



The Mazon Creek Lagerstätte: a diverse late Paleozoic ecosystem entombed within siderite concretions

Thomas Clements^{1,2*}, Mark Purnell¹ & Sarah Gabbott^{1*}

¹ Department of Geology, University of Leicester, Leicester LE1 7RH, UK

² School of Biological, Earth and Environmental Sciences (BEES), University College Cork, Cork, Ireland

T.C., 0000-0002-6563-4720; M.P., 0000-0002-1777-9220

* Correspondence: clements.taph@gmail.com; sg21@le.ac.uk

Abstract: One of the best records of late Paleozoic ecosystems, the Mazon Creek Lagerstätte is world famous for its striking flora and fauna preserved within siderite concretions. Distinct from other late Carboniferous concretionary Lagerstätten because of the remarkable fidelity of soft tissues and pigments that are frequently preserved, the Mazon Creek has seen a revival in investigations during the last 10 years using modern palaeontological techniques. However, many of these modern investigations build upon a literature that incorrectly interprets the palaeoenvironment of the Mazon Creek and the separate biotas: there is a lack of evidence to support a distinct freshwater fauna. Here, we present a detailed overview of the Mazon Creek Lagerstätte, including the palaeoenvironmental conditions, organisms present and the complex taphonomic processes involved in fossil formation. Investigation into the formation of siderite concretions and the complex taphonomic processes controlling soft-bodied preservation are still continuing but are reviewed in detail.

Received 27 April 2018; revised 7 August 2018; accepted 7 August 2018

The late Carboniferous (Pennsylvanian) Mazon Creek Lagerstätte, Illinois, USA, is exceptional for the diversity and abundance of preserved fauna and flora found within siderite concretions. It hosts the highest diversity of Carboniferous terrestrial plants (Horowitz 1979) and exceptionally preserved 3D animals representing over 300 species from 11 phyla and 23 classes (Shabica & Hay 1997; see Table 1 and Box 1). Unlike most Lagerstätten, it includes fossil organisms that inhabited a number of closely connected habitats including terrestrial swamps, nearshore and fully marine environments. This means that the Mazon Creek provides a unique ‘window’ into multiple Carboniferous animal and plant communities.

Exceptionally preserved fossils from the Mazon river area have been known since the mid-19th century (see Nitecki 1979), but it was only after intensive strip mining for coal began in the 1940s that the importance of the Mazon Creek Lagerstätte (Mazon Creek) was truly realized. The fossiliferous concretions of the Mazon Creek occur within the Francis Creek Shale Member of the Carbondale Formation, removed as overburden to one of the largest and most profitable coal seams in the northern USA (Wright 1979). Records indicate that over 83 shaft mines and 15 strip mines operated between the 1900s and 1980s across a 250 km² geographical area in northern Illinois (Shabica & Hay 1997). Several companies, including the ‘Peabody Coal Company’ (which operated the largest and most famous strip mine, the 14 km² ‘Pit 11’) extracted coal for over 50 years, resulting in the accumulation of immense spoil heaps that were picked over for fossil-bearing siderite (iron carbonate, FeCO₃) concretions by collectors and researchers for decades. This resulted in huge collections of fossil material being amassed; it is not uncommon for collectors to own tens of thousands of fossiliferous concretions, with many hundreds of thousands of Mazon Creek fossils being donated to museums worldwide or sold privately.

Owing to the flat topography of Illinois, very few natural exposures exist; the banks of the Mazon River reveal some outcrop (Fig. 1e); however, high river discharge, vegetation overgrowth and land ownership make collecting problematic. Unfortunately for palaeontological research, the majority of the coal mines were

closed and back-filled during the 1990s. Because of this, collecting localities are greatly diminished, especially the largest, Pit 11, which was deliberately flooded to create a fishing reserve and cooling lake for a nuclear power station. Nevertheless, study of the Mazon Creek is currently undergoing a revival (e.g. Sallan & Coates 2014; Clements *et al.* 2016; Cotroneo *et al.* 2016; Gabbott *et al.* 2016; Locatelli *et al.* 2016; McCoy *et al.* 2016; Murdock *et al.* 2016), predominantly utilizing the huge collections of fossiliferous material at several North American institutions such as the Field Museum of Natural History, Chicago, USA and the Royal Ontario Museum, Toronto, Canada.

Site location and age

The Mazon Creek is named after a tributary of the Illinois River SW of Chicago (Illinois, USA), that flows close to the town of Morris, Grundy County, Illinois, USA (Fig. 1). The fossiliferous concretions are found across an area of c. 150 km² spanning several counties; when found *in situ*, the concretions occur within the lower 3–8 m of the Francis Creek Shale Member.

Baird (1979) stated that the Francis Creek Shale Member was deposited at 290 Ma based on Eysinga (1975), whereas later work and reviews (i.e. Baird *et al.* 1985a; Shabica & Hay 1997; Schellenberg 2002) used an age of 296 Ma based on Harland *et al.* (1982). However, nearly all subsequent literature (i.e. Baird *et al.* 1985b, 1986; Sallan & Coates 2014; Clements *et al.* 2016; Cotroneo *et al.* 2016; McCoy *et al.* 2016, etc.) cited the Francis Creek Shale Member as having an age of 306–311 Ma. The latter age is based on studies utilizing palynological and palaeobotanical data (Pfefferkorn 1979; Wagner 1984; Peppers 1996), which indicate an age that equates to the upper part of the Moscovian stage, the top of which has been dated at 307.0 ± 0.1 Ma (Cohen *et al.* 2013).

Carboniferous Illinois

Late Carboniferous global-scale geological processes were dominated by the collision of Laurussia and Gondwana and the onset of

Table 1. *Fauna found in the Mazon Creek (amended from Shabica & Hay 1997, Appendix B)*

Phylum	Class	Orders represented	Number of sp.	Common name
Cnidaria	Cubozoa	1	1	Sea wasps and box jellyfish
	Scyphozoa	1	4	'True' jellyfish
	Hydrozoa	1	2	Hydras and siphophores
	Anthozoa	1	1	Sea anemones and corals
	Unknown	?	11?	
Nemertea		1	1	Ribbon worms
Nemotoda		1	1	Nematodes
Priapulida		1	1	Penis worms
Chaetognatha		1	1	Arrow worms
Annelida	Polychaeta	7	16?	Segmented worms
Onychophora		1	1	Velvet worms
Arthropoda	Chelicerata	12	43	Horseshoe crabs, arachnids and sea spiders
	Euthycarcinoidea†	1	3	Extinct arthropod group
	Diplopoda	2	17?	Millipedes
	Chilopoda	2	3	Centipedes
	Arthropleuridea†	1	2	Extinct giant millipedes
	Insecta	11	210+	Insects
	Remipedia	1	1	'Oar-footed' marine crustaceans
	Malacostraca	8	14	Crabs, lobsters, shrimps, etc.
	Phyllopoda	3	4	Fairy and clam shrimp
	Maxillopoda	3	7	Copepods, barnacles and tongue worms
	Thylacocephala†	2	3	Extinct 'head pouch' arthropods
Mollusca	Polyplacophora	1	1	Chitons
	Gastropoda	1	5	Slugs and snails
	Bivalvia	8	24	Bivalves
	Cephalopoda	4?	11?	Cephalopods
Brachiopoda	Inarticulata	2	2	Non-hinged brachiopods
	Articulata	1	1	Hinged brachiopods
Echinodermata	Holothuroidea	1	1	Sea cucumbers
	Crinoidea	1	1	Crinoids
Hemichordata	Enteropneusta	1	1	Acorn worms
Chordata	Cyclostomata	3	4?	Jawless fish
	Chondrichthyes	6	15?	Cartilaginous fish
	Osteichthyes	3	14	Ray finned fish
	Sarcopterygii	2	11	Lobe finned fish
	Amphibia	6	9	Amphibians
	Reptilia	1	1	Reptiles
<i>Incertae sedis</i>			9+	
Trace fossils			7+	
	Total:	103	465+	

†, extinct

Box 1 The Mazon Creek is exceptional for its fossil diversity and abundance

The flora and fauna of the Mazon Creek is exceptionally diverse with 350+ species of plant and 465+ animal species representing more than 100 orders (Table 1). Some of the organisms, like the famous *Tullimonstrum gregarium* and *Escumasia roryi*, are unique to the deposit; others, such as the lamprey *Mayomyzon pieckoensis* and chiton *Glaphurochiton concinnus* (see Fig. 3), are among the best-preserved fossil representatives of their groups. For other taxa, such as scolopendromorph centipedes *Mazoscolopendra richardsoni* and *Palenarthrus impressus* (Wilson 2003), the Mazon Creek provides some of the only known Paleozoic occurrences.

The concretions also preserve many remarkable aspects of ecology: direct evidence of invertebrate–plant interactions as well as some of the oldest examples of mimicry and structural camouflage. Similarities of the spines of the horseshoe crab *Euproops danae* and the foliage of the arborescent lycopod *Lepidodendron*, and the wing covers of the cockroach-like insects and *Odontopteris* pinnules have been suggested to be the earliest known examples of crypsis in the fossil record (Fisher 1979).

