EXCEPTIONAL PRESERVATION IN THE UPPER CARBONIFEROUS COSELEY LAGERSTÄTTE

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Abstract

The Late Carboniferous Coseley Lagerstätte of the West Midlands, UK, contains exceptionally preserved plant and animal fossils that occur as hard parts and mineralized soft tissues sealed within siderite concretions. The concretions were recovered from Westphalian B siltstones and mudstones that lie above the Thick Coal of the Coal Measure Group.

The Coseley plant fossils include a diverse range of plant groups including lycopsids, sphenopsids, ferns and pteridosperms. These are found as isolated fragments that include stems, leaves, cones, seeds and pollen sacs. The Coseley animal fossils comprise a diverse assemblage of arthropods that includes xiphosurans, crustaceans, arachnids, hexapods and myriapods, along with fish and molluscs. All of these organisms lived on and within a Coal Measure swamp forest occupying various niches at different trophic levels producing a complex trophic food web.

The Coseley fossils have been examined using various techniques including scanning electron microscopy and electron microprobe analysis that have revealed several phases of bacterially mediated preservation. Early framboidal pyrite growth accompanied decay of very volatile soft tissues, followed by the precipitation of open framework siderite concretions through bacterially mediated methanogenesis. This occurred either as a crystal phase around plant fossil or as a biofilm around animal ones and prevented compaction of the fossils. Bacterially induced void filling kaolinite mineralization then preceded the secondary phase of siderite precipitation which was then followed later on by void filling sphalerite, galena and pyrite sulphide mineralization, and carbonate mineralization.

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1. Introduction

The fossils of the Coseley Lagerstätte were recovered from lacustrine siltstones of the Upper Carboniferous (Westphalian B) Coal Measures Group from Coseley, West Midlands, UK. The fossils occur as refractory hard parts and mineralized soft tissues with various degrees of lability sealed within siderite concretions. The fossils were collected during active coal mining in the 18th century and now reside in museum collections. Siderite hosted fossil assemblages are a common feature of Carboniferous Coal Measures sedimentary sequences and active coal mining at the present day is still turning up new assemblages that require description and documentation, such as Crock Hey, Merseyside.

Even though siderite hosted fossil assemblages such as Coseley are relatively common in the fossil record they are less well studied than other types of fossil Lagerstätten. The mode of formation of mudrock–hosted carbonate concretions, such as siderite ones, has been intensely studied over the past three decades (Fisher *et al.* 1998) but the mode of fossil preservation within these types of concretions has largely been ignored. The research into the growth and formation of carbonate concretions has involved the study of Carboniferous and modern day concretions, and until recently it was widely accepted that mudrock–hosted concretions grew from the centre outwards by concentric accretion of successive layers of carbonate cements (Fisher *et al.* 1998). However, more recent research by Fisher *et al.* (1998) using back scattered electron microscopy, geochemical and isotope analysis has shown that these types of concretions do in fact form by the simultaneous nucleation of a series of crystallites across an entire concretion. With further concretion precipitation occurring by the growth of the individual crystallites (Fisher *et al.* 1998).

This research provides a model for the precipitation and growth of mudrock–hosted concretions but does not explain how such exceptionally well preserved fossils became encased in the concretions. Considering the relatively common occurrence of fossils within these concretions it is surprising that this question remains unanswered. Baird *et al.* (1986) has addressed this problem in the study of the Mazon Creek siderite hosted Lagerstätte, USA. He concluded that fossil preservation occurred by the rapid precipitation of siderite around a decaying organism producing a mould or impression in the resulting concretion (Baird *et al.* 1986). That study however did not address the formation of the various mineral phases found within the fossils or the taphonomical and chemical conditions that accompanied and induced nodule growth and fossil preservation.

Concretionary siderite–hosted fossil assemblages such as Coseley and Mazon Creek preserve an abundant and diverse assemblage of plant and animal fossils. These fossil assemblages preserve some of the most complete invertebrate animal faunas and some of the most diverse land plant floras known from the Palaeozoic (Baird 1990).

