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Russia-UK collaboration in palaeontology: past, present, and future

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Abstract–There is a long history of collaboration between Russia and the United Kingdom in palaeontology. This began, arguably, in 1821, with the seminal work by William Fox-Strangways, who produced a geological map of the area around St Petersburg. Most famously, Roderick Murchison carried out extensive surveying and observations throughout European Russia in 1840 and 1841, and published a major monograph on geology and palaeontology of European Russia in 1845. Since then, and continuing today, there have been many fruitful collaborations on Precambrian life, Palaeozoic marine organisms, terrestrialisation of plants and vertebrates, the Permian-Triassic mass extinction, fossil mammals, human evolution, and conservation palaeobiology.

INTRODUCTION

The Royal Society (RS) and Russian Academy of Sciences (RAN) agreed to hold meetings to discuss future collaborative research directions in different areas of mutual scientific interest. The first theme to be selected was palaeontology, and a Royal Society delegation of six palaeontologists travelled to Russia in October 2016 to explore possible collaborations with their Russian counterparts. Co-chaired by Professor Mike Benton FRS (Bristol) and Professor Sergei Rozhnov, Director of the Palaeontological Institute (PIN) and colleagues, it featured a diversity of presentations encompassing a vast range of geological time, from the Precambrian to the emergence of *Homo sapiens*.

In this account, we provide a perspective from the British side of the meeting, outlining themes that were presented and discussed during a day of symposium presentations at the Borissiak Paleontological Institute, Moscow (PIN), a key division of RAN. Sections of this paper were written as follows: Introduction (M.J.B.), The early years of collaboration (M.J.B.), Exceptional preservation reveals the early evolution of life in the oceans (DEGB), Terrestrialisation, early plants and changing earth systems (D.E.), Documenting major evolutionary transitions – the first tetrapods (J.C.), The impact of mass extinctions on the history of life (M.J.B.), The early human occupation of Britain (C.B.S. and J.G.-W.), and Conservation palaeobiology (S.T.T.)

THE EARLY YEARS OF COLLABORATION

Collaborations between Russian and British earth scientists and palaeontologists began at the very roots of geology as a science. An unusual early manifestation was an article entitled ‘Geological sketch of the environs of Petersburg’ published in the *Transactions of the Geological Society of London* in 1821. The author was William Fox-Strangways, 4th Earl of Ilchester (1795–1865), and he wrote it when he was attaché at the British Embassy in St Petersburg. Fox-Strangways ventured out around the glittering imperial capital city for some 40 versts (c. 30 miles) in all directions, exploring the alluvium and underlying rocks around the delta of the River Neva. Amongst his diverse observations on the roads, rivers, villages, soils, and rocks, Fox-Strangways mentioned fossil orthoceratites, ‘sometimes a yard in length’ and two species of trilobite in the ‘Pleta’ Limestone at Krasnoe Selo, identified as the Lower Silurian Orthoceratite

Limestone, known over parts of Finland and Sweden also, and subsequently widely used as a decorative stone in building. Fox-Strangways (1821) provided a coloured geological map of the St Petersburg region, distinguishing four rock types, as well as some cross-sections and scenic views along the river banks.

Fox-Strangways was writing at a time before the synoptic works of Lyell (1830–1833) and Murchison (1839), who did so much to establish the principles of methods in geological observation and the international stratigraphic system. In fact, Roderick Impey Murchison (1792–1871; Fig. 1) is regarded by many as the founder of geological research in Russia. Murchison first visited Russia in 1840, and saw the geology of the west and the Moscow Basin. His intention was to check the validity of the stratigraphic system of the Palaeozoic that he and Adam Sedgwick had established in the United Kingdom. He travelled through Germany and the Baltic coast, observing examples of the Silurian, Devonian, and Carboniferous systems as he went, and confirming their occurrence, including the Orthoceratite Limestone at St Petersburg. But his main quest was to fill the final gap in the universal stratigraphic scheme he had drawn up, namely identifying what happened between the already named Carboniferous and the Triassic.

After lengthy negotiations, Murchison had achieved the backing of Tsar Nicholas I, and he revelled in the royal parties and discussions. He was commissioned by the Tsar to carry out a much more extensive survey of the geology of European Russia, and he read extensively in planning for the trip. In particular, he benefited from the detailed accounts written by Alexander von Humboldt (1769–1859) who had travelled widely around Russia in 1829 exploring the Ural Mountains for their effects on topography and climate, but also the mines for valuable metals (Humboldt 1831). Murchison was enthralled by Humboldt’s adventures, especially since the Russian officials and princes themselves knew so little of the remoter parts of their own land. Murchison’s expedition was commissioned in a similar way to Humboldt’s: he was funded and instructed in his aims by Tsar Nicholas I and Russian Foreign Minister Count Georg von Cancrin.

Murchison began his second Russian expedition in 1841, setting out from St Petersburg with his scientific companions, the French palaeontologist Edouard de Verneuil (1805–1873), the German-Russian mining expert Alexander von Keyserling (1815–1891), and a young Russian mineralogist, Nikolai Koksharov (1818–1893). Their route took them to Moscow, and then east on the road to Nizhny Novgorod. They proceeded together to the old monastery city of Vladimir, and then Verneuil and

Keyserling took a southerly route to Kazan', and Murchison and Koksharov continued on the main road east. Details of the trip and Murchison's observations are recorded in detail in a series of 13 field notebooks as well as an autobiographical journal, in nine volumes, all preserved in the archives of the Geological Society of London (the latter transcribed and published: Collie and Diemer 2004).

At Vyazniki, a town 300km east of Moscow, Murchison noted how at last the party had passed from the grey-coloured Carboniferous rocks of the Moscow Basin into younger, redbed rocks that he later identified as equivalent in age to the marine Permian he saw in the Urals. This was his first sighting of the Permian (Benton et al. 2010). Murchison continued to Kazan', after passing down the Volga, and the party proceeded to explore the western flanks of the Ural Mountains, reaching Perm' a month later. Murchison saw gypsum-bearing white limestones, which he assigned to the lower part of the New Red Sandstone, and, on later days, marine beds of the Lower Permian. The party criss-crossed the Ural Mountains, exploring the Permian and Triassic redbeds around Orenburg in the south, and then swinging far west to examine the Donetz coal field. They finally returned through Moscow to St Petersburg, after a journey lasting for some 5 months. Before returning to the UK, Murchison (1841) wrote a short note in which he established the Permian System, founded primarily on the marine rocks around Kazan' and Perm itself, and Orenburg in the south: limestones with shells, gypsum, salt, and copper-bearing sandstones, lithologies that he had seen in the Zechstein of Germany and Magnesian Limestone of England. He used his information from Russia in numerous publications, and especially in his magisterial account of the whole expedition (Murchison 1845), published in lavish style at the expense of the Tsar (Fig. 1).

Further collaborations between Russia and the UK focused on more specialist topics. For example, bones had been reported as early as 1770 from the Permian Copper Sandstones of Orenburg, and Murchison brought specimens back in 1841 for Sir Richard Owen (1804–1892) to study. Various specimens had been described in the 1830s and 1840s by Russian geologists S.S. Kutorga, F. Wangenheim von Qualen, and G.I. Fischer von Waldheim (Ochev and Surkov 2000), at the same time that Owen was naming materials of similar age from the Karoo basin in South Africa. Eventually, Owen (1876) provided a thorough overview of the Russian synapsid reptiles, subsequently the subject of extensive expeditions in the South Urals and along the banks of the River North Dvina, and a major focus in modern Russian palaeontology (Ochev and Surkov 2000; Benton et al. 2000).

In this account, we summarise key palaeontological themes of international importance, emphasizing the potential for furthering collaboration between researchers in Russia and the UK. We see these as areas for future development. The topics range from the origin and early evolution of life in the Precambrian, exceptionally preserved Palaeozoic marine faunas, the origin of plants and animals on land, major mass extinctions – especially the Permo-Triassic mass extinction 252 million years ago, human evolution, and conservation palaeobiology.

EXCEPTIONAL PRESERVATION REVEALS EARLY EVOLUTION OF LIFE IN THE OCEANS

The marine fossil record is dominated by the biomineralized elements of organisms – shells, bones and teeth. Surveys of modern marine communities show that some 60% of animals lack biomineralized ‘hard’ parts (Schopf 1978), a proportion exceeded in some assemblages of exceptionally preserved fossils such as those of the Middle Cambrian Burgess Shale of Canada (Conway Morris 1986). It follows that hard parts alone provide a significantly impoverished sample of the organisms originally present. Conversely, exceptional preservations (Konservat-Lagerstätten) are critical to our understanding of the history of life on Earth. The soft-bodied fossils preserved in Konservat-Lagerstätten fill gaps in the record of groups with an otherwise poor fossil record. They are important in fleshing out the evolutionary history of these groups and they provide data on morphologies no longer represented today, which are critical for reconstructing phylogenies. The preservation of soft-bodied taxa also allows the calibration of molecular clocks, which provide estimates of the timing of events in clade evolution.

Biomineralization was rare prior to the Cambrian explosion. Fossilization in Precambrian rocks generally depends on the survival of organic remains, which requires exceptional conditions. Nonetheless there is a substantial record of microscopic organic fossils in the Precambrian of Russia which is too extensive to summarize here: Archean and Proterozoic examples are treated in reviews of global occurrences by Knoll and Sergeev (1995) and Sergeev et al. (2007, 2010) and important new discoveries continue to be made (e.g. Golubkova et al. 2015). The first large organisms, which are likewise non-biomineralized, became widespread during the Ediacaran Period. Some of the most celebrated examples are the classic Ediacara fossils of the White Sea area (Fedonkin et al. 2007). Such exceptional preservations are critical to understanding how the evolution of ocean ecosystems relates to environmental factors such as the chemistry of the atmosphere and oceans, and vice versa.

The White Sea fossils are preserved as three-dimensional impressions resulting from early cementation of the host sediment (Fig. 2a), but other fossils of Ediacaran age survive as organic material (both micro- and macrofossils) and as a result of diagenetic replacement in phosphate. Large Ediacara fossils are known worldwide, most notably from Mistaken Point in Newfoundland, the Flinders Ranges in Australia, and from Namibia. Their preservation has been explained by early precipitation of pyrite – the 'Death Mask' hypothesis developed by Gehling (1999) based on specimens from the Flinders Ranges. Recent evidence from Australian examples indicates that the pyrite coating forms later in the Flinders Ranges and fossilization appears to be a result of elevated concentrations of silica in the oceans (Tarhan et al. 2016) prior to the onset of silica biomineralization by sponges and radiolarians. This new model (Tarhan et al. 2016) remains to be tested by investigating occurrences elsewhere in the world where pyrite is associated with Ediacara fossils, including Mistaken Point (Liu 2016) and the White Sea (Ivantsov 2016).

Localities yielding Ediacara fossils are much rarer in the United Kingdom than in Russia but examples from Charnwood Forest were the first to be positively identified as Precambrian, in the 1950s (Fig. 2b). Recent research in the Charnwood Forest inlier has revealed some 14 taxa (P.R. Wilby, pers. comm.) and shown that the biota is most similar to the Avalon Assemblage of Newfoundland (Wilby et al. 2011). Bedding plane surfaces with hundreds of specimens have allowed population studies with the aid of new techniques for moulding and imaging (Wilby et al. 2015). A few examples of Ediacara fossils have also been recovered from the Carmarthen area in Wales.