The abundance of juvenile and diminutive fish and sharks has led some researchers to suggest that the Mazon Creek is a 'nursery' habitat (Baird *et al.*

1986; Sallan & Coates 2014), similar to modern estuaries where shallow, calm waters are used as spawning grounds and hatcheries (Gillanders *et al.* 2003). Indeed, the Mazon Creek contains the most diverse fossil record of chondrichthyan egg cases, with nine types currently described (Wittry, pers. comm., 2015). Evidence of ontogeny is also preserved in the Mazon Creek: spawn, hatchling and juveniles (with egg yolks still attached) have been discovered as well as sub-adult forms of several sharks and fish groups, further supporting the hypothesis of a nursery environment (Baird *et al.* 1986). However, there is also evidence for the presence of larger animals inhabiting this environment; ichthyoliths representing adult remains, large scales of dipnoans, individual adult shark teeth and hefty coprolites are regularly found within concretions. The near-absence of large body fossils has been explained by their ability to escape burial (Baird *et al.* 1986), although, alternatively, the sediment may have lacked the required interstitial iron for concretions to form around large carcasses (Baird 1990). That some concretions contain plants over a metre long counters this explanation.

A full description of the fauna found in the Mazon Creek is beyond the scope of this review; however, there are several excellent guides to the organisms from the Mazon Creek Lagerstätte (e.g. Shabica & Hay 1997; Wittry 2012) with illustrations of all major organisms found to the class level. A faunal list can be found in Table 1.

Mazon Creek: fossils entombed in siderite

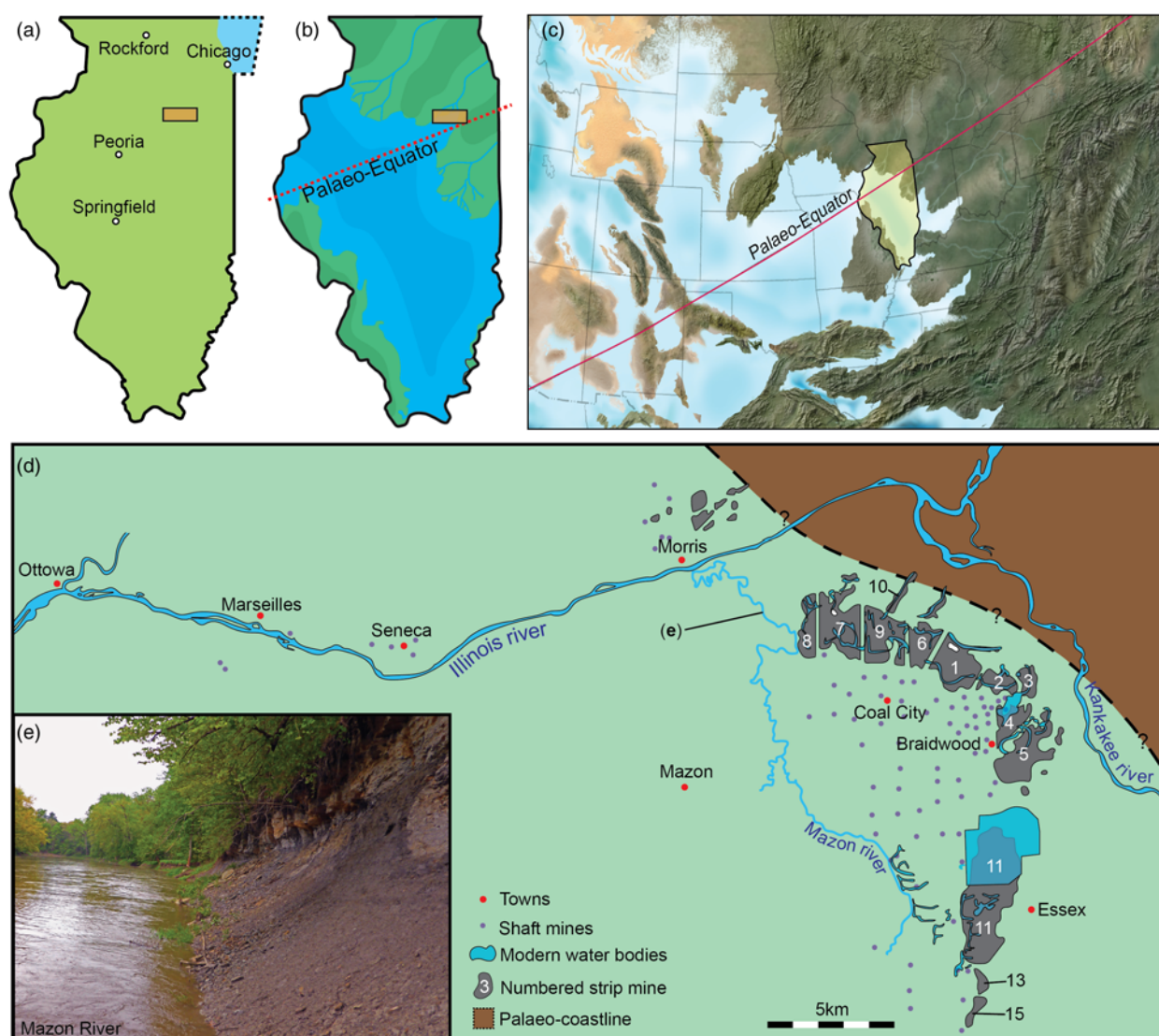


Fig. 1. (a) Locality of the Mazon Creek (brown box) in relation to major cities and towns in Illinois. (b) Illinois during the Pennsylvanian showing the epeiric sea and approximate landmasses in relation to the Mazon Creek Lagerstätte (brown box). (c) Illinois (highlighted) and surrounding US states (grey outline) during the Late Carboniferous. (d) Map of the current Mazon Creek area. The strip mines (or 'pits') are marked with their designate numbers. It should be noted that many of these are now infilled and no longer visible on topographical maps. To the NE, the hypothesized palaeo-coastline is marked. The inset photograph is marked as (e) on the Mazon River. Based on Baird *et al.* (1986). (e) Photograph of the type locality along the Mazon River banks (see (d) for location). Much of this area is on private land and is inaccessible. (c) Map © 2013 Colorado Plateau Geosystems, used with permission.

the Late Paleozoic Ice Age. Several discrete glaciations in both the southern and northern hemispheres and intermittent warming periods (Montañez & Poulsen 2013) caused sea-level oscillations during the late Carboniferous (Heckel 1986; Veevers & Powell 1987).

The Francis Creek Shale Member containing the Mazon Creek Lagerstätte was deposited on the NE margin of the Illinois Basin, which during the late Carboniferous was situated *c.* 4–10° south of the palaeoequator (Fig. 1) (Ziegler *et al.* 1979; Baird *et al.* 1985a, b; Rowley *et al.* 1985) in a vast epeiric sea that covered most of Illinois and the adjoining states (Wanless 1975; Wright 1979; Cecil *et al.* 2003). The unit underlying the Francis Creek Shale Member, the Colchester Coal (no. 2) Member, represents an extensive lycopod-dominated swampy forest found close to the palaeo-coastline (Pfefferkorn 1979; Phillips *et al.* 1985; Winston 1986) that grew in a warm, humid and wet climate (Schopf 1979a; Phillips & DiMichele 1981; Phillips *et al.* 1985; DiMichele 2014). Ultimately, a marine transgression inundated and drowned much of the forest adjacent to the palaeo-coast (Baird *et al.* 1985b). As this transgression occurred, the continuing Alleghanian orogeny to the NE disrupted atmospheric conditions and led to increased precipitation (Phillips *et al.*

1985; Cecil *et al.* 2003), which resulted in powerful erosive rivers that eventually deposited their load into newly formed shallow seas (Potter & Pryor 1961). In northern Illinois, the washout resulting from this upland flooding formed the Francis Creek Shale Member, an expansive and vertically thick member (25 m maximum thickness). The NE-flowing river delta systems created a large 'wedge-shaped' fan of terrigenous sediment (Baird *et al.* 1985b) that pinches out to the south and west (Baird 1997a). The Francis Creek Shale Member is overlain by stratigraphic units representing the continuing sea-level rise throughout the late Carboniferous (Baird 1979; Baird *et al.* 1985b).

Mazon Creek: a river today and in the Carboniferous? Untangling the depositional environment

The Mazon Creek Lagerstätte is characterized as an obrution deposit. Geological investigations have stated that the Francis Creek Shale Member represents a river delta system (e.g. Baird *et al.* 1985a, b, 1986). Subsequently, the Mazon Creek Lagerstätte has been hypothesized as resulting from a large-scale cataclysmic

