the Precambrian fossil *Eoentophysalis belcherensis* (Krings & Sergeev, 2019). There is no doubt that further cyanophytes will be identified from the Rhynie chert, to continue to develop our understanding of the Devonian terrestrial ecosystem as a whole.

Multiple algal species are known from Rhynie (Edwards & Lyon, 1983). *Rhyniococcus uniformis* is a palmelloid and coccoid member of the family Chroococcaceae. It is colonial, and consists of a uniform, flat, one-cell-thick sheet of cells arranged in rows. *Rhynchertia punctata* and *Mackiella rotundata* comprise unbranched, unattached, uniseriate multicellular filaments. Most *R. punctata* vegetative cells have poorly defined walls, and either contain a single dark body (which may represent a single large organelle) or many small ovoid bodies (interpreted as being reproductive structures). The species' affinities are still unknown (Edwards & Lyon, 1983). *M. rotundata* (Ulotrichales) cells are largely uniform with fine granular material and a darker body. The relatively small freshwater charophyte *Palaeonitella cranii* is described as having multicellular furcating branchlets with antheridia attached to the parent plant by a pedicel (Fig. 6k). It has been compared to extant Characeae and inhibited the ephemeral freshwater pools and potentially provided food for detritivores (Kelman *et al.* 2003). The earliest evidence of the genus *Cymatiosphaera* (Pyramimonadales), a prasinophycean alga, in a freshwater environment, has been identified from the Rhynie chert. These are solitary or in loosely clustered groups of two to ten individuals. In the chert matrix, they are associated with accumulations of decomposing plant matter, although a few examples are located within plant tissues (Dotzler *et al.* 2007). Two forms of *Cymatiosphaera* have been identified, distinguished by their surface ornamentation (Kustatscher *et al.* 2014*a*). The phycomata of another prasinophycean alga, *Pterospermella*, has been recognized from the Rhynie chert. This species is similar to extant *Pterosperma*; the fossils are located within a loosely packed accumulation of fungal hyphae and land plant debris. The presence of three phycomata records in
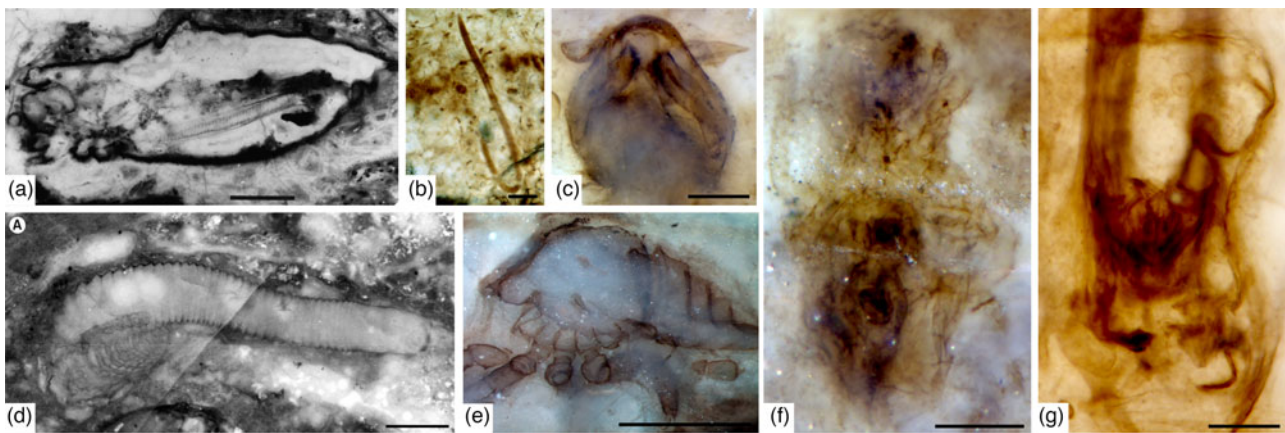
Fig. 7. (Colour online) Examples of the Rhynie chert fauna. (a) *Eophalangium sheari*, an opilionid arachnid – this specimen is a female. Scale bar 1 mm. (b) The nematode *Palaeonema phyticum*. Scale bar 100 μm. (c) Hexapod *Rhyniella praecursor*. Scale bar 100 μm. (d) Crustacean *Castracollis wilsonae*. Scale bar 0.5 mm. (e) A palaeocharinid trigonotarbid. Scale bar 1 mm. (f) An acariform mite. Scale bar 100 μm. (g) *Rhyniognatha hirsti*, a potential pterygote insect. Scale bar 100 μm. Photographs modified from: (a) Dunlop *et al.* 2004; (b, c, f, g) Dunlop & Garwood 2018; (d) Fayers & Trewin 2003; (e) Dunlop & Garwood 2014.

the Rhynie chert suggests that the ecosystem was home to a variety of prasinophyte algae (Kustatscher *et al.* 2014b).