A major area of palaeontological research is the nature of the transition from life in the Ediacaran to that in the Cambrian (Rozhnov 2010). Fortunately the Cambrian, like the Ediacaran, is characterized by an abundance of sites of exceptional preservation: there are many more Konservat-Lagerstätten of Cambrian age than in younger rocks. Investigation of the small shelly fossils that predate more familiar Cambrian macrofossils was pioneered by A. Yu. Rozanov and others in Russia (Rozanov and Missarzhevsky 1966; Matthews and Missarzhevsky 1975; see Bengtson 2005). These phosphatized shells were dissolved out of limestones, revealing a remarkable abundance and disparity of early Cambrian forms otherwise largely unknown. Diagenetic phosphatization can also promote the preservation of embryos and larval stages: so-called Orsten-type deposits are known from the Cambrian of Siberia (Müller et al. 1995; Bengtson and Zhao 1997). The Lower Cambrian of Siberia has also yielded some of the earliest sponge reefs, dominated by archaeocyaths (e.g. Riding and Zhuravlev 1995).

Our understanding of the Cambrian Explosion is intimately associated with Walcott's discovery of the Burgess Shale in the early 20th century and the reinvestigation of the biota initiated in the 1960s by the Geological Survey of Canada and carried out in Cambridge under the direction of Harry Whittington (Gould 1989). It is important to understand the factors that influence preservation so that we can distinguish real patterns in the diversification of life from those that reflect preservational biases. Burgess Shale-type preservations, like those of Ediacaran age, are global in distribution and it is likely that the controls on their occurrence were also global. A number of factors have been invoked, including the observation that burial may have placed potential fossils beyond the reach of burrowing animals, most of which could only penetrate to shallow depths during the Cambrian; deeper burrowing forms evolved later (but see Gaines et al. 2012b). There is mounting evidence, however, that ocean chemistry played a central role in fossil preservation. There may have been lower levels of sulphate in the Cambrian oceans, inhibiting decay by sulphate reducers. In addition marine waters were characterized by a higher concentration of alkalis, which promoted precipitation of carbonate cements, reducing diffusion and slowing degradation (Gaines et al. 2012a). Recent studies suggest that the composition of clay minerals in the early oceans may also have served to inhibit bacterial activity (Wilson and Butterfield 2014; McMahon et al. 2016; Naimark et al. 2016). Such considerations may explain why Sedgwick's classic Cambrian sequences in the UK have yielded nothing to match Burgess Shale-type preservation elsewhere in the world.

Our knowledge of the diversification of metazoans in the early Palaeozoic is increasing apace. Exploration of areas where exceptional preservations occur, in rocks of various ages, have demonstrated that Konservat-Lagerstätten are rarely unique: exceptional preservation occures where similar conditions prevail. Examples include the multiple occurrences of Burgess Shale fossils in the vicinity of Walcott's famous quarry in the Middle Cambrian of British Columbia (Briggs 2014). Spectacular new Cambrian assemblages have also been discovered in China, notably the older Chengjiang and Guanshan biotas and the middle Cambrian Kaili biota. Further excavations have augmented our knowledge of other early Cambrian biotas, including that from Sirius Passet in Greenland, and the Emu Bay Shale in Australia. Stratigraphic occurrences of some iconic Cambrian groups such as anomalocaridids have also been significantly extended by discoveries in the Ordovician of Morocco (Van Roy et al. 2010, 2015). The Early Cambrian Sinsk biota on the Siberian Platform near Yakutsk is an important source of data on Burgess Shale-type fossils, as they come not from shales but from a carbonate unit known as the Algal Lens. The biota is diverse, including trilobites, bradoriids, lobopods, other arthropods including *Phytophilaspis*, paleoscolecids, brachiopods, sponges, chancelloriids, eldoniids and probable pterobranchs, a range of taxa similar to that of Walcott's Burgess Shale (Ivantsov 1999; Ivantsov et al. 2005). The Middle Cambrian Zelenotsvetnaya Formation on the Ukukit River on the Siberian Platform has yielded rhabdopleurids with preserved zooids (Sennikov 2016). Burgess Shale-type preservations are rare in the interval between the Middle Cambrian and the Lower Ordovician, presumably reflecting a lack of suitable sedimentary facies (i.e. extensive deposits of mudstones introduce by episodic events). Recent research is filling this gap with data from small carbonaceous fossils (e.g. Smith et al. 2015; Slater et al. 2017).

Few marine Konservat-Lagerstätten have been reported from post-Cambrian strata in Russia, presumably reflecting the challenges involved in exploring such a vast country. The Palaeontological Institute in Moscow, however, holds significant material from a number of important terrestrial sites which have yielded prolific fossil insects of Permian, Triassic and Mesozoic age, together with similar collections from adjacent territories (Grimaldi and Engel 2005). Russian Konservat-Lagerstätten, both now and in the future, represent a fundamental resource for the investigation of the history of the planet.

TERRESTRIALISATION, EARLY PLANTS AND CHANGING EARTH SYSTEMS

The colonisation of the land by plants was not only a major event in the history of life on Earth, but one that had far wider impacts on the lithosphere and atmosphere.

Initially, intensive studies of terrestrialisation, which began in the 1960s, concentrated on the origins and radiations of vascular plants (tracheophytes) in the Late Silurian and Early Devonian, but 21st century work has yielded increasing evidence, beginning in the mid-Ordovician, for earlier land plants based on palynomorphs rather than megafossils. Configurations and ultrastructure of these spores, plus new phylogenetic trees, indicate affinities with bryophytes. More conjectural are hypotheses relating to the existence of further vegetation in which basal embryophytes (bryophytes + tracheophytes) were accompanied by associations of fungi, including lichens, algae, cyanobacteria and bacteria, collectively termed cryptogamic covers. These organisms today colonise habitats inhospitable to vascular plants. Research on early terrestrial animals has been less productive, but provides information on basal members of many lineages and the evolution of rudimentary food webs. Interactions between plants and fungi, particularly involving mycorrhizae, are being increasingly studied, as are the impacts of plants on sedimentological and environmental processes. These include their role in the chemical weathering of rocks, with implications for the evolution of atmospheric composition and the sequestration of carbon dioxide.

Returning to the evolution of tracheophytes, work on fossils from North America and Europe has shown an initial proliferation of plants of the *Cooksonia* type in the latest Silurian and earliest Devonian. This was followed by the diversification of plants with lateral sporangia and the beginnings of the lycophyte lineage in the basal Devonian (the Lochkovian *Zosterophyllum* Flora) and then the emergence and subsequent radiation of the euphyllophytes (the Pragian-Emsian *Psilophyton* Flora). This apparently stepwise chronological progression of ever increasing plant complexity was shattered by the discovery of the late Silurian lycophyte, *Baragwanathia* in Australia and zosterophylls in Arctic Canada, as well as the disparity and complexity displayed in Pragian/Emsian plants from Yunnan, China, many of which do not fit comfortably into existing classifications.

But what of palaeobotanical knowledge of Russian sequences of this age? In a landmark paper in 1967, Nina Petrosyan produced lists of Lower Devonian species collected from three geographical areas – the Tunguska region of western Siberia, central Kazakhstan, and the Volyno-Podolian margin of the Russian continental platform, and with, for the first time in English, a commentary on their palaeophytogeographic significance. These areas are considered here, emphasizing the role of Russian palaeobotanists in the collection, description and subsequent deposition of fossils in Russian Institutions, and includes the Ukraine for completeness.

The Siberian plant assemblages are important not only because they contain plants from Lochkovian through Emsian strata (termed the *Zosterophyllum* and *Psilophyton* Floras), but also because they were located on the Siberian palaeocontinent. This was the only major continent in the northern hemisphere in Devonian times, so its isolation potentially offers evidence for global provincialism in the early history of terrestrial plants. Comprehensive species lists were based initially on studies by A. Ananiev (e.g. 1955, 1960), who incorporated valuable geological data on the plant localities. Subsequent publications by Ananiev and Stepanov (1969), Stepanov (1975), and Zacharova (1981) testify to the legacy of his leadership. Data are supplemented by collections of Lepekhina, Petrosyan and Radchenko (1969), which D.E. was privileged to examine in St Petersburg on her first visit to Russia in the early 1970s. In 2002, she studied some of the Ananiev school's collections in the museum of Tomsk University, courtesy of Dr V.M. Podobina.

Interrogation of species lists and some personal observations indicate that there are a number of Siberian endemic genera, plus cosmopolitan representatives, that require reinvestigation. Thus, for example Stepanov (1975) described *Cooksonia pertoni* and *C. hemisphaerica* in the Kuznetsk Basin. These are important taxa in the Upper Silurian and basal Devonian of Europe, but the Russian specimens show much greater architectural complexity and should be assigned to a new genus. The difficulties of naming sterile spiny axes have been exemplified in European members of *Psilophyton* where it has been shown that *P. goldschmidtii* is a younger synonym of P. *burnotense.* Spiny axes from Siberia were named *P. goldschmidtii* by Ananiev and initially by Zacharova. The identity and affinities of the Russian material were subsequently resolved by the demonstration of its lateral sporangia, which necessitated its removal from the genus *Psilophyton* (with terminal sporangia) to the new genus *Margophyton* (Zacharova 1981). In a final twist, the demonstration of terminal sporangia in European *P. burnotense* has confirmed its trimerophyte status and hence cannot be the same taxon as the Siberian examples which belong to the lycophyte lineage and now require a new species name (Schweitzer 1989). Such are the pitfalls of recognising vegetative convergence in the absence of anatomy in compression and impression fossils and this example provides an indication of the extent of research activity required to confirm the presence of cosmopolitan taxa! Well-illustrated, intriguing endemics (e.g. *Christophyton kuznetzkianum*) need similar attention. A further characteristic is the lack of lycopsids in the Siberian assemblages. *Drepanophycus spinaeformis* is an exception, but is itself in need of revision.

The Karaganda and Junggar basins in Kazakhstan present different kinds of phytogeographic puzzles, because the area is an amalgam of a number of small plates, reflecting a very complex geological history. The plants of the central area (Karaganda) thus flourished on a plate distinct from that of the neighbouring Junggar Basin. Fossils from Karaganda, central Kazakstan, were described by Yurina (1969) whose collections D.E. was able to peruse in Moscow, and by Senkevich (1978, 1980). Marine incursions allow some independent dating involving brachiopods and graptolites. Again, representatives of cosmopolitan taxa such as *Cooksonia* (*C. crassiparietilis* Yurina, 1964, 1969), *Psilophyton* and *Zosterophyllum* need new assignation as do the numerous lycopsids which, in contrast to Siberia, dominate the assemblages. These lycopsids include European / North American taxa such as *Drepanophycus spinaeformis*, *D. gaspianus* and *Protolepidendron wahnbachense* and endemic *Lidasymophyton akermensis* (Senkevich 1980)—all in need of revision. Such uncertainties prevent adequate assessment of palaeogeographic relationships of the flora, although superficial scrutiny suggests great similarities with Laurussia rather than Siberia. Equally interesting are the older assemblages from the Junggar basin in the south. Fossils in the Tokrau Formation occur in terrestrial rocks interbedded with marine facies that yield graptolites which allow confident dating (Senkevich 1975, 1986) as uppermost Silurian (Přídolí). The plants include members of the rhyniophyte complex, but with organisations more complex than in coeval rocks elsewhere, plus spiny and 'leafy' axes. A similar composition is found in adjacent Xinjiang (China) where *Junggaria* is probably congeneric with Senkevich's *Cooksonella,* although there are further nomenclatural problems, while graptolites confirm the age as Přídolí (Cai et al. 1993). Intensive fieldwork near Hoboksar, north-west Xinjiang is proving very productive and demonstrates the importance of the Junggar assemblages to understanding possible provincialism early in the colonisation of the land by tracheophytes, while reinforcing the need for revision of the Kazakhstan fossils (Cai et al. 1993).