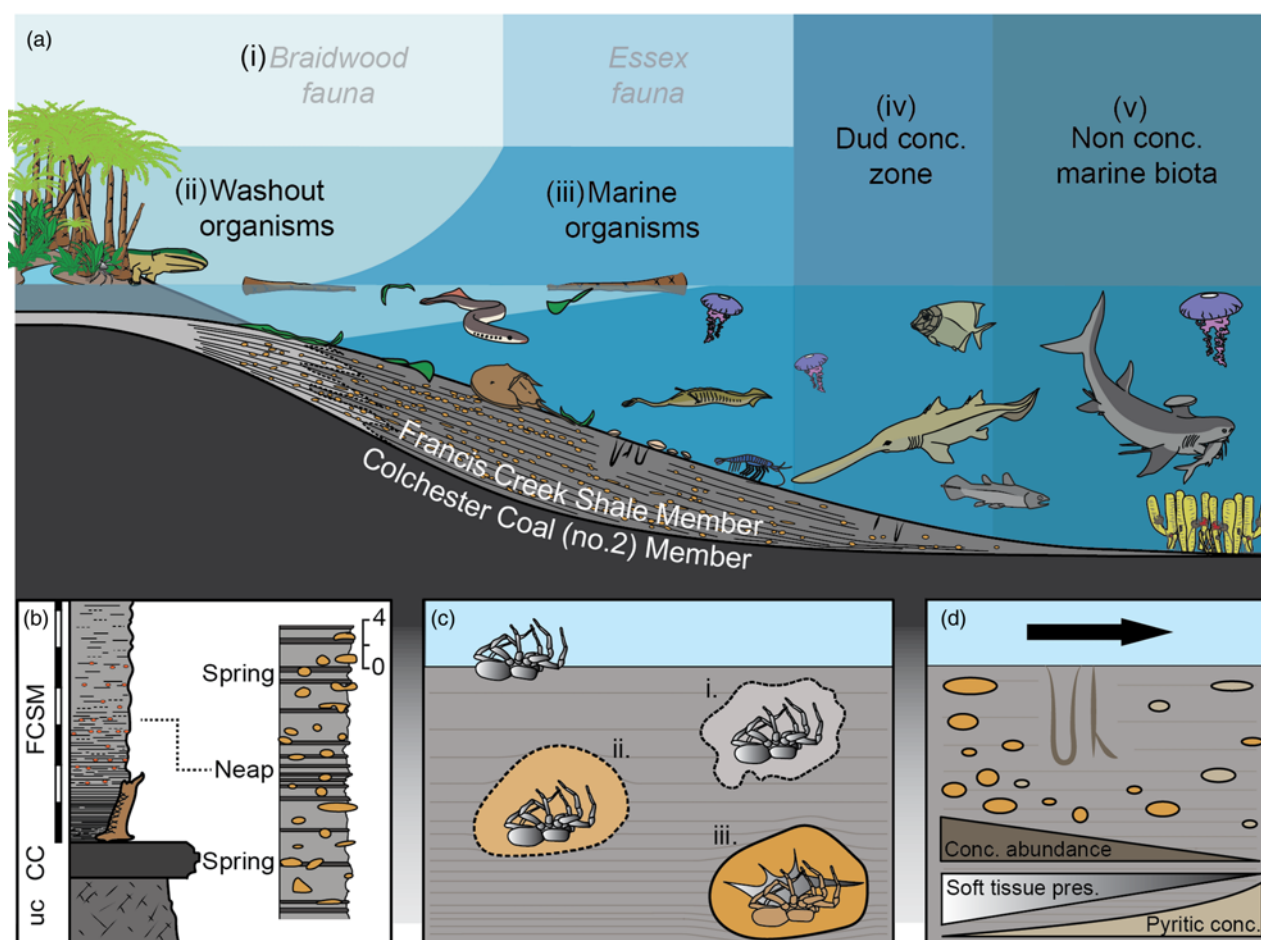


Fig. 2. (a) A geophantasmogram of the Mazon Creek Lagerstätte showing shore to marine distribution of fossils. The Francis Creek Shale Member was deposited largely from sediment washout from rivers, which created a shallow-dipping (2°) terrigenous wedge that extended out into the shallow sea and buried the previously drowned forest of the Colchester Coal Member. Proximally to the palaeo-coast the sediment was dominated by silts (lighter grey) whereas a large fan-shaped arc of distal sediment was dominated by finer clays (dark grey) (Baird 1997b). The literature divides the Mazon Creek into two distinct faunas: the freshwater Braidwood, a brackish community, and the marine Essex fauna (i). This is not supported by geology or fossil assemblages: we advocate categorization of fossils into those that were transported and washed out (including terrestrial plants) (ii) and organisms that inhabited the marine environments and colonized under the shifting freshwater plume (iii). In areas distal to the palaeo-coast, 'dud' (unfossiliferous) concretions are often found (iv). In areas where the Francis Creek Shale Member pinches out, 'normal' Carboniferous marine fauna fossils are found; however, they are not preserved within concretions (v). (b) Schematic stratigraphic sequence of the lower metres of the Francis Creek Shale Member and the associated members of the Carbondale Formation. The fossiliferous concretions can be found in the lower 3–8 m of the Francis Creek Shale Member. The fossiliferous Mazon Creek concretions are found in the lower 3–5 m of the Francis Creek Shale. Concretions found below this are typically pyrite rich. Higher order synodic neap–spring cycles can be seen on the right. Tidal cycles created the characteristic silt–clay paired laminae throughout the Mazon Creek Lagerstätte. These laminae are also commonly preserved within the siderite concretions (Kuecher *et al.* 1990). uc, underclay unit; CC, Colchester Coal No. 2 Coal Member; FCSM, Francis Creek Shale Member. Based on Baird *et al.* (1985a), Kuecher *et al.* (1990) and Shabica & Hay (1997). Scale left in metres and right in millimetres (mm). (c) Hypothesized sequence of events required for preservation in siderite concretions. (i) After rapid burial, decay of the organisms creates a geochemical microenvironment around the carcass and depletes interstitial sulphate. (ii) Siderite precipitation creates a 'proto-concretion' that acts to entomb the organism and resists compaction. (iii) Lithification of the concretion completes. Syneresis within the concretions can cause septarian fractures to occur. Secondary minerals may precipitate and fill voids left by decaying tissues. Tidal laminae are often compressed around concretions, suggesting that compaction of the sediment occurred after lithification of the proto-concretion (Kuecher *et al.* 1990). Based on Baird *et al.* (1986). (d) A schematic illustration of the so-called 'taphonomic discontinuity' seen in the Mazon Creek. Increased geographical distance from the river mouth correlates with an increase in the percentage of 'dud' or barren concretions (Fig. 2a (iv)). Similarly, soft-tissue preservation also dramatically decreases with distance from the shore. The most distal zone has no fossils found in concretions but poorly preserved 'normal' Carboniferous marine shelf fauna (Fig. 2a (v)). It is postulated that, in the distal region, high bioturbation and/or presence of epifaunal animals may have prevented or limited the formation of siderite concretions, increasing likelihood of pyritic cores forming and obliterating fossiliferous remains.

event such as bursting levees during storm events resulting in freshwater and sediment inundating and burying organisms rapidly (see Baird 1990; Shabica & Hay 1997; Schellenberg 2002). Other models include episodic incursion of turbid freshwater during periods of flash flooding (Baird *et al.* 1986), or storm surges (Johnson & Richardson 1966). Although these ideas are consistently cited in subsequent reviews, there are substantial issues with all these hypotheses.

These palaeoenvironmental interpretations are based on the entire 25 m thickness of the Francis Creek Shale Member, but the

fossiliferous Mazon Creek concretions are found only within the basal 3–8 m of the Francis Creek Shale Member. Sedimentary structures in this subsection indicate rapid deposition in a calm marine environment (Fig. 2) (Baird 1979). No sedimentary structures indicating turbulent deposition are found in the fossiliferous layers, making a high-energy mortality site unlikely (e.g. Baird & Sroka 1990). Rather, the fossiliferous section of the Francis Creek Shale Member represents voluminous sedimentation of muds and silts fed by one or more distributary channels into quiet water (Baird *et al.* 1985b) inundating and burying the already

submerged SW-sloping peat deposits. This rapidly deposited sediment smothered organism carcasses and engulfed the already drowned lycopod trees in life position, as seen at the base of Pit 11 (Shabica 1979).

Further evidence of this calmer embayment palaeoenvironment comes from highly regular cyclic laminations found throughout the fossil-bearing section of the Francis Creek Shale Member. Interpreted as flood–ebb tidal rhythmites (Kuecher 1983; Baird *et al.* 1985b; Kuecher *et al.* 1990; Feldman *et al.* 1993), these ‘pinstripe’ laminations record daily and twice a month neap–spring tidal cycles (Baird *et al.* 1985b; Kuecher *et al.* 1990) in both marine and freshwater areas (Fig. 2b) (Kuecher 1983; Kuecher *et al.* 1990), indicating that the entire Mazon Creek area was tidally influenced. It should be noted that the ebb tide band is far thicker than the flood band, suggesting a high sediment discharge rate (Baird *et al.* 1986). The presence of tidal laminae and rapid sedimentation rates, and the absence of high-energy sedimentary structures within the fossiliferous zone indicate that the organisms of the Mazon Creek inhabited an area around a river delta system that discharged large amounts of sediment and freshwater into a shallow, non-turbulent, brackish marine basin (Archer & Feldman 1994).

Palaeo-environmental information from organisms?

Much of the literature concerning the Mazon Creek considers the biota in terms of two separate faunas (e.g. Johnson & Richardson 1966; Baird *et al.* 1985a, b, 1986; Baird 1997b; Baird & Anderson 1997; Schellenberg 2002; Selden & Nudds 2012; Sallan & Coates 2014). Historically these biotas are based on communities found in distinct geographical localities: terrestrial wash-in and freshwater organisms make up the ‘Braidwood fauna’, whereas a predominantly stenohaline marine animal association is known as the ‘Essex fauna’ (Fig. 2a) (Johnson & Richardson 1966; the names come from the settlements near which the respective faunas are supposedly most prevalent). As with the palaeoenvironmental reconstructions, the evidence does not support this.

The ‘Essex’ marine fauna is dominated by cnidarians (locally known as ‘blobs’), arthropods (Schram 1974, 1981; Schram *et al.* 1997), polychaetes (Thompson 1979), lobopodians (Haug *et al.* 2012; Murdock *et al.* 2016), chitons (Yochelson & Richardson 1979), holothurians (Sroka 1988), fishes (agnathans, acanthodians, dipnoans, sarcopterygii and actinopterygii; Bardack 1979), chondrichthyans (Zangerl 1979), lamprey (Bardack & Zangerl 1968), hagfish (Bardack 1991), cephalopods (Kluessendorf & Doyle 2000; Mapes *et al.* 2007) and the famous *Tullimonstrum* (Richardson 1966; see Fig. 3). The Essex fauna (Box 1), although clearly marine, is not typical of a Pennsylvanian offshore shelf community (Baird 1997b); it is devoid of calcareous algae, sponges, corals, articulated brachiopods, crinoids and trilobites (Baird *et al.* 1985b, 1986); marine organisms sensitive to salinity and high sedimentary input, which would have struggled to cope close to a palaeo-river mouth (Baird 1997b).