9.f. Fauna

The animal component of the Rhynie chert fossils is limited to arthropods (chelicerates, crustaceans and hexapods; myriapods are reported from the Windyfield chert fauna), and a nematode worm – 11 genera in total. The Rhynie biota is largely associated with chert deposition in areas with a substrate or water temperature suitable for non-extremophile eukaryotes to thrive. For modern terrestrial and freshwater arthropods, vascular plants and mosses, the upper temperature limit is 45–50°C.

9.f.1. Arthropods

A significant component of the arthropod fauna comprises chelicerates. Of these the trigonotarbids of the genus *Palaeocharinus*, and the acariform mites currently placed within the genera *Protacarus*, *Protospeleorchestes*, *Pseudoprotacarus*, *Palaeotydeus* and *Paraprotocarus*, are currently in need of revision. Other arachnid taxa comprise the harvestman *Eophalangium sheari*, and enigmatic taxa *Palaeocteniza crassipes* and *Saccogulus seldeni*. *E. sheari* (Fig. 7a) is the oldest known harvestman (Opiliones; Dunlop *et al.* 2003). Male and female specimens have been preserved: internal anatomy includes a penis and ovipositor, in addition to tracheae. The genital and respiratory structures are similar in appearance to that of modern harvestmen (Dunlop *et al.* 2003, 2004), although recent cladistic analysis has placed the taxon as sister group to a Carboniferous taxon as a stem group to an extant suborder (Garwood *et al.* 2014), or within an opilionid polytomy (Garwood *et al.* 2017; Wang *et al.* 2018). Among the most abundant arachnids are trigonotarbid arachnids of the genus *Palaeocharinus* (Figs 7e, 8a, g). Five species were initially identified (Fayers *et al.* 2005), the first by Hirst (1923) and Hirst & Maulik (1926); however, only two are probably valid (Dunlop & Garwood, 2018). The presence of trabeculae and lamellar spines in palaeocharinid book lungs is unequivocal evidence that the organisms were fully terrestrial (Kamenz *et al.* 2008). It has been suggested that *P. crassipes* is also a trigonotarbid; the poor preservation quality prevents further conclusions being drawn (Selden *et al.* 1991). Similarly, *S. seldeni* – known from a single specimen showing

mouth with potential filtering device – is of uncertain affinities (Dunlop & Garwood, 2018). The mites from Rhynie chert (Fig. 7f) represent the oldest unequivocal record of the order Acariformes. They were first described by Hirst (1923), as a single species, before being split into an additional four (Dubinin, 1962): the latter was based on illustrations rather than restudy, and a taxonomic revision would be beneficial (Dunlop & Garwood, 2018).

Heterocrania rhyniensis, first described by Hirst & Maulik (1926), is now known to be a euthycarcinoid (Fig. 8d) having previously been identified as a chelicerate from fragmentary remains (Anderson & Trewin, 2003). *H. rhyniensis* likely inhabited isolated pools around the hot-spring system which suggests that by the Early Devonian some euthycarcinoids had begun to colonize isolated freshwater bodies on the continental interior after their initial Late Silurian colonization of fluvial environments (Anderson & Trewin, 2003).