The Volyno-Podolia margin of the Russian platform, Ukraine has yielded 'leafy' stems of uncertain affinity from the Late Silurian Skala horizon (Istchenko 1969).

Sections exposed in the banks of the Dniestr river extend into the Lower Devonian and preserve vascular plants and algae in a marginal facies. During a meeting of the International Submission of the IUGC on Silurian stratigraphy in 1983, led by academician Solokov, it was possible to examine the extensive collections of T.A. and A.A. Istchenko in Kiev. Plants from the Skala horizon (Přídolí) include algae (*Primochara*), rhyniophytes (*Cooksonia*, *Eorhynia* (*?Salopella*)) and possibly the earliest hepatic, *Prehepaticites* (see below), as well as the leafy forms (including *Lycopodolia*), whose lycopsid credentials need further scrutiny. In addition, the succeeding Lower Devonian assemblages (Istchenko 1965) contain plants also found in Laurussia, as well as less familiar taxa such as *Tirasiophyton europea*, but their age is based on the plants themselves

There is evidence of even older land plants from the Upper Ordovician of the Tungus Basin on the Siberian Platform, based on palynological assemblages (Raevskaya et al. 2016). They include, together with acritarchs, prasinophytes and chitinozoans, cryptospores in the form of naked and enveloped monads, dyads, tetrads and polyads, similar to those from rocks of the same age (Fig. 3). Previous ultrastructural studies had indicated hepatic affinities of the dyads, while the tetrad configuration is noted in certain extant hepatics. Basal embryophytes (bryophytes + tracheophytes) are poorly known worldwide. *In situ* dyads and tetrads found in sporangia in the Lower Devonian of southern Britain led to the recognition of a new group of basal embryophytes that possess both tracheophyte and bryophyte characters (Edwards et al. 2014). The mid Palaeozoic megafossil record of bryophytes is meagre. The Silurian Podolian fossil named *Prehepaticites* predates the oldest unequivocal hepatic in the Upper Devonian, as do the overlooked rosette-like thalloid fossils named *Sciadophytopsis* and *Riccielliopsis* from the Middle Devonian of Podolia (Istchenko and Sclyakov 1979), all of which are urgently in need of revaluation.

Finally, mention should be made of progress in disentangling the affinities of members of the Devonian order Spongiophytales, be they tracheophytes, algae or even lichens. They are united in being essentially axial organisms with very thick cuticles and include such disparate taxa as *Spongiophyton*, *Orestovia* and *Biteleria*. Space does not allow a detailed review of the controversies surrounding description and identification of specimens from Russia, but Broushkin and Gordenko’s (2009) description of a new tracheophyte, *Istchenkophyton filiciforme,* from the Kuznetsk Basin demonstrates how rigorous examination, especially employing electron microscopy, can resolve such issues.

In encouraging the search for new fossils, particularly with anatomy, and renewed activity on Russian assemblages, as well as those from other parts of the former Soviet Union, D.E. concurs with the late Sergei Meyen, the most influential and insightful palaeobotanist of his generation (Meyen 1987), when he wrote in a personal letter responding to her request for information on the Kazakhstan assemblages, 'This enigma will not disappear if we scrutinize now and again published lists and badly reproduced photographs. One should merely wait until a new generation of palaeobotanists clean the Augean stables'. Perhaps now is the time!

DOCUMENTING A MAJOR EVOLUTIONARY TRANSITION

The transition from aquatic vertebrates with fins and scales (fish) to those that had limbs with digits (tetrapods), and so could live on land, is one of abiding interest not only to palaeontologists, but also to the general public (Clack 2012). Over the past twenty years, our knowledge has expanded more or less exponentially, with discoveries of Devonian and earliest Carboniferous tetrapods, and the predecessors of the tetrapods, the tetrapodomorph fishes.

Nearly 20 taxa of Devonian tetrapods are now recognised, including some still awaiting description and analysis, and they occur worldwide (Clack 2012). Although originally only found in East Greenland, some of the most important subsequent finds were made in Russia (Fig. 4), and the same is true for the tetrapodomorph fishes closest to tetrapods. This section describes these discoveries and some of the collaborations between Russian, British and other European scientists that have helped build a picture of this important transition.

In 1984, Oleg Lebedev announced the Devonian tetrapod *Tulerpeton curtum* from the Tula Region. This specimen consisted of a nodule containing a few skull bones but also fore- and hind limbs, shoulder girdle and parts of the pelvic girdle, some vertebral elements and gastralia of a single partially articulated individual (Lebedev 1984, 1985). Intriguingly, it shows several traits that are more reminiscent of later Carboniferous tetrapods than the two then known Devonian forms, especially in the shoulder girdle and humerus. It was thought anomalous, however, in that the forelimb carries a complement of six digits rather than the conventional five. The hind limb, although the pes is incomplete, shows bases for six toes. A series of further publications, reconstructions and analyses followed, including comparison with the trackways made by Devonian tetrapods from Australia. Collaborations on more detailed descriptions were made with J.C. and Mike Coates, then in Cambridge (Lebedev and Clack 1993; Lebedev and Coates 1995).

Further discoveries of Devonian tetrapods with complete limbs put *Tulerpeton* in context. All three had more than five digits (Coates and Clack 1990). In fact, *Tulerpeton* was clearly part of a pattern of multidigited tetrapods, initiating new interest in the evolutionary developmental biology of tetrapod digits. It generated new collaborations between palaeontologists and developmental biologists, previously quite separate research endeavours, which continues to this day (e.g. Shubin et al. 1997; Davis et al. 2007; Standen et al. 2014).

The number of toes was not the only surprise of the *Tulerpeton* find. Its geological context was highly unusual and unexpected representing a hypersaline environment many kilometres from the nearest landmass (Alekseyev et al. 1994). It appeared to contradict the common previous assumption that tetrapods originated in fresh waters. Had it been washed out to sea as a mummified carcass? It surely could not have been living there. Based on the bias following the limited evidence provided by East Greenland, a freshwater origin had been assumed (but see Thomson 1980 for an early alternative view). Subsequent discoveries have increasingly shown that a marginal marine or lagoonal origin is much better supported (Lebedev 2004; Lukševičs and Zupins 2004). *Tulerpeton* was the first Devonian tetrapod discovery to prompt questions about our assumptions on this.

Since the discovery of *Tulerpeton*, other Devonian tetrapods have been found in Russia. *Jakobsonia*, described by Lebedev (2004), came from a new locality with the potential for further discoveries. In the northern province of Timan, further new material awaiting formal description consists of isolated skull and girdle bones preserved in a limestone matrix. These can be extracted by acid digestion and reveal not only that several of the bones can be fitted together and belonged to a single individual, but that this new genus shows some remarkably primitive features. Work is in progress with Pavel Besnosov and colleagues with J.C. and Per Ahlberg from Uppsala (Ahlberg et al. 2011). Unexplored Late Devonian sequences in Siberia also have great potential for new discoveries in this important field (P. Ahlberg pers. comm.).

These early tetrapod finds reveal the rich potential in Russia for illuminating this crucial transition in the history of life on earth, with significant impact in producing new ideas and overturning established hypotheses (Fig. 4).

The tetrapodomorph fishes represent another area in which Russian palaeontologists have made and can continue to make key contributions. Chief among the researchers in this area was the late Emila Vorobyeva. She described several Late Devonian tetrapodomorphs including *Panderichthys* and *Obruchevichthys* as well as a range of less well known earlier forms.

Panderichthys was regarded as a problematic taxon from some years, but with the discoveries of *Elpistostege* in the Frasnian of Canada, its significance became recognised. Vorobyeva and Schultze (1991) described the skull of *Panderichthys* in detail, drawing attention to features of its skull that foreshadowed those in limbed tetrapods. In 1992 with Alexandr Kuznetzov, Vorobyeva made an assessment of its likely locomotory mode based on its shoulder girdle and forelimb. Although most of its postcranium had not been fully described at that time, several articulated specimens exist and new techniques have increased our knowledge (Boisvert 2005; Boisvert et al. 2008). Features of *Panderichthys* and *Elpistostege*, further illuminated by the finds of *Tiktaalik* in Canada (Daeschler et al. 2006), reveal that these three taxa are members of a series of near-tetrapod taxa each of which shows tetrapod-like features of the skull and postcranium. The Russian collection of *Panderichthys* specimens remains to be more fully exploited.

Vorobyeva (1977) first described *Obruchevichthys* before the more recent studies of Devonian tetrapods had got under way. The specimens comprise two fragments of lower jaw. With the description of the lower jaw of *Elginerpeton* from the Frasnian of Scotland, *Obruchevichthys* was recognized as a tetrapod (Ahlberg 1991). The phylogeny of the Tetrapodomorpha is currently in need of revision with the addition of members of the clade from Russia. These need urgent restudy in the light of more recent finds and of current systematic practice (Fig. 4).

The end of the Devonian was marked by an extinction event that terminated the reign of many fish taxa common in the so-called ‘Age of Fishes’. It marked the demise of both the fish-like tetrapods and the near-tetrapod fishes, as well as other more archaic groups, at least as far as the fossil record shows (Sallan and Coates 2010). Following that extinction, a dearth of finds of continental vertebrates suggested that life on land took a very long time to recover, in an interval colloquially known as 'Romer's Gap' (Coates and Clack 1995). By the end of this interval, tetrapods had radiated into more familiar forms and generated fully terrestrially capable animals. Recent discoveries in the Tournaisian of Scotland have inserted several new tetrapods in this gap (Clack et al. 2016). Some of these indicate cross-over taxa between the Devonian and Carboniferous – of which *Tulerpeton* is an earlier indication – suggesting that the extinction event might not have been so drastic for tetrapods (Anderson et al. 2015). Many new lungfish (Smithson et al. 2015) and chondrichthyan taxa (Richards et al. 2015) have also been found. Few indisputably Tournaisian lungfish were previously known: one from Russia, *Parasagenodus*, from the 'Lower Carboniferous' was poorly dated and was likely not Tournaisian (Vorobyeva 1972; Lebedev pers. comm.). Studies in Scotland show that tetrapods, lungfishes and chondrichthyans all diversified rapidly following the extinction event and that continental Tournaisian strata could provide rich palaeontological rewards. Although Russian Tournaisian strata are generally considered to be mainly marine, there are presumably sequences that are marginal marine (e.g. Lebedev 1996) or even continental. Studies of Famennian–Tournaisian sequences might help resolve some of the current disputes regarding the cause of the end-Devonian extinction, and its extent (McGhee 2013). Continental vertebrates are also poorly known in Visean strata, and these too could yield rich rewards for those determined enough to seek them out.