The ‘Braidwood’ biota is dominated by flora including horsetails, lycopods and pteridosperm tree fern material (Darrah 1969; Peppers & Pfefferkorn 1970). The vast diversity of plants has been attributed to the washout of plant material from the entire drainage basin of the rivers (DiMichele 2014) and this has resulted in a grossly inflated estimation of the diversity of Pennsylvanian wetland landscapes (DiMichele 2014; Moore *et al.* 2014). Animal fossils are significantly rarer, including reptiles and litter-dwelling invertebrates such as myriapods (Mundel 1979; Hannibal 2000), arachnids (Dunlop 1995), scorpions (Tetlie & Dunlop 2008) and insects, including some of the earliest known cockroach-like animals (Carpenter 1943; Burnham 1983). These plants and organisms represent allochthonous wash-out from their upstream terrestrial ecosystems. In fact, only freshwater bivalves and amphibians are

considered autochthonous representatives of a freshwater biota (Milner 1982). However, poor preservation of the bivalves makes identification difficult; furthermore, their occurrence with known marine organisms (i.e. polychaetes) demonstrates that they are not good freshwater indicators (Baird *et al.* 1985b; Schultze 2009). Moreover, amphibians are not good salinity indicators either; some Devonian amphibians are known to be marine (George & Blieck 2011) and Carboniferous forms had the capability to disperse through coastal marine environments and may have spawned there (Godfrey 1992; Parker & Webb 2008).

Currently, there is no clear evidence, fossil or sedimentological, to support that a distinct truly freshwater ecosystem extended into the bay. Investigations have not identified any distinct geographical demarcation between freshwater and marine organisms (Baird 1997a; Schultze 2009) nor have any sedimentary structures that differentiate these environments been identified (Schultze 2009); in fact, tidal laminae have been described throughout ‘Braidwood’ areas (Kuecher *et al.* 1990; Baird 1997c). Previous work on the ‘one-directional mixing’ between the Braidwood and the Essex faunas is based not on animal fossils, but on fossilized terrestrial plant remains decreasing in size, abundance and diversity distally from the palaeo-coastline (Baird *et al.* 1985b, 1986). Most of the major groups found in the Mazon Creek could tolerate varying degrees of salinity; these groups include palaeoniscoid fish (Schultze & Bardack 1987), horseshoe crabs (Fisher 1979; Anderson 1994), syncarid shrimps, polychaetes, eurypterids (Kjellesvig-Waering 1963), ostracods and shark egg cases (*Palaoxyris*). Stenohaline organisms have been found within the ‘Braidwood’ fauna (Schultze 2009), further diminishing the argument for a distinct freshwater biota. Therefore, rather than a distinct freshwater biota, it is more likely that the Mazon Creek represents a brackish marine environment.

Areas that have previously been identified as freshwater (i.e. Braidwood) are actually part of the bay closer to the palaeo-coast (Schopf 1979b). This area was most probably influenced by the freshwater discharge of nearby rivers, with the discharge, sedimentary load and tidal influence acting as biogeographical filters, explaining why benthic organisms in the northern Mazon Creek have ‘patchy’ distributions occurring in dense concentrations locally (Baird *et al.* 1985b; Baird & Anderson 1997). Where large river systems enter the sea, the freshwater often exists as a hypopycnal plume overlying marine water. In this situation, marine faunas, both benthic and nektonic, can rapidly colonize and inhabit areas with normal marine salinity that occur beneath freshwater (Moura *et al.* 2016). These areas tend to exhibit lower biodiversity than ‘true’ marine environments (e.g. Carriker 1967) and this reduced diversity has been noted in northern Mazon Creek fossil assemblages (Baird 1997b). Pit 11, famous for its ‘true’ marine fossils, is bioturbated by benthic invertebrates such as polychaetes and holothurians, but only in the northern section of the pit. Only nektonic organisms, including fish, shrimp and *Tullimonstrum* (Box 2), are found in the southern end, which exhibits very little bioturbation and is deemed to be closer to the palaeo-coast (Baird *et al.* 1985b). Similar patterns of distributions have been observed in modern marginal marine environments (Moura *et al.* 2016). The brackish and sediment-rich water of the Mazon Creek would also explain why typical Carboniferous marine communities of corals, articulate brachiopods, bryozoans, trilobites and nuculid bivalves are found only in areas distal to the palaeo-coast, where the Francis Creek Shale Member pinches out, and are not preserved in concretions (see fig. 1a (iv) of Baird *et al.* 1986).

Forming a sideritic tomb for Mazon Creek organisms

Although fossil-bearing sideritic concretions are known from several late Carboniferous Lagerstätten, such as Sosnowiec,



Fig. 3. A selection of fossils within siderite concretions from the Mazon Creek Lagerstätte. (a) *Rhabdoderma* sp. (ROM56774). (b) Chiton *Glaphurochiton concinnus* (PE29045). (c) *Rhabdoderma* (*exiguum*?) (Burpee/Lauer Foundation LF836). (d) Polychaete *Esconites zelus* (ROM47529). (e) Priapulid *Priapulites konecniorum* (FMNHPE25135). (f) Actinopterygian *Platyosomus circularis* (FMNHPE7333). (g) Unidentified trigonotarbid arachnid, most probably *Aphantomartus pustulatus*. (BMRP2014MCP850). (h) The seed fern *Alethopteris* sp. (ROM43584). (i) *Asterophyllites* sp. ROM 43576. (j) *Annularia stellate*(?) that has been overgrown with sphalerite (LEIUG83622). (k) Chondrichthyan tooth; *Phoebodus*? (ROM56812A) demonstrates, that despite an absence of large fossils, larger animals lived in the Mazon Creek area. (l) Concretion with pyritic core from pit 11 (not accessioned). (m) Holothurian *Achistrum*? (P69TG22a). (n) *Saurerpeton obtusum* (ROM56804B). Scales: 20 mm. Accurate locality data for fossils are often sparse, and most are often referred to by the associated strip-mine ‘pit’ number; however, some pits (such as Pit 11) are geographically wide, making this information less useful.

Box 2 *Tullimonstrum gregarium*

Fig. 4. The holotype of *Tullimonstrum gregarium* (PE 10504). Image by Paul Mayer (FMNH).

In contrast to other famous Lagerstätten, such as the Burgess Shale or Chengjiang, the flora and fauna of the Mazon Creek are largely recognizable but an extraordinary exception is *Tullimonstrum gregarium* (Figure 4). Discovered in 1955 by a local collector, Francis Tully, and found only in the Mazon Creek Lagerstätte, the enigmatic ‘Tully Monster’ is a popular fossil organism, recognized by the public as the State fossil of Illinois and by its use in advertising campaigns by U-Haul™.

The ‘Tully Monster’ is an anatomically bizarre animal. Described in 1966 (Richardson 1966), *Tullimonstrum* has a long slender segmented body, broad flattened asymmetrical tail, a distinctive ‘transverse bar’ that runs perpendicular to the body with associated organs at either end and an anterior elephantine proboscis that terminates in a claw or jaw lined with teeth (Johnson & Richardson 1969). Over the last five decades numerous studies have allied it to a suite of disparate phyla including Mollusca (Foster 1979), Annelida (Johnson & Richardson 1969; Schram 1991), Nemotoda (Johnson & Richardson 1969; Foster 1979) and Chordata (Beall 1991).

Recently, two studies have reclassified *Tullimonstrum* as a vertebrate. McCoy *et al.* (2016) reinterpreted a suite of anatomical features of *Tullimonstrum* by examining thousands of specimens and using synchrotron X-ray images to propose new hypotheses of homology, identifying a notochord, arcualia, dorsal fin, keratinous teeth, a single nostril and the presence of tectal cartilage. A phylogenetic analysis using these new data placed *Tullimonstrum* as a stem-lamprey.

A separate and contemporaneous study investigated the transverse bar organs, identifying dark structures found terminally on stalks as being eyes (Clements *et al.* 2016). The eyes of *Tullimonstrum* were found to contain melanosomes, the intracellular organelles that synthesize and store the pigment melanin. Importantly, Clements *et al.* identified two distinct melanosome morphologies, each occurring in distinct layers. These layers reflect preservation of the reticulated pigmented epithelium (RPE: a screening layer of the retina). This microanatomical complex was interpreted as an synapomorphy of total group vertebrates, and suggested that *Tullimonstrum* could form a clear visual image with its stalked eyes.

However, these findings have been questioned. Miyashita & Diogo (2016) noted that placing *Tullimonstrum* as a stem vertebrate, stem cyclostome or stem gnathostome (Clements *et al.* 2016) would question the traits identified on the basis of a lamprey model (McCoy *et al.* 2016). More recently, Sallan *et al.* (2017) also questioned the placement of *Tullimonstrum*, disagreeing with most of the anatomical characters described by McCoy *et al.* (2016). Sallan *et al.* (2017) noted that eye structures and characters exhibit high levels of homoplasy, convergence and parallel evolution across the tree of life, although they were unable to demonstrate that the RPE character complex has been identified in non-vertebrates.