Three of the Rhynie arthropods – *Lepidocaris rhyniensis*, *Castracollis wilsonae* and *Ebullitiocaris oviformis* – are branchiopod crustaceans. *L. rhyniensis* (Fig. 8h) was the first crustacean to be described from Rhynie (Scourfield, 1926). Both male and female specimens have been identified, in various ontogenetic stages. Whilst originally placed within the Anostraca, a lack of stalked eyes, and other morphological differences have resulted in the species being since placed in a monotypic class, Lipostraca (Scourfield, 1926). Strullu-Derrien *et al.* (2016) describe spinose structures that they interpret as resting eggs of *Lepidocaris* associated with a new species of Chytridiomycete fungus. *C. wilsonae* (Figs 7d, 8e) was described more recently. It is known from exuveae which are markedly different in morphology *L. rhyniensis*, and is classified as an *incertae sedis* calmanostracan branchiopod (Fayers & Trewin, 2003). Because of a high concentration of *Castracollis*, specimens of different ontogenetic sequences have been found within a single, thin chert horizon, it is suggested that this is evidence of a short life cycle, similar to modern notostracans, with rapid development and moults after hatching (Fayers & Trewin, 2003). The most recently discovered Rhynie crustacean is *E. oviformis* (Fig. 8f), a univalved diplostracan branchiopod (Anderson *et al.* 2003), which authors suggest might have had desiccation-resistant eggs (as modern Cladocera do) due to their mode of life in ephemeral freshwater pools. All three branchiopods are aquatic, with fossils found in areas of the chert with a 'clotted'
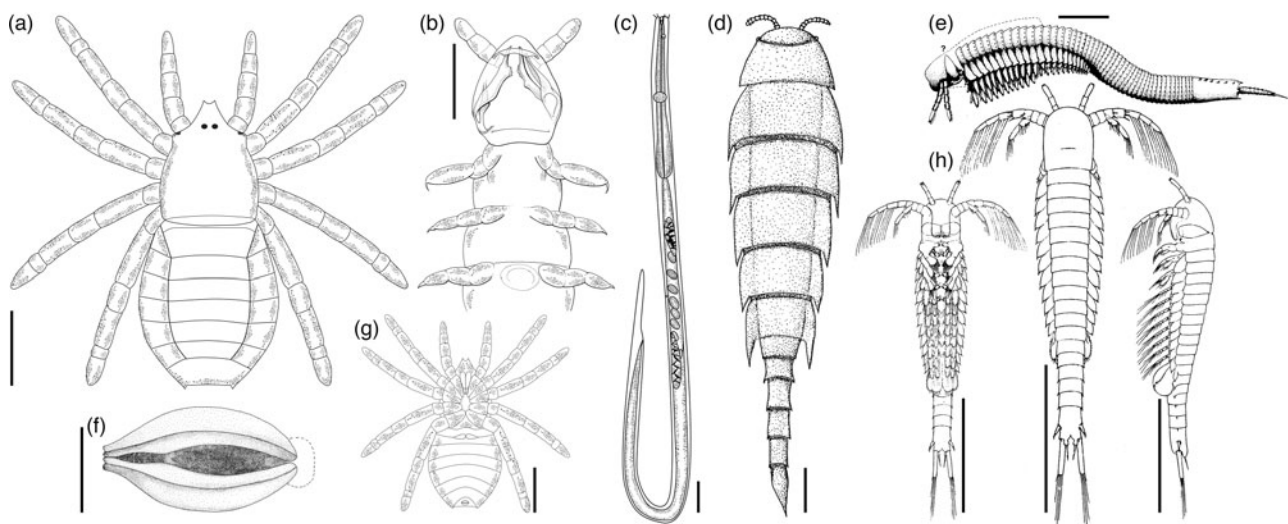
Fig. 8. Reconstructions of Rhynie chert fauna. (a) A palaeocharinid trigonotarbid, based on members of the genus *Palaeocharinus*, which is in need of revision. Scale bar 1 mm. (b) The hexapod *Rhyniella praecursor*. Scale bar 0.2 mm. (c) The nematode *Palaeonema phyticum*. Scale bar 39 µm. (d) *Heterocrania rhyniensis*, a euthycarcinoid. Scale bar 1 mm. (e) The crustacean branchiopod *Castracollis wilsonae*. Scale bar 1 mm. (f) A univalve branchiopod crustacean *Ebullitiocaris oviformis*. Scale bar 0.5 mm. (g) Ventral view of a palaeocharinid trigonotarbid. Scale bar 1 mm. (h). The crustacean *Lepidocaris rhyniensis* shown in ventral, dorsal and then lateral aspect. Scale bars 1 mm. Figures modified after: (a, g) Garwood & Dunlop (2010). (b) Grimaldi & Engel (2005). (d) Anderson & Trewin (2003). (e) Fayers & Trewin (2003). (f) Anderson *et al.* (2003). (h) Scourfield (1926).

texture characteristic of organic matter in freshwater pools (Anderson *et al.* 2003; Fayers & Trewin, 2003).

There are also two Rhynie hexapod genera: *Rhyniella praecursor* and *Rhyniognatha hirsti*. *R. praecursor* (Figs 7c, 8b) has long been considered the oldest hexapod (Dunlop & Garwood, 2018). It is a collembolan (springtail), a flightless group closely related to insects, and is very similar to modern springtails (Tillyard, 1928; Scourfield, 1940; Whalley & Jarzembowski, 1981; Greenslade & Whalley, 1986). It has been proposed that *R. hirsti* (Fig. 7g) is the earliest known winged insect based on its mandible morphology: these bear two pivots, or condyles (Engel & Grimaldi, 2004, but for an alternative interpretation see Haug & Haug, 2017). Both genera are terrestrial (Dunlop & Garwood, 2018).