THE IMPACT OF MASS EXTINCTIONS ON THE HISTORY OF LIFE

There have been many extinction events in the history of life, times when large numbers of plant and animal species have died out in a single event, often triggered by some shock environmental change. Largest of these events are the mass extinctions, when 50% or more of species have disappeared, and the most famous of these happened 66 Myr ago, when the dinosaurs, marine reptiles, and ammonites disappeared at a time of shock environmental change triggered by the impact on Earth of a giant asteroid. This event is not well documented in either Russia or the UK, and attention has focused on older events, most notably the largest mass extinction of all time, the Permian-Triassic mass extinction (PTME), which happened 252 Myr ago.

There are extensive basins of largely terrestrial Permian and Triassic rocks between Moscow and the Ural Mountains, and extending for some 2000 km from the Arctic coast to the borders of Kazakhstan. The Permo-Triassic boundary (PTB) has been identified at many sites throughout these basins, and evidence for the PTME found among the terrestrial tetrapods in particular (Benton et al. 2004; Benton 2015). The scale of the PTME was huge. Global compilations of data show that more than 50% of families of animals in the sea and on land went extinct, and regionally based studies show that this equates to 90% of species loss. The cause of the PTME has long been debated, but it was obviously catastrophic, and the balance of current opinion indicates that the Siberian Traps large igneous province provides the smoking gun.

The Siberian Traps comprise 3 million cubic kilometers of basalt lava that cover 5 million square kilometres of eastern Russia to a depth of 400–3000 m. It is widely accepted now that these massive eruptions, confined to a time span of less than 2 myr in all, were a significant factor in the PT crisis (Reichow et al. 2009). Eruptions of these basaltic lavas were accompanied by the escape of huge volumes of gases such as methane, carbon dioxide, sulphur dioxide, and others. Mixing with water in the atmosphere, these gases produced acid rain, which killed the land plants, and this released the soils that were also stripped off the land. With no food, land animals died. Warming is often associated with loss of oxygen, and seabeds became anoxic, so killing life in the sea. The CO_2 from the eruptions also caused ocean acidification, which doubtless led to further distress among shelled organisms.

Much of the evidence for this ‘standard’ killing model (Wignall 2015) comes from studies of marine sediments across the PTB in North Italy, western Canada, Spitsbergen, Greenland, and especially South China. In marine sections, the end-Permian sediments are often bioclastic limestones or intensely bioturbated mudstones and sandstones, indicating richly-oxygenated bottom conditions for life. In contrast, sediments deposited immediately after the extinction event, in the earliest Triassic, are dark-coloured, often black and full of pyrite. They largely lack burrows and indeed any fossils. The sediments and isotope geochemistry confirm a remarkable shift to anoxic conditions just at the time of the PTME. Further, a dramatic shift in oxygen isotope values indicates a global temperature rise of around 16°C. Climate modellers have shown how global warming can reduce ocean circulation, and the amount of dissolved oxygen, to create anoxia on the seabed. The oxygen spike is matched by an equally dramatic carbon excursion, indicating a dramatic increase in the light carbon isotope (^{12}C), coming from dead organisms, volcanic sources, and even massive releases of gas hydrates from frozen reserves on the ocean floor. The warming became self-reinforcing, a so-called "runaway greenhouse" effect, and the ocean-atmosphere system apparently spiraled out of control, leading to the biggest crash in the history of life.

Evidence for conditions on land comes primarily from Russia, South Africa, and northern China. Indeed, one key component in providing linkages from land to sea came from studies in the Russian Permo-Triassic red beds in the 1990s. Geomin geologist Valentin Tverdokhlebov (Fig. 5a) had plotted great alluvial fans that spread westwards from the Ural Mountains at the very beginning of the Triassic. The alluvial fans spread for 100–150 km over the low-lying Permian lakes and meandering rivers on the great plain. Tverdokhlebov identified the boulders in the different basal Triassic alluvial fans and tracked them to their sources high in the Ural Mountains. The conglomerate boulders include blocks of Devonian or Carboniferous limestones, often with fossils, and metamorphic and igneous rocks.

During collaborative field trips in the 1990s, led by Valentin Tverdokhlebov (Benton 2008), we investigated the PTB, and especially this remarkable shift in sedimentary regime (Fig. 5a). The uppermost Permian sedimentary succession consists of repeated fining-upward cycles, each beginning with a cross-bedded sandstone, and then fining upwards into siltstones and mudstones and ending with a palaeosol. The palaeosols are sometimes associated with plant remains and are nearly always invested with carbonate. These cycles are interpreted as the deposits of cyclical lakes, with occasional influx of sediment (the coarser sands), then finer lake deposits and finally a palaeosol when the lake dried out – all perhaps the result of a broadly monsoonal climate (Newell et al. 1999). The earliest Triassic conglomerates were unexpected, marking an entirely new rock type, and evidence of a huge change in sedimentary regime from meandering to braided streams.

Earlier workers had interpreted this shift as evidence for renewed uplift of the Ural Mountains. The Urals had been uplifted primarily in the late Carboniferous and early Permian as the separate Eurasian and Siberian continental plates came into contact, and they could well have become active again. Another idea attributed the switch from low- to high-energy deposition to a dramatic increase in rainfall at the PTB. Both suggestions were rejected by Newell et al. (1999) because, firstly, the sedimentary regime switch is also evident in South Africa, Australia, India, and Spain, and so was apparently worldwide. Secondly, independent climatic evidence pointed to increasing aridity across the PTB, not increasing rainfall. Newell et al. (1999) argued for a third model, linking increasing aridity and mass stripping of forests. Climates worldwide switched from a semi-arid/sub-humid climate in the latest Permian to greater aridity in the earliest Triassic, and this could increase sediment yield by reducing vegetation cover. If vegetation is stripped from the surface of the land, rates of erosion can increase perhaps tenfold. Local data confirms the short-term loss of plants at the PTB in Russia and elsewhere, as well as a global 'forest gap', lasting for some 10 Myr of the Early and Middle Triassic, when forests were absent worldwide. Without extensive forests and their role in generating and binding soils, erosion on land may have reverted to early Palaeozoic levels. This has subsequently been confirmed by studies in other parts of the world, and especially by the observation of a sudden spike in sand washed from land into shallow marine sediments around the world (Algeo and Twitchett 2010).

The Russian research provides key evidence that links land and sea in the PTME killing model, and there is enormous scope for future studies of the Russian Permian-Triassic red beds. Recent work continues to reveal new examples of fossil tetrapods, and these are studied in relation to coeval animals from around the world (Fig. 5c). The associated plants, molluscs, insects, and fishes have been studied extensively by Russian palaeontologists, but much of the work remains unpublished because it formed part of the mapping programmes by Geomin. For example, well established stratigraphic schemes based on palynomorphs, bivalves, ostracods, and fishes, as well as magnetostratigraphy (Fig. 5b), are only in part, and these require substantial re-study and publication. The potential to use the Russian red beds to document events through much of the Permian and Triassic relies on secure stratigraphy and extensive correlation with developing schemes in South Africa and China. In addition, increasing focus on the detail of the Siberian Traps should allow researchers to identify how the killing agency rolled out around the world. Such work will enhance our understanding of how mass extinctions have affected life on land in general, but also provide deeper insights into the devastating PTME.

Early hominin occupation in Russia includes the intriguing remains from Denisova Cave (Altai Mountains, Siberia), which has had a history of excavation by Russian archaeologists since the 1970s. The 'Denisovans', a group of hominins currently represented by only a fragmentary manual distal phalanx (Krause et al. 2010), two large adult molars (Sawyer et al. 2015), and a deciduous molar (Slon et al. 2015; Stringer and Barnes 2015) from the cave, received considerable attention when the preservation of the fossils permitted DNA extraction, revealing a lineage genetically distinct from modern humans and Neanderthals (Krause et al. 2010). The reconstructed genome indicated the Denisovans are more closely related to early Neanderthals than modern humans (Reich et al. 2010), diverging from the Neanderthal lineage ~450 kya, roughly contemporary to the early Neanderthals at Sima de los Huesos (Atapuerca, Spain) to which they were compared (Meyer et al. 2014). The Denisovan material was uncovered from multiple sequences within the cave indicating an extended period of occupation (Sawyer et al. 2015), 150-50 kya (Stringer and Barnes 2015). Neanderthal fossils too have been discovered from Late Pleistocene deposits (Prüfer et al. 2014), suggesting the cave was alternately occupied by Neanderthals and Denisovans (Stringer and Barnes 2015); though attribution of the archaeology dated to these periods is consequently ambiguous. Subsequently, the cave was also occupied by modern humans, based on the presence of Upper Palaeolithic tools from ~40 kya (Derevianko et al. 2000).

Morphologically, the molars are distinct from those of Neanderthals and modern humans in their large size and root and crown morphology, with some archaic traits generally considered reminiscent of early *Homo* (Sawyer et al. 2015). The genetic evidence of introgression with an additional, currently unknown hominin species has been suggested to account for these archaic features (Sawyer et al. 2015), though at present the small and fragmentary nature of the Denisova fossils are not sufficient to make any significant morphological comparisons with the majority of other fossils, which have not yielded genetic data. However, the genetic diversity of the four separate individuals whose genomes have been sequenced indicate that the Denisovans had a population size greater than that of Neanderthals, and their geographic range likely extended beyond the Altai region (Pennisi 2013). Furthermore, the concentration of Denisovan DNA in modern Oceanic populations (Reich et al. 2010, 2011; Meyer et al.

2012), with minimal amounts in modern mainland Asian populations (Prüfer et al. 2014), suggests that the Denisovan range extended significantly beyond Siberia, perhaps even having crossed the Wallace line (Cooper and Stringer 2013). If this is the case, the potential range of the Denisovans extended into areas of mainland Asia for which there is already an extensive fossil record. In fact, several taxonomically ambiguous specimens from mainland Asia have been suggested to represent the Denisovans, given their relative mosaicism and combinations of traits associated with Neanderthals, *H. heidelbergensis* and *H. erectus* (Cooper and Stringer 2013; Xing et al. 2015; Li et al. 2017).

While collaborations between British and Russian researchers within palaeoanthropology have been rare historically, the wealth of information derived from the Denisova materials has led to some collaborative research, particularly in dating the site (e.g. Brown et al. 2016; Douka et al. 2015). However, there is still room to develop a large-scale interdisciplinary approach to understanding human occupation in northern Asia. Increasingly, patterns of human occupation during the Late Pleistocene in Asia appear to have been extremely complex, with multiple species occupying the region and occasionally interbreeding, as exemplified by the data emerging from Denisova and reflecting the complexity that has also emerged in the western European fossil record.