Fossil Lagerstätten such as Coseley can be termed conservation deposits due to the quality of the fossil preservation (Seilacher *et al.* 1985). These qualitative conservation deposits are synonymous with incomplete decay and consequent exceptional preservation. The preservation of organisms within concretions in Carboniferous coal swamps was a widespread phenomenon calling for a large scale cause for arrested decay. These stratiform conservation deposits can be divided into two groups: obrution deposits formed from sediment smothering and stagnation deposits formed due to widespread anoxia (Seilacher 1990). Concretionary fossil Lagerstätten are therefore a subset of stagnation deposits (Seilacher *et al.* 1985). Concretionary Lagerstätten such as Coseley can also be described as diagenetic fossil concentrations as they are the result of post burial physical and chemical processes (Fürsich 1990). The Coseley and Mazon Creek fossil assemblages also represent allochthonous death assemblages where elements of an original life assemblage have been transported and broken down prior to decay (Fürsich 1990).

Time averaging is an important factor to consider when analysing fossil assemblages, and may be defined as the mixing of remains of non-contemporaneous populations and communities of a period of time into one geological plane (Fürsich 1990). The larger the time period between death and burial the more information is lost therefore reducing the quality of the fossil assemblage. Exceptionally preserved concretionary assemblages such as Coseley result from relatively rapid burial and will more faithfully reflect the original life assemblage (Fürsich 1990).

Fossil Lagerstätten such as Coseley and Mazon Creek therefore preserve rapidly buried, un-compacted, exceptionally preserved, stratiform conservation stagnation deposits that represent transported death assemblages.

The aim of this study is to determine the mode of exceptional preservation of the Coseley siderite hosted fossils and produce a model that can be applied to other such Lagerstätten. A number of objectives were undertaken to fulfil this aim.

- Palaeoenvironmental and sedimentological analysis of siderite bearing Coal Measures sediments in the South Staffordshire Coalfield (Chapter Two).
- Biostratinomical analysis of the Coseley fossils to identify the influence of transportation processes on the assemblage (Chapter Two).
- Palaeoecological analysis of the biota to determine modes of life, trophic niches and structure of a Carboniferous swamp forest community (Chapter Two).
- Investigation of an undocumented and un-described siderite–hosted Lagerstätte form the Lancashire Coalfield (Crock Hey). To analyse siderite concretions *in situ* to more closely constrain the sedimentological parameters that led to concretion growth and fossil preservation (Chapter Three).

- Sedimentological, biotic and taphonomic comparison of UK siderite hosted Lagerstätten with that of the North American Mazon Creek Lagerstätte (Chapter Four).
- Detailed mineralogical and chemical investigation of the Coseley, Crock Hey and Mazon Creek fossils to determine the mode of preservation (Chapter Five).
- Finally an investigation into the chemical and taphonomical controls on siderite concretion growth and fossil preservation to produce a fully integrated model for siderite fossil preservation that can be applied to Coseley and other such siderite hosted Lagerstätten (Chapter Six).

2. Palaeoenvironments, palaeoecology and biostratinomy of the Upper Carboniferous Coseley Lagerstätte.

2.1 Palaeoenvironment of the Upper Carboniferous Coseley Lagerstätte.

2.1.1 Tectonic and depositional setting

Coseley is situated in the English Midlands (Fig. 2.1), which during the Carboniferous was located on the southern margin of the Pennine Basin. The Pennine Basin extended over an area that included central and northern England, and formed part of the foreland of the Variscan Orogenic Belt. The Pennine Basin was bounded to the south by the Wales-London-Brabant High and to the north by the Southern Uplands High (Guion *et al.* 2000). The Pennine Basin was formed through active rifting that had developed in response to northwards lithospheric stretching during the Variscan Orogeny. The Pennine basin, and in particular the southern margin around Staffordshire, was greatly affected by Variscan tectonics during the Westphalian, resulting in foreland basin sedimentation, rapid subsidence and associated accumulation of thick sedimentary sequences (Warr 2000).