9.f.2. Nematodes

The only non-arthropodan Rhynie animal is a nematode worm, *Palaeonema phyticum* (Figs 7b, 8c). The 0.1–1 mm worm has been placed in the extinct family Palaeonematidae within an extant order, Enoplia. The fossils represent the oldest unequivocal nematode body fossil. They were identified within the stomatal chambers of *Aglaophyton major*, and because multiple ontogenetic stages of the species are found here, from eggs through to adults, it has been suggested the species reproduced within the plant tissue. This would represent one of the oldest examples of a relationship between an animal and a terrestrial plant (Poinar *et al.* 2008; Poinar, 2015).

9.f.3 Coprolites, trace fossils and palaeoecology

Further evidence regarding the Rhynie animals can be found through the numerous coprolite ichnofossils identified in the deposit. These suggest a range of feeding strategies, but one dominated by detritivory. Coprolites comprise plant spores, fungal spores and hyphae, macerated plant cells, mineral grain and amorphous organic materia (Habgood *et al.* 2003). One specimen of the taxon *Rotundafaex aggregata* additionally contains arthropod remains. In general, coprolites appear to have been produced by detritivores (collembolans and myriapods being likely producers).

In addition to this, *Bacillafaex constipata* coprolites are similar to the cluster pellets produced by modern microherbivores: Habgood *et al.* (2003) suggest these could have been produced by oribatid mites or collembolans. The nematode fossil outlined previously represents a potential herbivore. Spore and sporangia feeders have been suggested from the presence of spore-rich coprolites (Kevan *et al.* 1975), but the evidence for this remains inconclusive (Habgood *et al.* 2003; Dunlop & Garwood, 2018). Sap-sucking by organisms, which pierce the axes of plants to extract the phloem, has been the suggested cause of wounds on plant axes (Kevan *et al.* 1975), but subsequent work has suggested that the cause of the damage remains ambiguous (Dunlop & Garwood, 2018). Based on functional morphology, rather than coprolite evidence, it is clear that predators were present. Dunlop & Garwood (2018) provide an overview of the potential ecological role of the terrestrial Rhynie animals, and Haug (2018) uses functional morphology of the fossils to suggest the arthropods of the Rhynie ecosystem used a wide range of feeding strategies. A key outstanding question regarding the Rhynie fauna, as with its flora, is whether this is representative of a typical terrestrial fauna, or rather if it was a community specialized to the Rhynie hot-spring environment. Given the lack of contemporary terrestrial arthropod faunas, and lack of study of modern systems, providing a definitive answer regarding whether this was the case remains challenging (Dunlop & Garwood, 2018).

10. Conclusions and future research

Since its discovery a century ago, despite its lack of exposure, the Rhynie chert has provided a wealth of knowledge about early terrestrial ecosystems. This results from both the level of preservation of its fossils, and the timing of its deposition, during an interval when terrestrial fossils are otherwise rare, and seldom well preserved. Edwards *et al.* (2018) provide an excellent overview of potential future research directions on the study of Rhynie fossils. In general, it seems likely that with continued study and the development of novel imaging techniques such as confocal microscopy,

new species from the deposit are likely to be discovered, and previously described ones better understood. For example, much of the work to understand the contribution of fungi and bacteria to the Rhynie ecosystem has been conducted in the last decade, propelled by electron microscopy, more widespread use of other novel techniques (e.g. confocal laser microscopy) and the observation that primary producers are key to the growth of modern ecosystems. Indeed, a key path for future research will be the interactions between the organisms preserved at Rhynie, allowing us to understand the ecosystem better. Here key questions remain, such as how representative Rhynie is of early Devonian ecosystems more generally. Another likely area for development is the application of novel geochemical analysis to Rhynie fossils. Preston & Genge (2010) demonstrated the potential for FTIR and GC-MS in understanding the organic composition of these deposits, and Abbott *et al.* (2018) have used X-ray photoelectron spectroscopy and time-of-flight secondary ion mass spectrometry to provide chemical maps. This approach of mapping of organic and inorganic compounds associated with the fossil material has the potential, as in other areas (e.g. Wacey *et al.* 2017), to have a transformative impact on our understanding of the taphonomy and physiology of Rhynie organisms.

Author ORCIDs. Russell J Garwood 0000-0002-2803-9471; Alan R T Spencer 0000-0001-6590-405X

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