In 2001, the first of three phases of a large-scale consortium project called the Ancient Human Occupation of Britain (AHOB) began, funded by the Leverhulme Trust. Over its 12 years, AHOB collected and analysed data from assemblages at new and existing sites that relate to the colonisations of western Europe during the Pleistocene (Stringer 2007, 2011). During this time (Fig. 6), data have continued to indicate that mainland Britain became increasingly isolated from continental Europe between Marine Isotope Stage (MIS) 11 (~400 ka) and MIS 7 (~200 ka). From this point, Britain was apparently without human occupation until the end of MIS 5 (~71 ka), after which time Neanderthals recolonised, followed by modern humans entering Britain for the first time around 40 ka. During the Last Glacial maximum, as well as for periods of the Younger Dryas, Britain again seems to have been devoid of human occupation, though humans recolonised Britain rapidly following these periods, as indicated through improvements in radiocarbon dating (see, e.g. Jacobi and Higham 2009). These episodic and fragmented occupations of Britain provide a model that is probably applicable to many regions of Eurasia, including Russia, where severe climatic and environmental changes must have also regularly disrupted the patterns of early human settlement.

In the 1970s, two conflicting viewpoints emerged concerning the number and sequence of glacials and interglacials recognisable in Britain during the Quaternary. The first focused on pollen data informed by vegetational changes, which indicated that there were four interglacials in Britain, with three intervening glaciations (Mitchell et al. 1973). The alternate viewpoint was that mammalian biostratigraphy was more accurate than pollen alone. This opinion was reinforced by work on molluscan aminostratigraphy (Bowen et al. 1986) – together these indicated that the record was more complex than the pollen data indicated. However, debates about the aminostratigraphic methods meant that the debate was not quickly resolved. Eventually, the mammalian biostratigraphic approach inspired Mammal Assemblage Zones (MAZ), which have been invaluable for AHOB (Currant and Jacobi 2001), and aminostratigraphy was also placed on a more secure footing (Penkman et al. 2013).

Work to better understand the Thames deposits was also carried out during this time, which was relevant to the debate about the British Pleistocene sequence. During the early history of the Thames, the river has been displaced progressively southwards, a movement that meant it accumulated large amounts of sediment critical to the biostratigraphy of the early human occupation of Britain. Crucially, these data suggest that the largest diversion of the Thames was caused by Anglian ice, and this can be correlated with MIS 12 (Bridgland et al. 2004). The significance of this is marked for sites such as Swanscombe in MIS 11, with post-diversion interglacial deposits. Additionally, Swanscombe and MIS 11 have been correlated with the Hoxnian Interglacial (see, e.g. Bridgland et al. 2004; Penkman, et al. 2013).

Interpretations of the Swanscombe hominin have varied greatly since the discovery of its first cranial bone in 1935, including being used as support for the Piltdown finds and later as a member of a pre-*sapiens* lineage. Since re-evaluations in the 1960s, however, it has more widely been considered to represent an early Neanderthal (Weiner and Campbell 1964; Stringer 1974; Hublin 1988). Its similarities in cranial morphology to the Steinheim skull from the Middle Pleistocene, in addition to hominins from the large assemblage at Atapuerca, Spain, in the Sima de los Huesos (SH) (Bermúdez de Castro et al. 2004; Martinón-Torres 2012; Arsuaga et al. 2014), provide support for the archaic affinities of the Swanscombe hominin and its potential conspecificity with Neanderthals.

It may be that human occupation in Britain is even more complex than we recognise, given the continuing enigma of the Clactonian industry. The Lower Loam, a deposit of silt and sand beneath the Middle Gravels of the Swanscombe skull (McNabb 2007), contains an assemblage of artefacts that are characterised by flake tools and that do not include handaxes attributable to the Acheulian. That assemblage is representative of the Clactonian industry, which was originally described based on material from Clacton in Essex. At one time, Clactonian artefacts were thought to be the oldest technology in Britain, either being replaced by handaxes once they arrived in Britain, or representing a precursor industry. However, the dating of handaxe sites such as Boxgrove as older than deposits containing Clactonian artefacts refutes this idea. This has raised the question of whether the tools produced by the Swanscombe and other peoples had different functions. Or did the people represented by the Clactonian have a distinct pattern of living, with the absence of handaxes signifying either the inability to produce such tools or a cultural tradition that inhibited their production (McNabb 2007; Stringer 2007)?

A partial skeleton of *Palaeoloxodon antiquus,* associated with Clactonian tools, was found in 2003, at Ebbsfleet in Kent. It is likely that this Clactonian occupation was towards the beginning of the same interglacial period as the Clactonian occupation at Swanscombe. For butchery, it had previously been suggested that handaxes were the favoured tools during the later British Lower Palaeolithic, and therefore this find was significant, as it associated Clactonian tools (and an absence of handaxes) with a large mammal skeleton. This supported the idea that there must have been separate populations with different lithic traditions (Wenban-Smith et al. 2006). This view has been reinforced by a repetition of the same Clactonian-Acheulian sequence at the MIS 11 site of Barnham in Suffolk (Ashton et al. 2016).

An additional part of the Clactonian puzzle was provided by a discovery in 1911 at Clacton - a piece of yew wood sharpened to a point. While it could not be confirmed that it had been hardened in a fire, microscopic analyses showed that it had been carefully shaped (Oakley et al. 1977). The artefact was broken, and at 33 cm in length, had many interpretations. Its significance was amplified, however, by the discovery of several wooden spears at Schöningen in Germany (Conard et al. 2015). It is thus possible that the Clacton wooden artefact represents an important component of Lower Palaeolithic technology that was unsuspected until the Schöningen discoveries. Neither the Clacton nor Schöningen sites had human remains associated with the wooden artefacts. However, another German site, the Steinrinne travertine quarry near Bilzingsleben, did yield some fossil evidence approximately contemporary with Clacton and Schöningen. Cranial remains of three individuals were found, and floral and faunal evidence at the site indicates that the remains derived from a warm Middle Pleistocene interglacial (probably MIS 11, or perhaps MIS 9). These have been reconstructed as either *Homo erectus* (Vlček et al. 2000) or possibly *Homo heidelbergensis* (Stringer 2012).

At one time, Swanscombe was considered as the oldest site in the UK to yield archaeological and fossil remains of human occupation in Britain. While the Mauer mandible of *Homo heidelbergensis* from Germany indicated that early humans had reached northern Europe comparatively early in the Middle Pleistocene, no convincing evidence suggested that humans had arrived to Britain until after the Anglian ice advance and its resultant diversion of the Thames southwards. It was argued that, given the climatic conditions of Britain at the time, the humans of the earlier Middle Pleistocene could not have weathered the conditions by producing clothing, shelters, or fire. Furthermore, they were considered to be largely opportunistic hunters and scavengers rather than hunters of large game, and would have been vulnerable and unable to compete with the large carnivores of the period.

Archaeological remains from cave deposits at Westbury-sub-Mendip threw this into question, indicating that humans were present in Britain during a warm stage prior to the Anglian. Based on biostratigraphic faunal analyses, Bishop (1975) suggested that there might have been human occupation during an unrecognised interglacial between the Cromerian and the Hoxnian (~600 ka and ~400 ka respectively). Further excavations recovered more artefacts and also identified cut-marked bones at Westbury (Andrews et al. 1999). These finds were complemented by subsequent discoveries at Boxgrove, that were also found to be from interglacial deposits earlier than the Hoxnian, based on the represented fauna, and therefore also predating the Anglian Thames diversion (and probably belonging to MIS 13, ~500 ka; Roberts and Parfitt 1999). In addition to about 400 handaxes that have been excavated at Boxgrove and assigned to this period, bones of large fauna with cutmarks have also been recovered, and these encouraged researchers to re-evaluate their assumptions about the hunting capabilities of these early humans. The subsequent discovery of fossil human remains - a partial tibia and two lower incisors - in the early 1990s heightened the significance of the archaeological remains. Provisionally assigned to *H. heidelbergensis* (Stringer et al. 1998; Stringer 2007; Hillson et al. 2010), these remains represent the earliest known fossil evidence of humans in Britain. Scratches and pits on the labial surfaces of the incisors have been interpreted as the result of damage by tools, perhaps as pieces of food gripped between the front teeth were cut by stone tools. Aided by the Boxgrove specimens, a 'Short Chronology' was developed to describe the first human occupation in Europe, which was represented by sites such as Boxgrove and Mauer from ~500 ka (Roebroeks and van Kolfschoten 1994). Prior to this date, the evidence was considered to be sparse and unconvincing.

However, since then, earlier sites have emerged that suggest some earlier forays into Europe. These include the Orce site in southern Spain, where a fossil hominin tooth has been discovered, as well as tools and fauna, that dates to ~1.4 ma (Toro-Moyano et al. 2013) and at Pirro Nord, which is of a similar age (Arzarello et al. 2012). Furthermore, in northern Spain at Gran Dolina fossil human remains dated to ~850 ka have been excavated (Bermúdez de Castro et al. 2004; Bermúdez de Castro and Martinón-Torres 2014) and assigned to a new taxon *Homo antecessor* (Carbonell et al. 2005; Lacruz et al. 2013). Similarly, an even older Atapuerca site, Sima del Elefante, has yielded fragmentary human remains, flake and core tools, and fauna with evidence of butchery. Sima del Elefante has been dated to between 1.1 and 1.2 ma (Carbonell et al. 2008). Together, the evidence at Gran Dolina and Sima del Elefante has led researchers to argue that these humans represent early Eurasian lineages that may have gone extinct. Increasingly, archaeological evidence in combination with the Sima del Elefante material suggests that the first hominins may have entered southern Europe soon after the hominin dispersal represented by the Dmanisi fossils in Georgia, and this has consequently falsified the previously popular hypothesis of a Short Chronology in European occupation.

For a while, some researchers supported a Short Chronology north of the Alps, given the absence of convincing evidence for human occupation before 500 ka, if Mauer and Boxgrove could be dated to that time period (Roebroeks 2001). However, a flint handaxe was discovered on the Happisburgh foreshore in Norfolk, in 2001, which is dated to at least an MIS 13 age (Ashton *et al.* 2010). Reanalysis of a Happisburgh assemblage from a 19th century collection led to the discovery of a bison foot bone with cutmarks (Parfitt et al. 2005), which represents the first strong evidence of human occupation from a Cromerian locality in East Anglia (Parfitt et al. 2005). Subsequently, systematic at the site of Happisburgh 1 have yielded over 50 artefacts and several large faunal specimens with evidence of impact damage and cutmarks.

A site on the shoreline at Pakefield, in Suffolk, had been yielding 'Cromerian' fossils since the 19th century. Then, human-modified flint was also recovered, which prompted formal excavations in 2004, ultimately producing over 40 flint flake and core artefacts (Parfitt et al. 2005). Provisionally, Pakefield has been assigned to the warm peak of an interglacial correlated with MIS 17 (~700 ka), pushing back human occupation in Britain to the early Middle Pleistocene (Fig. 6).

In 2006, further excavations at a new Happisburgh locality, site 3, uncovered signs of an even earlier occupation of Britain, lying between ~850 and 950 ka, based on biostratigraphy and palaeomagnetism, with evidence of less favourable palaeoclimatic signals. Modified flint in the form of scrapers, notches, and flakes was discovered, and analyses of the fauna and flora of the site indicated that Happisburgh at this time would have been at the border of the boreal zone (Parfitt et al. 2010). In 2013, correlated deposits at Happisburgh revealed evidence of more than 40 human footprints made in river muds of what was then the Thames River system (Ashton et al. 2014). Unfortunately, there are currently no human fossils associated with either the Pakefield or Happisburgh 3 deposits, and therefore the identity of these early northern European inhabitants is still unknown. Generally, it has been supposed that the hominins represented at Happisburgh 3 and Pakefield were derived from northern waves of migration from southern Europe, and therefore likely linked to *H. antecessor*. However, *H. antecessor* is currently only known from the Gran Dolina locality, and it is unclear how it and *H. heidelbergensis* relate phylogenetically to the shared ancestry of Neanderthals and *H. sapiens* (Stringer 2016).