With the public interest in such a unique fossil and the current controversy in its identification, more research on the ‘monster’ is sure to follow.

Poland (Krawczynski *et al.* 1997; Pacyna & Zdebska 2002), Montceau-les-Mines, France (Perrier & Charbonnier 2014), and Coseley (Wilson & Almond 2001; Garwood *et al.* 2009), Crock Hey (Prokop *et al.* 2006; Garwood & Dunlop 2011) and Bickershaw, UK (Anderson *et al.* 1997), the Mazon Creek is distinctive, not only for the high diversity of organisms, but also because the fidelity of highly labile soft tissues preserved is unparalleled in the other Carboniferous concretionary fossil deposits.

The controls on concretion formation (Box 3) and the taphonomic pathways before, during and after concretion growth are under renewed investigation. Rapid and constant terrigenous

Box 3 Collecting, opening and mode of preservation within concretions

Fossils of the Mazon Creek are found within concretions (not nodules), which generally occur parallel to the bedding plane and come in a range of colours, shapes and sizes; most are relatively spheroidal–oblate in shape but discoidal, flattened and other shapes occur, including the colloquially named ‘nipple nodules’. The entombed fossils also exhibit a remarkable amount of variability in orientation. Within the concretions they are predominantly found parallel to the bedding plane; however, fossils such as bivalves and polychaetes also occur at oblique orientations (Baird *et al.* 1986). In concretions that preserve tidal laminae, multiple fossils can be found partitioned into separate layers vertically through the concretion (personal observation). Infrequently, plant material may protrude beyond the concretion margins, giving the illusion of it ‘growing’ out of the siderite. Moreover, extremely rarely, impressions of fossil organisms, such as fish, occur on the external surface of concretions (personal observation).

After collection, fossils can be revealed within the concretions by hammering them open, although this tends to cause the concretions to shatter and may damage fossils. The method used most commonly, by private collectors and academic institutions, is freeze–thaw (often over several years), which tends to split the siderite along planes of weakness revealing fossils within. Stories of collectors trying to speed the process by using microwave-ovens are a famous fable amongst the collecting community and certainly a health hazard!

Plant fossils in concretions are preserved as 3D moulds comprising an organic, coaly residue, although voids are infilled with kaolinite, calcite, pyrite, sphalerite or galena (Baird *et al.* 1986). These fossils typically show minimal compression; fruiting bodies often exhibit uncrushed coalified exterior walls, infilled with secondary minerals (Baird *et al.* 1986). Recent taphonomic studies of Mazon Creek plants illustrate that rapid entombment in siderite concretions preserves important taxonomic information of both marattialean ferns and medullosan seed ferns in high fidelity regardless of differing anatomy and preservation potential (Locatelli *et al.* 2016).

Animal skeletal remains and recalcitrant tissues preserve in a similar mode to the plant material: as 3D moulds with much of the original material missing owing to decay and dissolution. In some vertebrate skeletal remains, arthropods and polychaetes, degraded remnants of original material have been identified (Baird *et al.* 1986); however, this is yet to be analysed by modern techniques. Similar to the plant fossils, voids may be overgrown or infilled by secondary minerals previously mentioned, but they are frequently empty leaving exquisite impressions of integument (see Fig. 3). Soft tissues are preserved as ‘flattened composite moulds’ (Baird *et al.* 1986); either as 2D light-on-dark stains or as stains combined with impressions of the organism. The eyes of chordates such as sharks, fish, amphibians, hagfish, lampreys and *Tullimonstrum* preserve melanin (Clements *et al.* 2016; Gabbott *et al.* 2016), some of the oldest pigment known in the fossil record. A full taphonomic investigation of Mazon Creek organisms is currently under way.

sedimentary input from the upland peaty forests created the ideal scenario to bury organic matter and carcasses quickly, preventing scavenging and retarding aerobic decay. It is important to note that the kill mechanism that caused the mortality of Mazon Creek organisms is unclear, although pulses of freshwater, water column anoxia or water poisoning could be conceivable stresses on marine life. The burial of organisms obliquely to bedding planes suggests that some organisms were, however, smothered and buried *in situ*. The high fluxes of terrigenous sediment supply also had the secondary effect of supersaturating porewaters with sufficient interstitial iron for siderite formation. In normal marine conditions, pyrite is the primary reduced-iron precipitate as it is thermodynamically and kinetically favourable for iron to form sulphide minerals at the expense of carbonate precipitation (Cotroneo *et al.* 2016). However, in environments lacking sulphate, such as freshwater, or marine systems where sulphate is exhausted, iron carbonate (siderite) will preferentially precipitate (see Cotroneo *et al.* 2016, and references therein).

Although the presence of marine communities and the occurrence of tidally influenced sedimentary structures indicate that a

persistent head of freshwater did not exist above the sediment (Kuecher *et al.* 1990), the Francis Creek Shale Member is dominated by illite–chlorites, which reflect deposition in low-salinity oxygen-rich water (Hughes 1970). Rapid deposition, tidal pumping and limited bioturbation probably limited the penetration of seawater into the sediment. This scenario would restrict sulphate supply (sulphate poisons the precipitation of siderite) and minimize the diffusion of oxygen, creating a reducing environment ideal for siderite formation. Furthermore, waters from upland forests would have decreased Eh and pH, further enhancing Fe⁺ activity, increasing the likelihood of siderite formation (Woodland & Stenstrom 1979), although oxygen isotopes suggest that the concretions formed in marine waters (Cotroneo *et al.* 2016). Although oxygen levels in the Mazon Creek are poorly constrained, it is likely that the muds were anoxic: studies on modern estuaries demonstrate that high bacterial and detrital content of the sediment can generate varying, but significant, levels of anoxia (Jonas 1997).

Decay of soft tissues was probably retarded by inhibition of both oxidant diffusion and bacterial activity by rapid authigenic precipitation of ‘proto-concretions’ around organic-rich remains (Fig. 2c). Oxygen, carbon and sulphur isotopic signals indicate that the closed environmental conditions were depleted of sulphate, swiftly changing from the precipitation of pyrite to siderite and forcing methanogenesis to become the dominant metabolic pathway for anaerobic bacteria (Cotroneo *et al.* 2016). Subsequently, methane fermentation is posited to have cemented the proto-concretion by supplying the carbonate required for diagenetic siderite to form (Cotroneo *et al.* 2016). Siderite tends to form pervasively within the sediment rather than concentrically, filling pore space and resisting compression, protecting the fossil from compaction or obliteration (Raiswell & Fisher 2000). Post-lithification, minerals including kaolinite, galena and sphalerite fill cracks and overgrow fossils, although it is not known if this happens during late diagenesis or as a result of weathering. The high carbonate content, isotopic stability and fossilized soft tissues establish that the concretions formed rapidly (Woodland & Stenstrom 1979; Baird 1990; Cotroneo *et al.* 2016). It has been suggested that tidal pumping may have been important to the rapid growth of the concretions (Allison & Pye 1994).

What initiated the formation of a concretion is not fully understood. The close relationship between concretion size and shape and the fossil within suggests that organic remains acted as passive nuclei (Baird 1997c). Large amounts of macerated, compressed and carbonized plant matter and infrequent fragments of insect or crustacean cuticle are found in the Francis Creek Shale Member along bedding planes (Baird *et al.* 1986), suggesting that the sediment was saturated with organic remains. It has been suggested that the decay of larger ‘juicer’ organic remains may have created geochemical microenvironments that triggered siderite precipitation (Baird *et al.* 1986; Baird 1997c), but the preservation of small animals and plant fragments brings this into question. Moreover, many concretions in the Mazon Creek are ‘dud’ (barren) and seemingly devoid of fossil material.

Such barren concretions may have nucleated around detrital organic remains or small carcasses, and the lack of organic carbon may have limited the bacterial respiration required for the lithification of the proto-concretion (Baird *et al.* 1986; Cotroneo *et al.* 2016). Potential retardation of the formation of a proto-concretion and prolonged aerobic bacterial activity prior to entombment in siderite would allow organic remains to decay before preservation. The formation of barren concretions is likely to have been exacerbated by the slower deposition and higher bioturbation commonly seen distally from the sedimentary source. This hypothesis is supported by analysis of fossiliferous versus barren concretions; in the areas closer to the palaeo-coastline 40% of

concretions are barren ($n = 56\,974$), whereas in the marine section 63% are barren ($n = 229\,979$) (Baird & Anderson 1997).

Distance from the palaeo-coast also considerably affected the preservational fidelity of organisms (see Fig. 2d). Concretions found close to the palaeo-coast mouth are rich in soft-tissue fossils (Baird *et al.* 1985b, 1986; Baird 1997b) whereas areas up to 50 km west of this are characterized by concretions that preserve only small bivalve shells or are barren (Baird 1997a). Towards the towns of Galesburg and Peoria, 170 km SW of the Mazon River, the Francis Creek Shale Member thins, and comprises a highly bioturbated and non-concretionary marine siltstone containing a more typical Carboniferous marine shelf fossil fauna, including trilobites, bryozoans, brachiopods and bivalves (Smith *et al.* 1970; Shabica 1979; Baird *et al.* 1985b; Baird 1997b; Baird & Anderson 1997). Between the concretion zone and this ‘normal’ non-concretionary deposit, the Francis Creek Shale Member contains pyritic/calcite concretions almost completely devoid of any fossils, except for a few poorly preserved marine organisms (see fig. 1a of Baird 1979). These areas are typified by high levels of bioturbation that obliterated the tidal laminae that probably slowed the formation of concretions either by aerating or allowing sulphate-rich marine waters into the sediment, or both (Baird *et al.* 1986). Coupled with the slower rates of sedimentation around the outer margins of the delta fan, this may explain the taphonomic variation (termed a ‘taphonomic discontinuity’ by Baird *et al.* 1986) observed within the Francis Creek Shale Member.