The AHOB projects have answered many questions concerning the earliest human occupations of Britain, and suggest that Britain was colonised at least 9 times by successive human populations during the Pleistocene (Fig. 6). But new questions have also arisen, in particular with the discovery that the earliest known occupants at Happisburgh, at more than 800 ka, were already coping with climatic conditions somewhat cooler than our present interglacial. This suggests that they must have had either better cultural means to cope with the cold than currently recognised, or that they had evolved physiological adaptations to cope with the cold, or perhaps both. This raises the possibility that human tolerances to cold in the Lower Palaeolithic were sufficient to have colonised northern regions elsewhere in Eurasia, at least during the interglacial periods. Perhaps a multidisciplinary consortium approach like that of AHOB could reveal evidence of such early occupations in Russia too.

CONSERVATION PALAEOBIOLOGY

In addition to providing the primary source of data on the historical pattern of human evolution, fossil and archaeological records from the Neogene, and especially the Quaternary, provide unique insights into the composition of past ecosystems and past human interactions with biodiversity. Humans are now a dominant driver of patterns in global biodiversity; well-documented ongoing anthropogenic transformation of the biosphere is responsible for catastrophic declines across a broad range of taxa and disruption to the structure and functioning of ecosystems, and it is widely accepted that we are experiencing a human-mediated global biodiversity crisis (McClellan 2014; McGill et al. 2015). For Russian ecosystems alone, recent historical records provide evidence for the human-caused global extinction of Steller's sea cow (*Hydrodamalis gigas*), Japanese sea lion (*Zalophus japonicus*), spectacled cormorant (*Phalacrocorax perspicillatus*) and crested shelduck (*Tadorna cristata*) in the Russian Far East, the regional loss or major range reduction of a wide variety of species including tarpan or wild horse (*Equus ferus*), saiga (*Saiga tatarica*), sociable lapwing (*Vanellus gregarius*) and slender-billed curlew (*Numenius tenuirostris*), and extensive anthropogenic modification to ecosystems across the country (Josephson et al. 2013; IUCN 2016). However, the Quaternary record demonstrates that human activities have substantially affected species and ecosystems through a much longer period of recent prehistory. As a result, insights into key properties of biodiversity—for example, ecosystem structure and composition in the absence of human modification, or the specific ecological requirements of threatened species now restricted to remnant distributions in potentially suboptimal habitat—will remain incomplete and biased by an "extinction filter" if only assessed using modern-day data (Balmford 1996). There is therefore increasing awareness of the need for a new discipline of 'conservation palaeobiology' that integrates a range of long-term archives into conservation research and management, to identify past environmental baselines and provide novel insights into regional biodiversity, extinction dynamics and ecosystem properties that are unavailable from short-term studies (Bonebrake et al. 2010; Rick and Lockwood 2013; Davies et al. 2014; Barnosky et al. 2017).

There is strong evidence that early humans caused the extinction of many large mammals. During the Late Pleistocene, almost two-thirds of terrestrial megafaunal vertebrate taxa (at least 97 genera), mostly mammals, disappeared without ecological replacement from the world's continents during a series of "eco-catastrophic" (Haynes 2002) events, and with very little corresponding extinction of small-bodied species (Martin 1984; Koch and Barnosky 2006; Stuart 2015). Some form of human involvement in Late Pleistocene megafaunal extinction dynamics is now widely accepted by most palaeontologists, as the stepwise nature of these extinctions across different continents correlates with the arrival of technologically modern humans in each region. However, the mechanism by which humans may have driven these megafaunal species losses is unclear (e.g. rapid direct overhunting, or ecosystem-level interactions such as habitat modification). Extinctions also occurred during an interval of major global-scale climatic shifts during the transition from glacial to interglacial conditions near the Pleistocene–Holocene boundary, so that the relative importance or possible interactions of prehistoric human activity and natural environmental change in driving this extinction event have been debated extensively since the nineteenth century (Grayson 1984).

The diversity, evolution, ecology, and extinction chronology and dynamics of the Late Pleistocene megafauna of Russia have been the subject of extensive research, supported by excellent preservation of abundant Late Quaternary material under cool boreal environmental conditions (e.g. in permafrost). This research has been conducted in part through considerable collaboration between Russian and UK academics (e.g. Lister and Sher 2001; Stuart et al. 2004, 2005; Barnes et al. 2007). Current radiometric data indicate that several representatives of the northern Eurasian megafauna, including woolly mammoth (*Mammuthus primigenius*), woolly rhinoceros (*Coelodonta antiquitatis*) and cave lion (*Panthera spelaea*), disappeared from mainland Russian ecosystems during the Late Glacial between *c.* 11,000–14,000 years ago (ya), with several other large mammals also becoming regionally extirpated during this interval

(MacPhee et al. 2002; Stuart 2015). Megafaunal disappearance is associated with the disappearance of vast areas of high-productivity open grass/forb/sedge-dominated vegetation, representing an ecosystem with no exact modern analogue known as 'mammoth steppe' or 'steppe-tundra', and its replacement with wet mossy tundra, shrubs, and coniferous and deciduous forest (Zimov et al. 2012).

This vegetation biome change is often interpreted as having occurred in response to increasing temperatures at the end of the Last Glacial, and may have been responsible for driving the extinction of the large mammal community that was adapted for mammoth-steppe landscapes (e.g. Stuart 2015). However, it has also been argued that this ecosystem shift may represent an example of top-down rather than bottom-up regulation, with the mammoth-steppe ecosystem actually maintained by megaherbivores and disappearing when these keystone species became extinct due to human activity. Heavy mammalian cropping and trampling would likely have suppressed woody growth and stimulated growth of grasses, leading to high rates of transpiration of soil moisture and likely increased carbon storage in dry soils and permafrost, and rapid nutrient cycling from megaherbivore dung supported high ecosystem productivity; conversely, megaherbivore extinction would have allowed shrubs and trees to exclude grasses, rising water tables would have further suppressed grasses and favoured cool, waterlogged moss-covered soils, and decreased nutrient cycling would have led to decreased soil fertility (Zimov 2005; Zimov et al. 2012). This novel hypothesis suggests that mammoth-steppe may represent a stable ecosystem that can potentially be recreated in Russia under current-day environmental conditions if large herbivores are present.

Investigating this possibility is now the focus of the 'Pleistocene Park' project led by Sergei Zimov, which has reintroduced extant large mammals formerly present during the Late Pleistocene (including feral horses, muskoxen *Ovibos moschatus*, and European bison *Bison bonasus*) to a nature reserve on the Kolyma River in Sakha Republic, to test predictions about ecosystem change and potential reduction in greenhouse gas emissions associated with predicted reduction in permafrost thawing, and ultimately aiming to restore regional ecosystem processes that may be 'natural' throughout Quaternary glacial–interglacial cycles (Zimov 2005). Comparable but smaller-scale rewilding projects (e.g., at Oostvaardersplassen in the Netherlands; Lorimer and Driessen 2014) are also underway elsewhere to assess changes in ecosystem structure and productivity associated with reintroduction of regionally extirpated large herbivores, and there is considerable potential for future research in this area to better understand extinction dynamics and ecosystem stability.

Extensive evidence for further human involvement in prehistoric biodiversity loss is documented across the subsequent Holocene Epoch. This was an interval of modest or minimal climatic variation under broadly “modern” environmental and climatic boundary conditions; evidence for human involvement in nearly all Holocene extinctions and ecosystem change is not confounded by major climatic factors and is therefore relatively undisputed (Turvey 2009). Most Holocene extinctions are documented from island systems, including the well-documented extinction of Russia’s final remnant mammoth population on Wrangel Island *c*. 4000 ya (Vartanyan et al. 1993; Stuart et al. 2004). Continental regions experienced reduced levels of postglacial species-level extinction before the recent historical era, leading to use of the term ‘Holocene underkill’ to contrast with hypothesized ‘Pleistocene overkill’ (Grayson 2008). However, it is increasingly apparent that continental ecosystems also underwent considerable anthropogenic modification throughout the Holocene, associated with extensive regional species losses and population depressions (Grayson 2001; Johnson 2006; Crees and Turvey 2014). Reconstructing the magnitude and nature of prehistoric human-caused biodiversity change under postglacial, ‘modern’ environmental conditions is necessary to identify regionally extirpated species for potential reintroduction projects, and the true evolutionary or ecological basis of their geographic distributions before disruption by human activity. Such reconstruction would also provide wider novel insights into important concerns in modern conservation biology, such as the determinants of variation in population vulnerability or resilience through time across different species and landscapes.

Russian ecosystems experienced further postglacial Holocene species losses before the recent historical era. These include (Fig. 7) global extinctions of the final remnant populations of two Pleistocene survivors, the steppe bison *Bison priscus* (persisted until 9,800 ya in Taimyr and 8,900 ya in western Chukotka; MacPhee et al. 2002; Kirillova et al. 2013) and the giant deer *Megaloceros giganteus* (persisted until 7,700 ya in the Urals; Stuart et al. 2004), and the more recent disappearance of aurochs (*Bos primigenius*) in the late Holocene (Crees et al. 2016). The Holocene record also shows that many still-extant species had much broader postglacial geographical distributions in Russia. For example, all wild populations of European bison were extirpated by the early 20th century, but the species formerly occurred across a large area of European Russia as far north as Lake Ladoga (Sipko 2009) (Fig. 7); and archaeological remains demonstrate that multiple sturgeon species (*Acipenser sturio*, *A. oxyrinchus*) occurred in the North Sea during the Holocene (Ludwig et al. 2002; Thieren et al. 2016). A large number of mammal and bird species alone are now known to have become regionally extirpated elsewhere in Europe, e.g. Britain, during the Holocene (Yalden and Albarella 2009; O'Connor and Sykes 2010), and it is likely that future research into postglacial long-term archives will reveal greater levels of human-caused biodiversity loss from "modern" Russian ecosystems.

Data from Holocene long-term archives have so far been used to guide species recovery and environmental restoration programmes, such as the reintroduction of European bison to landscapes within its former distribution in Russia and elsewhere in Europe (Sipko 2009; IUCN 2016), and the proposed reintroduction of Caspian tiger (*Panthera tigris virgata*) to sites in Central Asia (Chestin et al. 2017). However, wide-scale macroecological analysis of patterns of mammalian range loss across Europe, including data from Russia, has revealed that prehistoric human impacts on postglacial biodiversity began early on during the Holocene, and that the dynamic pattern of progressive faunal modification of European mammal assemblages across the Holocene challenges easy identification of 'static' past baselines that could act as benchmarks for current-day environmental management and restoration (Crees et al. 2016). Furthermore, different terrestrial vertebrate guilds have been disrupted to different extents by human activity through the Holocene (e.g. large-bodied mammalian grazers and browsers experienced significantly earlier declines than mammalian carnivores; Crees et al. 2016). It is again likely that reduction or removal of distinct faunal guilds during the Holocene would have triggered wider ecological knock-on effects, such as shifts in plant community composition following both removal of large herbivores (cf. Zimov et al. 2012), and removal of large carnivores and the 'landscapes of fear' that they maintain (Kuijper et al. 2013); however, the potential consequences of this Holocene loss of functional diversity and potential keystone species has not been adequately studied in Russian ecosystems.

Incorporating data from long-term archives is essential for environmental management, but conservation palaeobiology raises important and challenging questions. Ultimately, is it even possible to identify or define what constitutes a 'natural' Russian ecosystem, whether any such systems still occur today—and in the face of conflicting pressures of human resource use and dependency on high-productivity landscapes, could, or should, any Russian ecosystems be restored to incorporate now-lost biodiversity or ecological processes?

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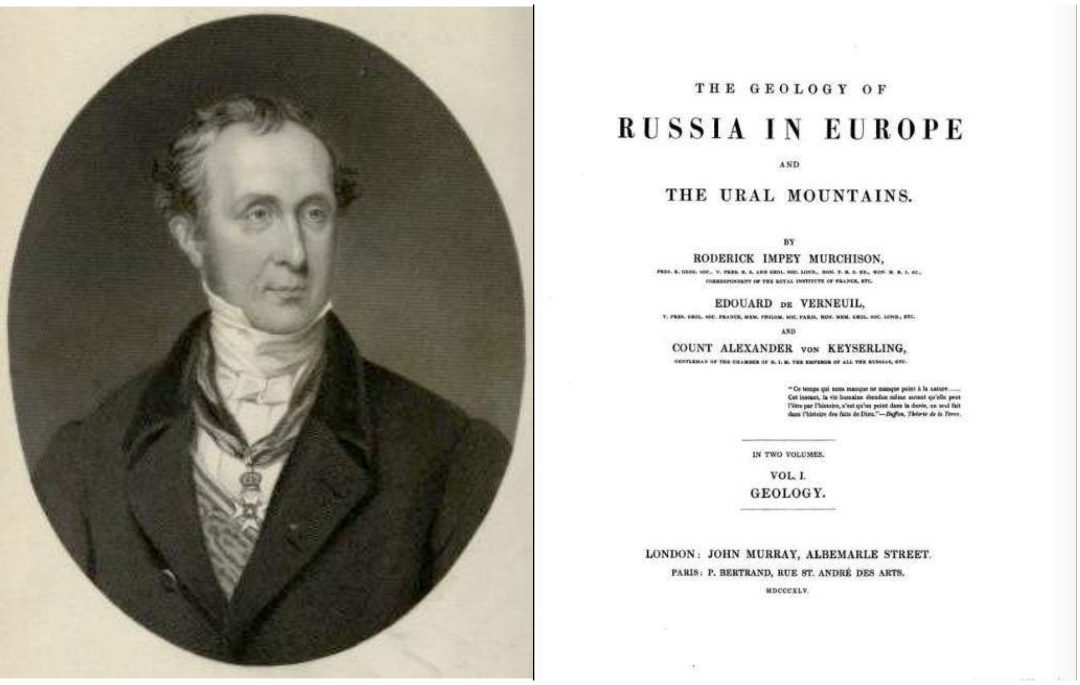

THE GEOLOGY OF
RUSSIA IN EUROPE
AND
THE URAL MOUNTAINS.

BY
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Fig. 1. Sir Roderick Murchison (1792–1871), about the time he visited Russia in 1840, and the title page of his major monograph on Russian geology, published in London, Paris, and St Petersburg in 1845.

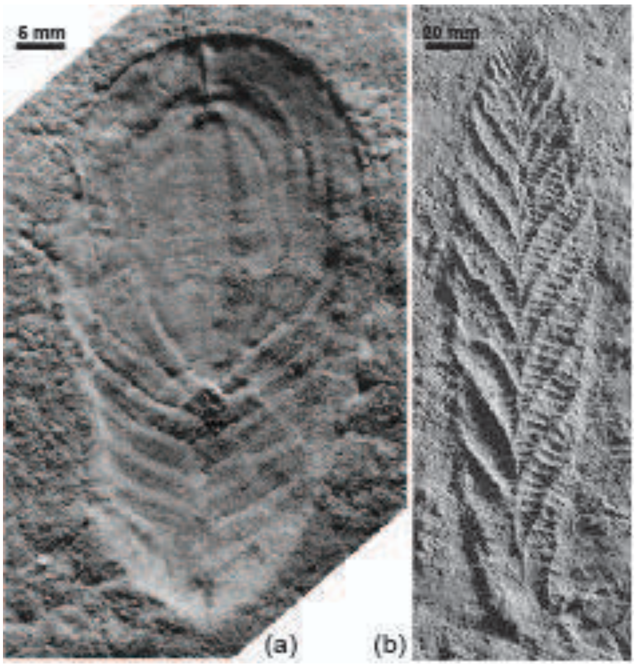

Fig. 2. Ediacara fossils. (a) *Dickinsonia* sp., Zimnii Gory, White Sea, Russia (photo J. Vinther, see Fedonkin et al. 2007, fig. 222). (b) *Charnia masoni*, Charnwood Forest,

Leicestershire, UK (the holotype, copyright British Geological Survey, Natural Environment Research Council).

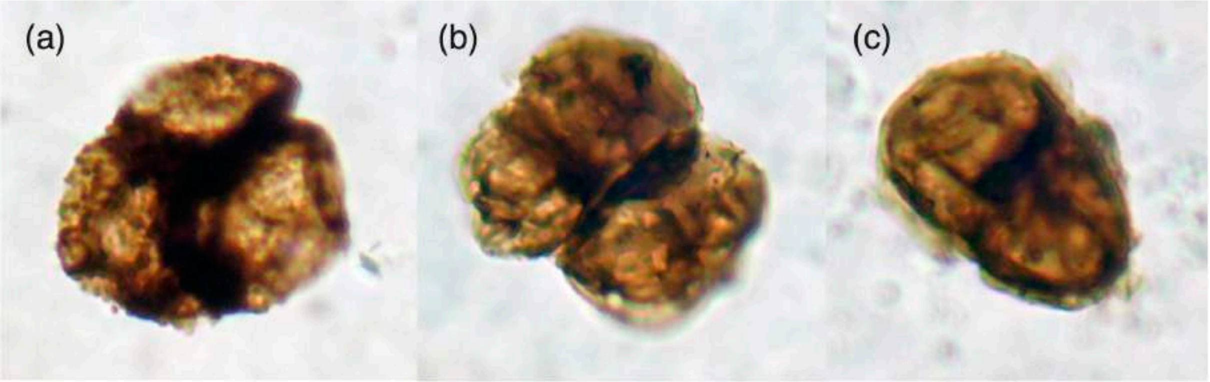

Fig. 3. Cryptospores from the Upper Ordovician of Siberia, evidence for some of the earliest vascular plants. (a, b) Permanent tetrad enclosed in a laevigate envelope, ?*Velatitetras laevigata* Burgess, 1991. (c) Pseudodyad enclosed in a laevigate envelope, *Segestrespora laevigata* Burgess, 1991.

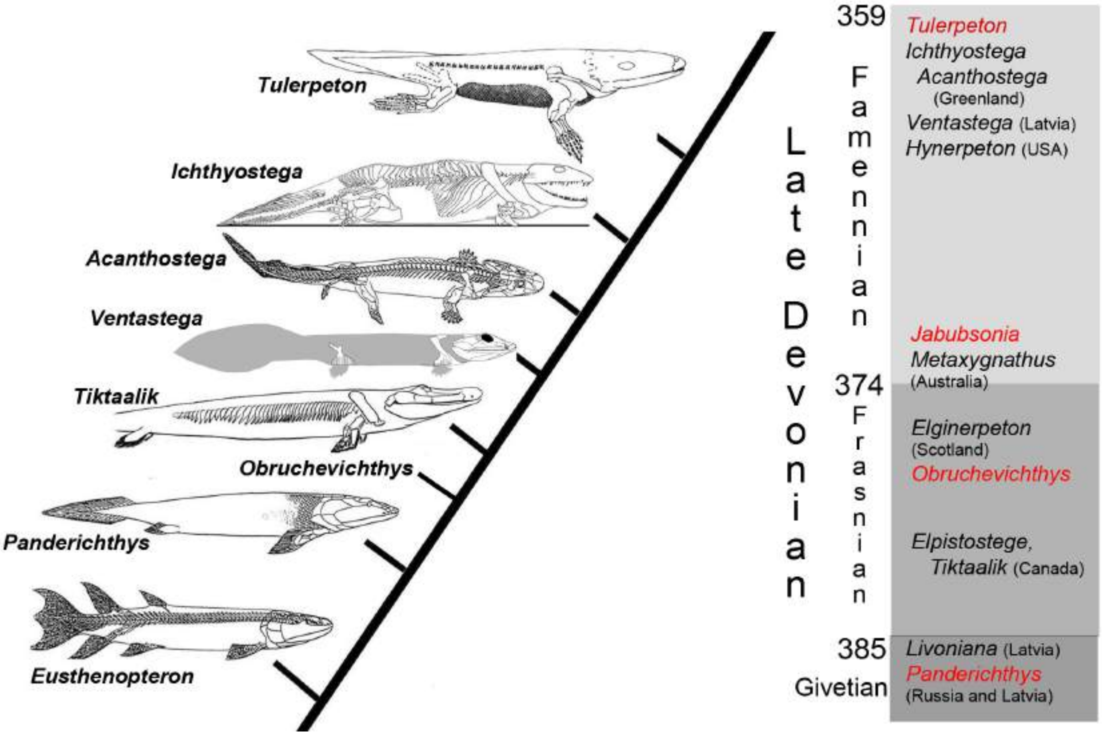

Fig. 4. The cladogram shows the relationships as a present understood between some of the Devonian tetrapods. The stratigraphical column at the right shows the Russian taxa in red in the context of a selection of other taxa and their countries of origin. Russian taxa contribute key parts of this assemblage both phylogenetically and stratigraphically.