Recent isotope analysis of Mazon Creek concretions has yielded some interesting preliminary results. Concretions found in the Braidwood area tend to have very little sulphide mineral content compared with Essex concretions, suggesting different diagenetic pathways (Cotroneo *et al.* 2016). This may be due to proximity to the palaeo-coast; however, further geochemical investigation with a rigorous sampling strategy with more than one Braidwood site is required to accurately constrain this.

Summary and future work

The Mazon Creek represents a marine bay where allochthonous terrestrial and native marine organisms were buried in an environment favourable for siderite concretion formation. Rapid entombment of the flora and fauna led to exquisite soft-tissue preservation, fossilizing entire organisms rarely seen in the fossil record such as polychaetes, chitons and holothurians. In areas distal to the sedimentary source, burial was slower and increased bioturbation retarded the formation of siderite, preventing exceptional preservation and creating a taphonomic bias. In the most distal areas, where sedimentary input was extremely low, ‘typical’ offshore shelf communities flourished but were not preserved in concretions, nor are any fossils with soft tissues found in these areas.

The Mazon Creek is arguably the most complete record of a late Carboniferous equatorial ecosystem, and renewed research on familiar and in some cases commonly found fossils is providing new insights. For example, recent work on the Tully Monster (*Tullimonstrum*) has shown the benefits of using modern analytical techniques for detailed anatomical re-evaluation of taxa that have been largely neglected since their original descriptions. The current revival of Mazon Creek research has highlighted several gaps in our current understanding of how this marvellous fossil deposit formed. Investigation of modern estuarine environments has elucidated some of the controls on the formation of siderite concretions, which can now be applied to the Mazon Creek. This work, in particular, will lead to a better understanding of the unique mode of preservation seen in this Lagerstätte when compared with other Carboniferous sideritic concretionary deposits. Additional high-resolution geochemical investigations through the interval and across the geographical area have yet to be attempted; these would complement and validate the isotope studies that

Mazon Creek: fossils entombed in siderite

have recently been reported. In-depth geochemical investigations on the shale host rock may also better constrain the depositional environment and influence of freshwater on the Mazon Creek. Investigation of analogous deltaic settings would also benefit Mazon Creek research.

Although these large complex research questions will require considerable integrated research to answer, there is scope for citizen science to have a significant impact on the current understanding of the Mazon Creek. There are thousands upon thousands of unopened and unsorted concretions at many major North American museums and new material is still being collected from the last few exposures by collectors and amateur organizations. The sheer amount of fossil material available and the fidelity of soft-tissue preservation makes the Mazon Creek an ideal Lagerstätte for large-scale taxon-specific investigations, many of which are under way. These studies, along with descriptions of the many undescribed taxa, mean that the Mazon Creek is a vital Lagerstätte for reconstructing Carboniferous ecosystems.

Acknowledgements Staff at The Lapworth Museum of Geology, Oxford University Museum of Natural History, Burpee Museum of Natural History, Field Museum of Natural History (FMNH) and Royal Ontario Museum (ROM) are thanked for assistance with this project. The Leicester University Palaeobiology, Palaeoenvironments & Palaeoclimates Research Group is thanked for inputs and advice. A. Clements, E. Dunne, P. Orr and M. Williams are thanked for proofreading and helpful comments. Thanks go to R. Garwood for his constructive review, which greatly added to this paper.

Funding This work was funded by the Natural Environment Research Council (P14DF19).

Scientific editing by Philip Donoghue

References

- Allison, P.A. & Pye, K. 1994. Early diagenetic mineralization and fossil preservation in modern carbonate concretions. *Palaaios*, **9**, 561–575.
- Anderson, L.I. 1994. Xiphosurans from the Westphalian D of the Radstock Basin, Somerset Coalfield, the South Wales Coalfield and Mazon Creek, Illinois. *Proceedings of the Geologists' Association*, **105**, 265–275.
- Anderson, L.I., Dunlop, J.A., Horrocks, C.A., Winkelmann, H.M. & Eagar, R. 1997. Exceptionally preserved fossils from Bickershaw, Lancashire UK (Upper Carboniferous, Westphalian A (Langsettian)). *Geological Journal*, **32**, 197–210.
- Archer, A.W. & Feldman, H.R. 1994. Tidal rhythmites in fine-grained Carboniferous limestones, USA. *Geobios*, **27**, 275–281.
- Baird, G. 1979. Lithology and fossil distribution, Francis Creek Shale in northeastern Illinois. In: Nitecki, M.H. (ed.) *Mazon Creek Fossils*. Academic Press, New York, 41–67.
- Baird, G. 1990. Mazon Creek. In: Briggs, D. & Crowther, P.R. (eds) *Palaeobiology: a Synthesis*. Blackwell Scientific, Oxford, 279–282.
- Baird, G. 1997a. Francis Creek diagenetic events. In: Shabica, C.W. & Hays, A.A. (eds) *Richardson's Guide to the Fossil Fauna of the Mazon Creek*. Northeastern Illinois University, Chicago, IL, 30–34.
- Baird, G. 1997b. Geological setting of the Mazon Creek area fossil deposit. In: Shabica, C.W. & Hays, A.A. (eds) *Richardson's Guide to the Fossil Fauna of the Mazon Creek*. Northeastern Illinois University, Chicago, IL, 16–20.
- Baird, G. 1997c. Paleoenvironmental setting of the Mazon Creek biota. In: Shabica, C.W. & Hays, A.A. (eds) *Richardson's Guide to the Fossil Fauna of Mazon Creek*. Northeastern Illinois University, Chicago, IL, 35–51.
- Baird, G. & Anderson, J. 1997. Relative abundance of different Mazon Creek organisms. In: Shabica, C.W. & Hays, A.A. (eds) *Richardson's Guide to the Fossil Fauna of Mazon Creek*. Northeastern Illinois University, Chicago, IL, 27–29.
- Baird, G. & Sroka, S. 1990. Geology and geohistory of Mazon Creek area fossil localities, Illinois. In: Hammer, W.R. & Hess, D.R. (eds) *Geology Field Guidebook: Current Perspectives on Illinois Basin and Mississippi Arch Geology*. Western Illinois University, Macomb. *Preservation in Late Paleozoic Deltaic Environments*, Macomb, IL, **201**, C1–C70. <https://trove.nla.gov.au/work/178576252?q&versionId=194396123>
- Baird, G.C., Shabica, C.W., Anderson, J.L. & Richardson, E.S. Jr, 1985a. Biota of a Pennsylvanian muddy coast: habitats within the Mazonian delta complex, northeast Illinois. *Journal of Paleontology*, **59**, 253–281.
- Baird, G., Sroka, S., Shabica, C., Beard, T., Scott, A. & Broadhurst, F. 1985b. Mazon Creek-Type fossil assemblages in the US Midcontinent Pennsylvanian: their recurrent character and palaeoenvironmental significance [and discussion]. *Philosophical Transactions of the Royal Society of London, Series B*, **311**, 87–99.
- Baird, G.C., Sroka, S., Shabica, C. & Kuecher, G. 1986. Taphonomy of Middle Pennsylvanian Mazon Creek area fossil localities, northeast Illinois: Significance of exceptional fossil preservation in syngenetic concretions. *Palaaios*, 271–285.
- Bardack, D. 1979. Fishes of the Mazon Creek fauna. In: Nitecki, M.H. (ed.) *Mazon Creek Fossils*. Academic Press, New York, 501–528.
- Bardack, D. 1991. First fossil hagfish (Myxinoidea): a record from the Pennsylvanian of Illinois. *Science*, **254**, 701–703.
- Bardack, D. & Zangerl, R. 1968. First fossil lamprey: a record from the Pennsylvanian of Illinois. *Science*, **162**, 1265–1267.
- Beall, B. 1991. The Tully Monster and a new approach to analyzing problematica. In: Simonetta, A.M. & Conway Morris, S. (eds) *The Early Evolution of Metazoa and the Significance of Problematic Taxa*. Cambridge University Press, Cambridge, 271–285.
- Burnham, L. 1983. Studies on Upper Carboniferous insects: 1. The Geraridae (Order Protorthoptera). *Psyche*, **90**, 1–58.
- Carpenter, F.M. 1943. *Carboniferous insects from the vicinity of Mazon creek, Illinois*. State Museum, Springfield, IL.
- Carriker, M.R. 1967. Ecology of estuarine benthic invertebrates: a perspective. *Estuaries*, **83**, 442–487.
- Cecil, C.B., Dulong, F.T., West, R.R., Stamm, R., Wardlaw, B. & Edgar, N.T. 2003. Climate controls on the stratigraphy of a Middle Pennsylvanian cyclothem in North America. In: Cecil, C.B. & Edgar, N.T. (eds) *Climate Controls on Stratigraphy*. SEPM Special Publications, **77**, 151–182.
- Clements, T., Dolocan, A., Martin, P., Purnell, M.A., Vinther, J. & Gabbott, S.E. 2016. The eyes of *Tullimonstrum* reveal a vertebrate affinity. *Nature*, **532**, 500–503.
- Cohen, K., Finney, S., Gibbard, P. & Fan, J.-X. 2013. The ICS international chronostratigraphic chart. *Episodes*, **36**, 199–204.
- Cotroneo, S., Schiffbauer, J., McCoy, V., Wortmann, U., Darroch, S., Peng, Y. & Laflamme, M. 2016. A new model of the formation of Pennsylvanian iron carbonate concretions hosting exceptional soft-bodied fossils in Mazon Creek, Illinois. *Geobiology*, **14**, 543–555.
- Darrah, W.C. 1969. *A critical review of the Upper Pennsylvanian floras of eastern United States with notes on the Mazon Creek flora of Illinois*. Gettysburg.
- DiMichele, W.A. 2014. Wetland–dryland vegetational dynamics in the Pennsylvanian ice age tropics. *International Journal of Plant Sciences*, **175**, 123–164.
- Dunlop, J.A. 1995. Redescription of the Pennsylvanian trigonotarbid arachnid *Lissomartus Petrunkevitch* 1949 from Mazon Creek, Illinois. *Journal of Arachnology*, 118–124.
- Eysinga, F.v. 1975. *Geological Time Table*. Elsevier, Amsterdam.
- Feldman, H.R., Archer, A.W., Kvale, E.P., Cunningham, C.R., Maples, C.G. & West, R.R. 1993. A tidal model of Carboniferous Konservat-Lagerstätten formation. *Palaaios*, **8**, 485–498.
- Fisher, D. 1979. Evidence for subaerial activity of *Euproops danae* (Merostomata, Xiphosurida). In: Nitecki, M.H. (ed.) *Mazon Creek Fossils*. Academic Press, New York, 379–448.
- Foster, M. 1979. A reappraisal of *Tullimonstrum gregarium*. In: Nitecki, M.H. (ed.) *Mazon Creek Fossils*. Academic Press, New York, 269–301.
- Gabbott, S.E., Donoghue, P.C., Sansom, R.S., Vinther, J., Dolocan, A. & Purnell, M.A. 2016. Pigmented anatomy in Carboniferous cyclostomes and the evolution of the vertebrate eye. *Proceedings of the Royal Society of London, Series B*, 20161151.
- Garwood, R.J. & Dunlop, J.A. 2011. Morphology and systematics of Anthracomartidae (Arachnida: Trigonotarbita). *Palaeontology*, **54**, 145–161.
- Garwood, R., Dunlop, J.A. & Sutton, M.D. 2009. High-fidelity X-ray microtomography reconstruction of siderite-hosted Carboniferous arachnids. *Biology Letters*, **5**, 841–844.
- George, D. & Blicek, A. 2011. Rise of the earliest tetrapods: an early Devonian origin from marine environment. *PLoS One*, **6**, e22136.
- Gillanders, B., Able, K., Brown, J., Eggleston, D. & Sheridan, P. 2003. Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: an important component of nurseries. *Marine Ecology Progress Series*, **247**, 281–295.
- Godfrey, S.J. 1992. Fossilized eggs from Illinois. *Nature*, **356**, 21.
- Hannibal, J.T. 2000. *Hexecontasoma*, a new helminthomorph millipede (Hexecontasomatidae, n. fam.) from the Mazon Creek, Illinois, fauna (Carboniferous, North America). *Fragmenta Faunistica*, **43**, 19–35.
- Harland, W., Cox, A., Llewellyn, P., Pickton, C., Smith, A. & Walters, R. 1982. *A Geologic Time Scale*. Cambridge University Press, Cambridge.
- Haug, J.T., Mayer, G., Haug, C. & Briggs, D.E. 2012. A Carboniferous non-onychophoran lobopodian reveals long-term survival of a Cambrian morphotype. *Current Biology*, **22**, 1673–1675.
- Heckel, P.H. 1986. Sea-level curve for Pennsylvanian eustatic marine transgressive–regressive depositional cycles along midcontinent outcrop belt, North America. *Geology*, **14**, 330–334.
- Horowitz, A. 1979. The Mazon Creek flora: review of research and bibliography. In: Nitecki, M.H. (ed.) *Mazon Creek Fossils*. Academic Press, New York, 143–158.
- Hughes, R.E. 1970. Clay minerals associated with the Colchester (no. 2) Coal of the Illinois basin. In: Smith, W. H., Nance, R. B., Hopkins, M. E., Johnson, R. G., & Shabica, C. W. (eds) *Depositional environments in parts of the Carbondale Formation, western and northern Illinois: Frances Creek and Mazon Creek biota*. Illinois Geological Survey Guidebook Series, **8**, 119.

- Johnson, R.G. & Richardson, E.S., Jr. 1966. A remarkable Pennsylvanian fauna from the Mazon Creek area, Illinois. *Journal of Geology*, **74**, 626–631.
- Johnson, R.G. & Richardson, E.S. 1969. *Pennsylvanian invertebrates of the Mazon Creek Area, Illinois: the morphology and affinities of Tullimonstrum*. Field Museum of Natural History, Chicago, IL.
- Jonas, R.B. 1997. Bacteria, dissolved organics and oxygen consumption in salinity stratified Chesapeake Bay, an anoxia paradigm. *American Zoologist*, **37**, 612–620.
- Kjellesvig-Waering, E.N. 1963. *Pennsylvanian Invertebrates of the Mazon Creek Area, Illinois: Eurypterida*. Chicago Natural History Museum, Chicago, IL.
- Kluessendorf, J. & Doyle, P. 2000. *Pohlsepia mazonensis*, an early ‘octopus’ from the Carboniferous of Illinois, USA. *Palaeontology*, **43**, 919–926.
- Krawczynski, W., Filipiak, P. & Gwozdziwicz, M. 1997. Fossils assemblage from the Carboniferous sideritic nodules (Westfalian A) of the NE margin of the Upper Silesia Coal Basin, southern Poland. *Przegląd Geologiczny*, **45**, 1271–1274.
- Kuecher, G. 1983. *Rhythmic sedimentation and stratigraphy of the middle Pennsylvanian Francis Creek Shale near Braidwood*. Master’s thesis, Northeastern Illinois University, Chicago, IL.
- Kuecher, G.J., Woodland, B.G. & Broadhurst, F.M. 1990. Evidence of deposition from individual tides and of tidal cycles from the Francis Creek Shale (host rock to the Mazon Creek Biota), Westphalian D (Pennsylvanian), northeastern Illinois. *Sedimentary Geology*, **68**, 211–221.
- Locatelli, E., Krajewski, L., Chochinov, A. & Laflamme, M. 2016. Taphonomic variance between marattialean ferns and medullosan seed ferns in the Carboniferous Mazon Creek Lagerstätte, Illinois, USA. *Palaios*, **31**, 97–110.
- Mapes, R.H., Mutvei, H. & Doguzhaeva, L.A. 2007. A Late Carboniferous coleoid cephalopod from the Mazon Creek Lagerstätte (USA), with a radula, arm hooks, mantle tissues, and ink. In: Landman, N.H., Davie, R.A. & Mapes, R.H. (eds) *Cephalopods Present and Past: New Insights and Fresh Perspectives*. Springer, Berlin, 121–143.
- McCoy, V.E., Saupe, E.E. *et al.* 2016. The ‘Tully monster’ is a vertebrate. *Nature*, **532**(7600), 496.
- Milner, A.R. 1982. Small temnospondyl amphibians from the Middle Pennsylvanian of Illinois. *Palaeontology*, **25**, 635–664.
- Miyashita, T. & Diogo, R. 2016. Evolution of serial patterns in the vertebrate pharyngeal apparatus and paired appendages via assimilation of dissimilar units. *Frontiers in Ecology and Evolution*, **4**, 71.
- Montañez, I.P. & Poulsen, C.J. 2013. The Late Paleozoic Ice Age: an evolving paradigm. *Annual Review of Earth and Planetary Sciences*, **41**, 629–656.
- Moore, L.C., Wittry, J. & DiMichele, W.A. 2014. The Okmulgee, Oklahoma fossil flora, a Mazon Creek equivalent: Spatial conservatism in the composition of Middle Pennsylvanian wetland vegetation over 1100 km. *Review of Palaeobotany and Palynology*, **200**, 24–52.
- Moura, R.L., Amado-Filho, G.M. *et al.* 2016. An extensive reef system at the Amazon River mouth. *Science Advances*, **2**, e1501252.
- Mundel, P. 1979. The centipedes (Chilopoda) of the Mazon Creek. In: Nitecki, M.H. (ed.) *Mazon Creek Fossils*. Academic Press, New York, 361–378.
- Murdock, D.J., Gabbott, S.E. & Purnell, M.A. 2016. The impact of taphonomic data on phylogenetic resolution: *Heliodora inopinata* (Carboniferous, Mazon Creek Lagerstätte) and the onychophoran stem lineage. *BMC Evolutionary Biology*, **16**, 1.
- Nitecki, M. 1979. Mazon Creek fauna and flora: a hundred years of investigation. In: Nitecki, M.H. (ed.) *Mazon Creek Fossils*. Academic Press, New York, 1–12.
- Pacyna, G. & Zdebska, D. 2002. Upper Carboniferous plant macrofossils from sideritic concretions in Sosnowiec (Upper Silesian Coal Basin) and Mazon Creek (Illinois, USA). In: Lipiarski, I. (ed.) *Geology of Coal-Bearing Strata of Poland, Proceedings of the 25th Symposium*, University of Mining and Metallurgy, Krakow, 123–127.
- Parker, K.E. & Webb, J.A. 2008. Estuarine deposition of a mid-Visean tetrapod unit, Ducabrook Formation, central Queensland: implications for tetrapod dispersal. *Australian Journal of Earth Sciences*, **55**, 509–530.
- Peppers, R. 1996. *Palynological correlation of major Pennsylvanian (Middle and Upper Carboniferous) chronostratigraphic boundaries in the Illinois and other coal basins*. Geological Society of America, Boulder, CO.
- Peppers, R. & Pfefferkorn, H.W. 1970. A comparison of the floras of the Colchester (No. 2) Coal and Francis Creek Shale. In: Smith, W.H., Nance, N.B., Hopkins, M.E., Johnson, R.G. & Shabica, C.W. (eds) *Depositional environments in parts of the Carbondale formation*. Illinois State Geological Survey Guidebook Series, **8**, 61–72.
- Perrier, V. & Charbonnier, S. 2014. The Montceau-les-Mines Lagerstätte (Late Carboniferous, France). *Comptes Rendus Palevol*, **13**, 353–367.
- Pfefferkorn, H. 1979. High diversity and stratigraphic age of the Mazon Creek flora. In: Nitecki, M.H. (ed.) *Mazon Creek Fossils*, Vol. 1. Academic Press, New York, 1–29.
- Phillips, T. & DiMichele, W. 1981. Paleoecology of Middle Pennsylvanian age coal swamps in southern Illinois/Herrin coal member at Sahara Mine No. 6. In: Niklas, K.J. (ed.) *Paleobotany, Paleoecology, and Evolution*, Praeger, New York, 231–284.
- Phillips, T.L., Peppers, R.A. & DiMichele, W.A. 1985. Stratigraphic and interregional changes in Pennsylvanian coal-swamp vegetation: environmental inferences. *International Journal of Coal Geology*, **5**, 43–109.
- Potter, P.E. & Pryor, W.A. 1961. Dispersal centers of Paleozoic and later clastics of the Upper Mississippi Valley and adjacent areas. *Geological Society of America Bulletin*, **72**, 1195–1249.
- Prokop, J., Smith, R., Jarzembowski, E.A. & Nel, A. 2006. New homiopterids from the late Carboniferous of England (Insecta: Palaeodictyoptera). *Comptes Rendus Palevol*, **5**, 867–873.
- Raiswell, R. & Fisher, Q. 2000. Mudrock-hosted carbonate concretions: a review of growth mechanisms and their influence on chemical and isotopic composition. *Journal of the Geological Society, London*, **157**, 239–251, <https://doi.org/10.1144/jgs.157.1.239>
- Richardson, E.S. 1966. Wormlike fossil from the Pennsylvanian of Illinois. *Science*, **151**, 75–76.
- Rowley, D.B., Raymond, A., Parrish, J.T., Lottes, A.L., Scotese, C.R. & Ziegler, A.M. 1985. Carboniferous paleogeographic, phytogeographic, and paleoclimatic reconstructions. *International Journal of Coal Geology*, **5**, 7–42.
- Sallan, L.C. & Coates, M.I. 2014. The long-rostrum elasmobranch *Bandringa* Zangerl, 1969, and taphonomy within a Carboniferous shark nursery. *Journal of Vertebrate Paleontology*, **34**, 22–33.
- Sallan, L., Giles, S., Sansom, R.S., Clarke, J.T., Johanson, Z., Sansom, I.J. & Janvier, P. 2017. The ‘Tully Monster’ is not a vertebrate: characters, convergence and taphonomy in Palaeozoic problematic animals. *Palaeontology*, **60**, 149–157.
- Schellenberg, S.A. 2002. *Exceptional fossil preservation: a unique view on the evolution of marine life*. Columbia University Press, New York.
- Schopf, J. 1979a. Pennsylvanian paleoclimate of the Illinois Basin. In: Palmer, J.E. & Dutcher, R.R. (eds) *Depositional and structural history of the Pennsylvanian System of the Illinois Basin, Part 2*, Illinois State Geological Survey, Urbana, 1–3.
- Schopf, J.M. 1979b. Evidence of soft-sediment cementation enclosing Mazon plant fossils. In: Nitecki, M.H. (ed.) *Mazon Creek Fossils*. Academic Press, New York, 105–128.
- Schram, F.R. 1974. *The Mazon Creek caridoid Crustacea*. Field Museum of Natural History, Chicago, IL.
- Schram, F.R. 1981. Late Paleozoic crustacean communities. *Journal of Paleontology*, **55**, 126–137.
- Schram, F. 1991. Cladistic analysis of metazoan phyla and the placement of fossil problematica. In: Simonetta, A.M. & Morris, S.M. (eds) *The early evolution of Metazoa and the significance of problematic taxa*, Cambridge University Press, Cambridge, 35–46.
- Schram, F.R., Vonk, R. & Hof, C.H. 1997. Mazon Creek Cycloidea. *Journal of Paleontology*, **71**, 261–284.
- Schultze, H.-P. 2009. Interpretation of marine and freshwater paleoenvironments in Permo-Carboniferous deposits. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **281**, 126–136.
- Schultze, H.-P. & Bardack, D. 1987. Diversity and size changes in palaeonisciform fishes (Actinopterygii, Pisces) from the Pennsylvanian Mazon Creek Fauna, Illinois, USA. *Journal of Vertebrate Paleontology*, **7**, 1–23.
- Selden, P. & Nudds, J. 2012. *Evolution of Fossil Ecosystems*. Elsevier, Amsterdam.
- Shabica, C. 1979. Pennsylvanian sedimentation in Northern Illinois: examination of delta models. In: Nitecki, M.H. (ed.) *Mazon Creek Fossils*. Academic Press, New York, 13–40.
- Shabica, C.W. & Hay, A. (eds) 1997. *Richardson’s guide to the fossil fauna of Mazon Creek*. Northeastern Illinois University, Chicago, IL.
- Smith, W., Nance, R., Hopkins, M., Johnson, R. & Shabica, C. 1970. *Depositional environments in parts of the Carbondale Formation, western and northern Illinois: Frances Creek and Mazon Creek biota*. Illinois Geological Survey Guidebook Series, **8**.
- Sroka, S. 1988. Preliminary studies on a complete fossil holothurian from the Middle Pennsylvanian Francis Creek Shale of Illinois. In: Balkema, A.A. (ed.) *Echinoderm Biology. Proceedings of the Sixth International Echinoderm Conference, Victoria 1987*. Balkema, Rotterdam, 159–160.
- Tetlie, O.E. & Dunlop, J.A. 2008. *Geralinura carbonaria* (Arachnida: Uropygi) from Mazon Creek, Illinois, USA, and the origin of subchelate pedipalps in whip scorpions. *Journal of Paleontology*, **82**, 299–312.
- Thompson, I. 1979. Errant polychaetes (Annelida) from the Pennsylvanian Essex fauna of northern Illinois. *Palaeontographica Abteilung A*, **163**, 169–199.
- Veevers, J.J. & Powell, C.M. 1987. Late Paleozoic glacial episodes in Gondwanaland reflected in transgressive-regressive depositional sequences in Euramerica. *Geological Society of America Bulletin*, **98**, 475–487.
- Wagner, R.H. 1984. Megafloral zones of the Carboniferous. *Compte Rendu: Congrès international de Stratigraphie et de Géologie du Carbonifère*, **2**, 109–134.
- Wanless, H.R. 1975. Distribution of Pennsylvanian coal in the United States. In: McKee, E.D., Crosby, E.J. *et al.* (eds) *Paleotectonic Investigations of the Pennsylvanian System in the United States, Part II. Interpretive Summary and Special Features of the Pennsylvania System*. US Geological Survey, Professional Papers, **853**, 33–47.
- Wilson, H.M. 2003. A new scolopendromorph centipede (Myriapoda: Chilopoda) from the Lower Cretaceous (Aptian) of Brazil. *Journal of Paleontology*, **77**, 73–77.
- Wilson, H.M. & Almond, J.E. 2001. New euthycarcinoids and an enigmatic arthropod from the British Coal Measures. *Palaeontology*, **44**, 143–156.