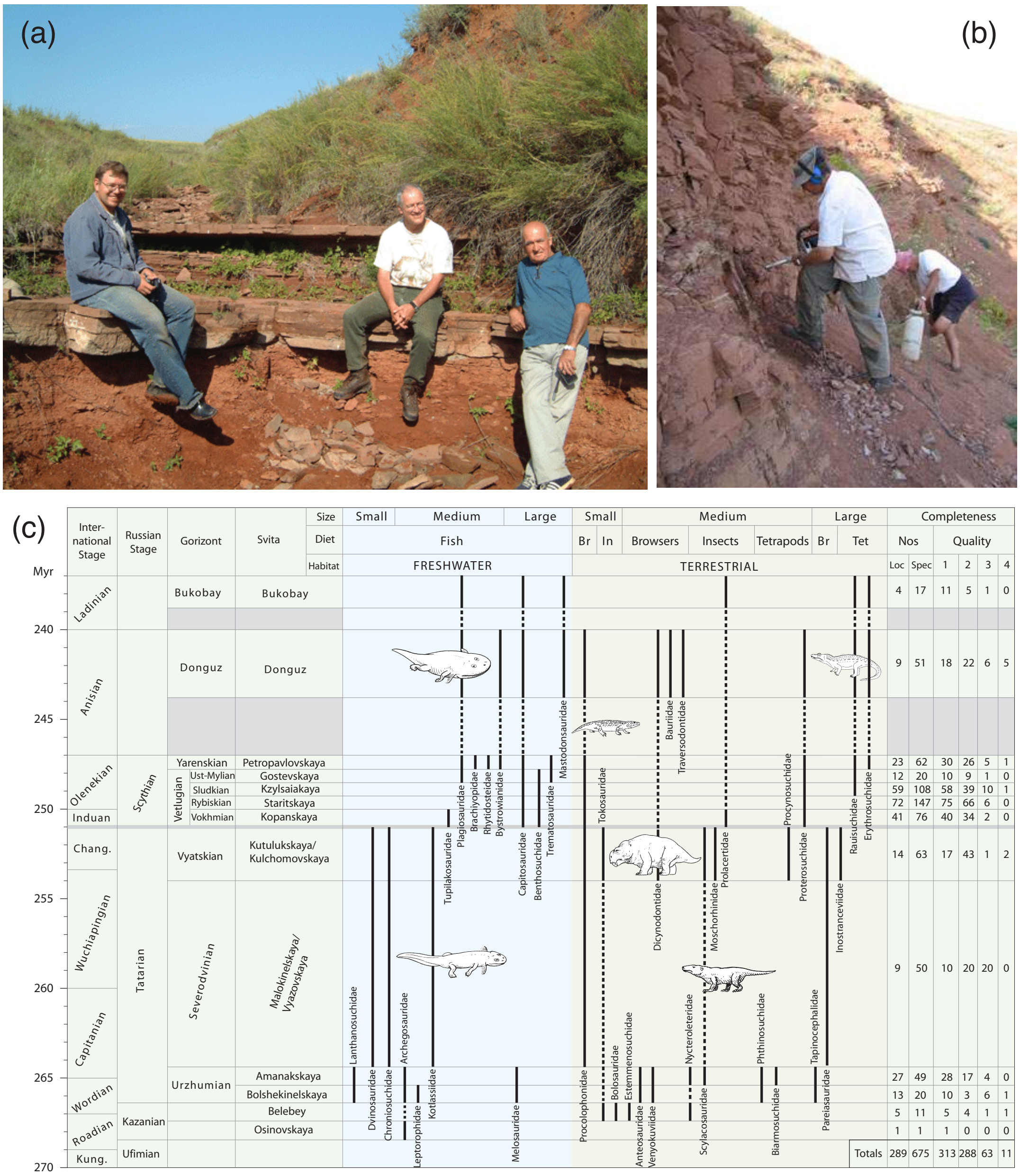

Figure 5. The Permo-Triassic boundary in Russia. (a) The Kulchomovskaya Svita (latest Permian) below the ledge, and the Kopanskaya Svita (basalmost Triassic) above, in the Korolki Ravine, near Sol-Iletsk, on the south-western margin of the Urals, Asiatic Russia. Mikhail Surkov, M.J.B. and Valentin Tverdokhlebov inspect the sandstone lying right at the boundary. (b) Graeme Taylor drills rock plugs for magnetostratigraphic analysis in the Boyevaya Gora PTB section, South Urals, assisted by M.J.B. (c) Overview of the fates of tetrapods from the Middle Permian to Middle Triassic, showing that only prcocolophonids and dicynodonts survived the Permo-Triassic mass extinction.

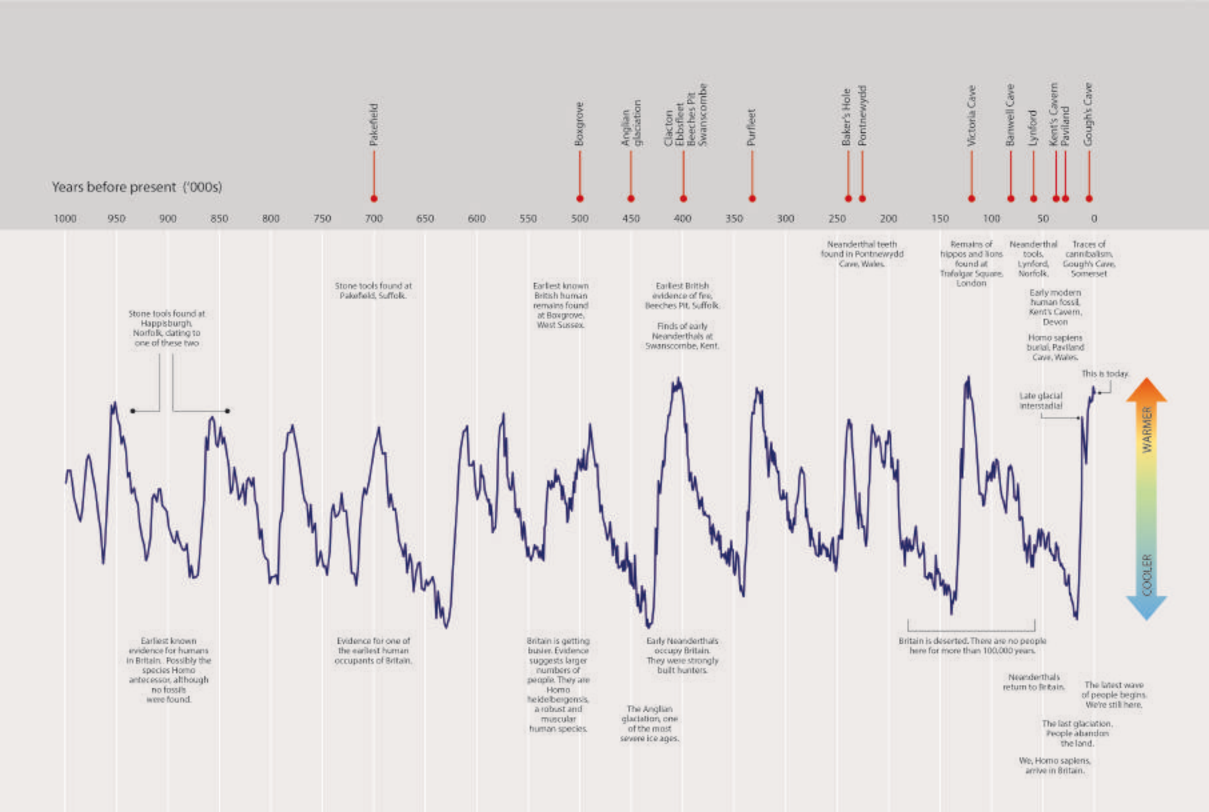

Figure 6. A timeline of key sites and events in Britain's human past. The climate curve is a combination of deep-sea records, and corresponds to global ice volume. This gives an indication of changing climatic conditions through time. Copyright The Trustees of the Natural History Museum, London.

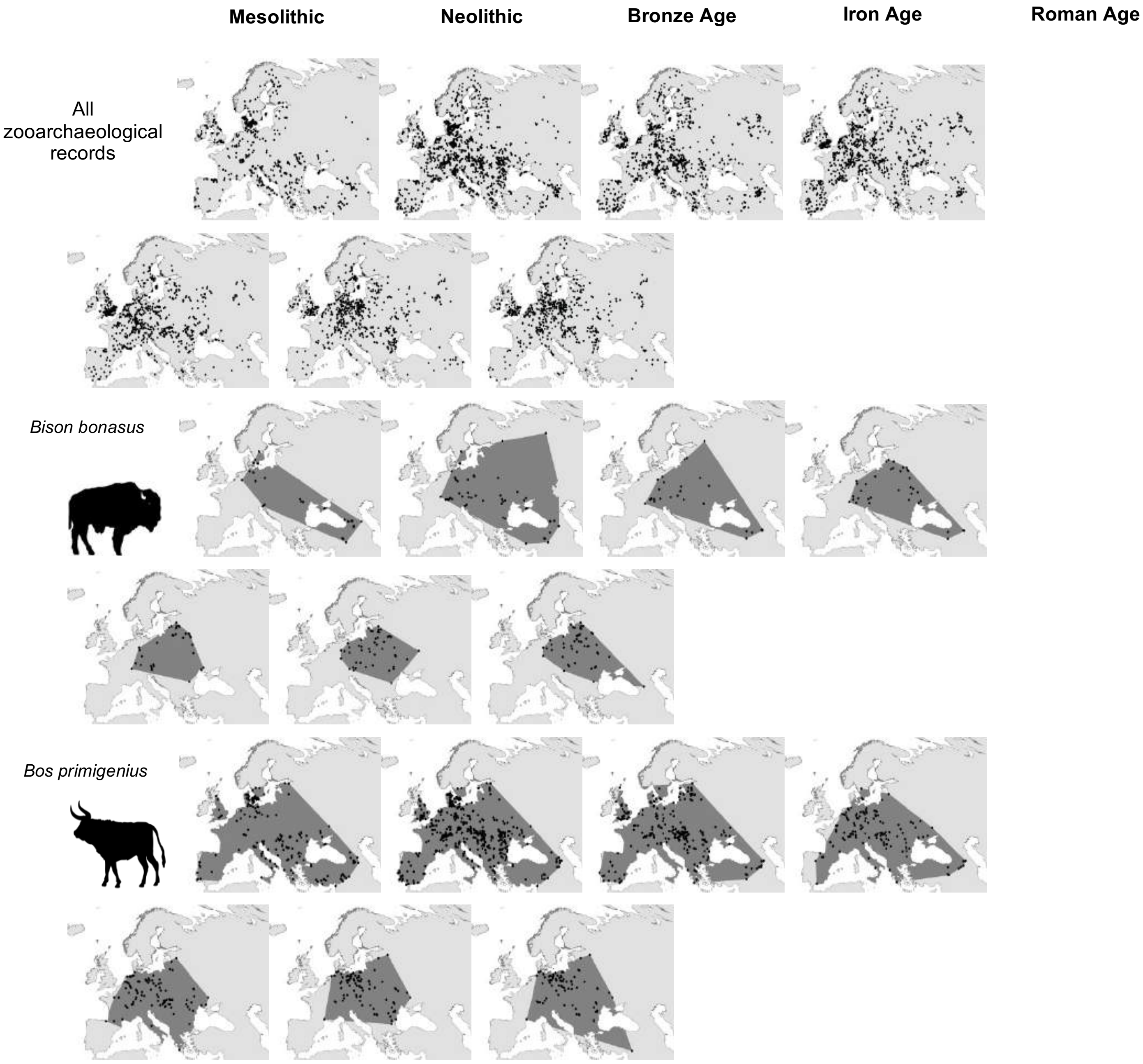

Figure 7. Reconstructed Holocene ranges across eight archaeological periods for two large mammal species now extirpated from Russia (top: European bison *Bison bonasus*; bottom: aurochs *Bos primigenius*), showing minimum convex polygons of available locality records from archaeological sites. Range extent is artefactually biased by variation in number and spatial distribution of archaeological sites across different periods (i.e., sampling bias), but available data demonstrate the persistence of both species in Russia into the Late Medieval. Modified from Crees et al. (2016).