Mazon Creek: fossils entombed in siderite

- Winston, R.B. 1986. Characteristic features and compaction of plant tissues traced from permineralized peat to coal in Pennsylvanian coals (Desmoinesian) from the Illinois basin. *International Journal of Coal Geology*, **6**, 21–41.
- Wittry, J. 2012. *The Mazon Creek Fossil Fauna*. Escon.
- Woodland, B. & Stenstrom, R. 1979. The occurrence and origin of siderite concretions in the Francis Creek Shale (Pennsylvanian) of northeastern Illinois. *In*: Nitecki, M.H. (ed.) *Mazon Creek Fossils*. Academic Press, New York, 69–103.
- Wright, C. 1979. Depositional history of the Pennsylvanian System in the Illinois Basin – a summary of work by Dr. Harold Wanless and associates. *In*: Palmer, J.E. & Dutcher, R.R. (eds) *Depositional and structural history of the Pennsylvanian System of the Illinois Basin*, Illinois State Geological Survey Guidebook Series, **15a**, 21–27.
- Yochelson, E. & Richardson, E., Jr. 1979. Polyplacophoran molluscs of the Essex Fauna (Middle Pennsylvanian, Illinois). *In*: Nitecki, M.H. (ed.) *Mazon Creek Fossils*. Academic Press, New York, 321–332.
- Zangerl, R. 1979. New chondrichthyes from the Mazon Creek fauna (Pennsylvanian) of Illinois. *In*: Nitecki, M.H. (ed.) *Mazon Creek Fossils*. Academic Press, New York, 449–500.
- Ziegler, A., Scotese, C.R., McKerrow, W., Johnson, M. & Bambach, R. 1979. Paleozoic paleogeography. *Annual Review of Earth and Planetary Sciences*, **7**, 473.