Coseley lies within the South Staffordshire Coalfield which during the early to mid - Westphalian was dominated by low lying delta plains, where low sinuosity rivers meandered across the landscape depositing sands and muds (Rippon 1996). These low-lying deltas supported forest forming vegetation, which accumulated as peat. Britain at this time lay at equatorial latitudes and suffered a humid non seasonal climate (Glover & Powell 1996). The Coal Measures of the Westphalian thin rapidly to the south of the basin and condense to form thick coal seams indicating more rapid rates of subsidence in the north of the basin (Waters *et al.* 1994).

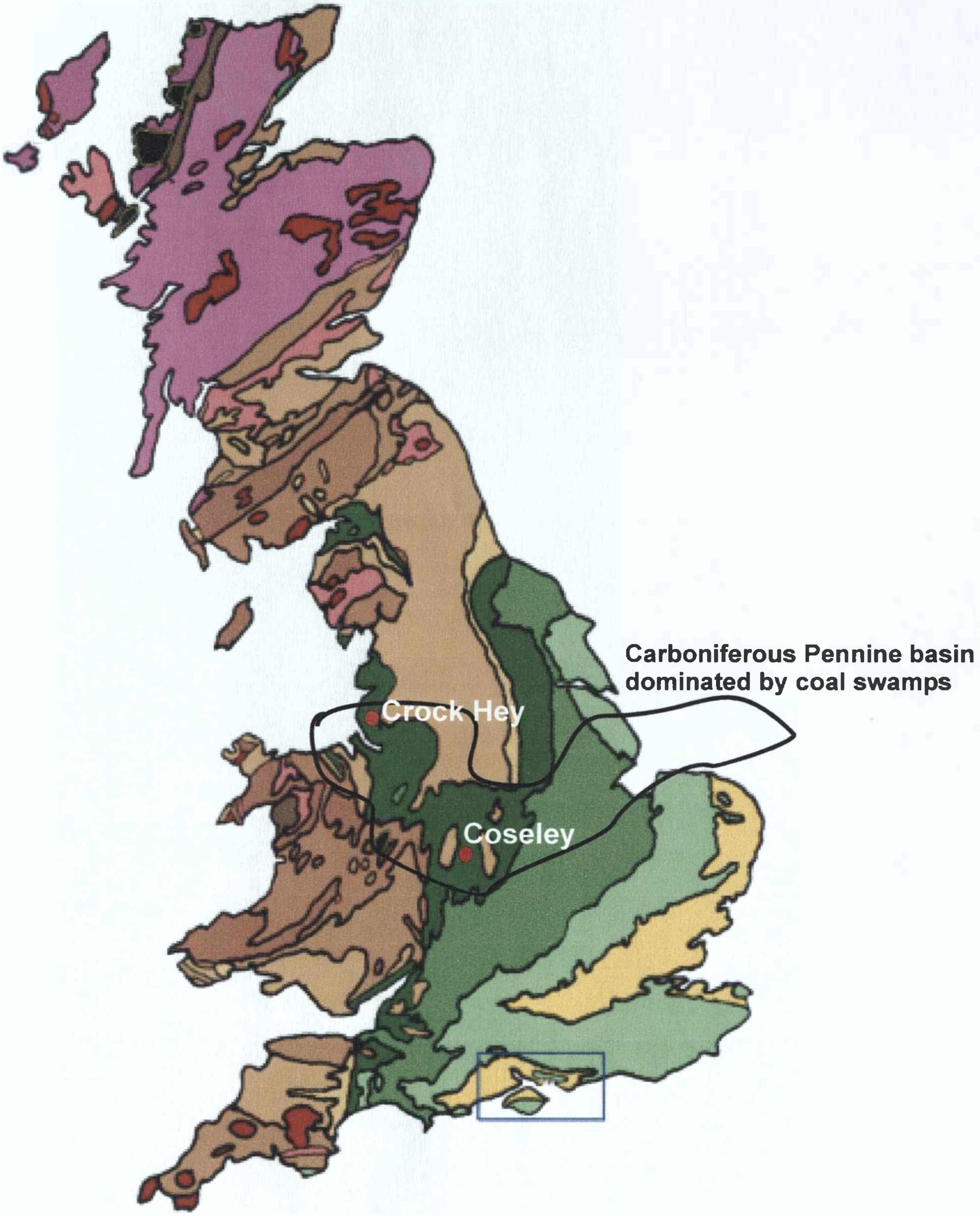


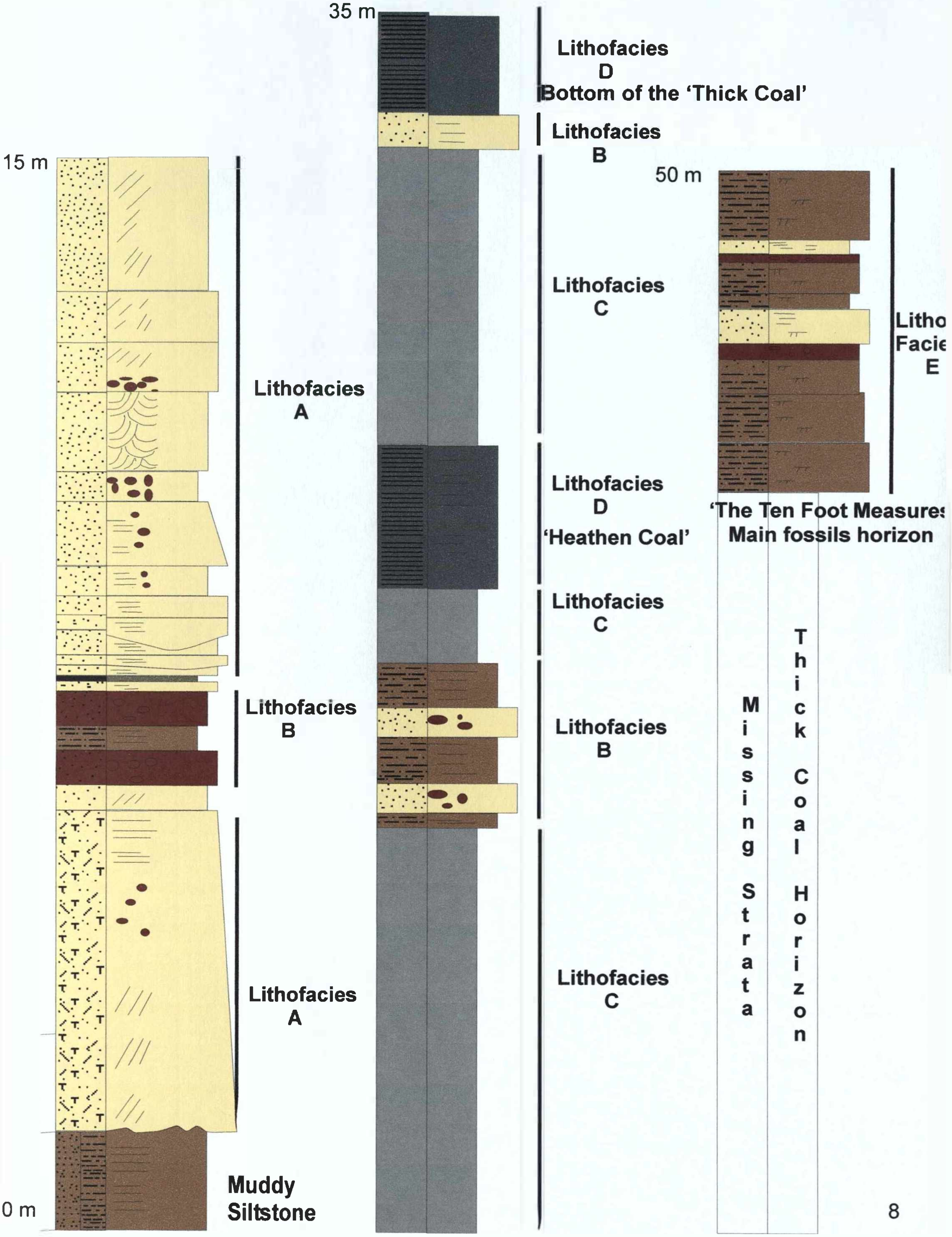
Fig 2.1 Geological map of the UK showing where the Carboniferous Pennine Basin was located and the position of Coseley and Crock Hey. (Adapted from www.bbm.me.uk/portsdown.co.uk)

2.1.2. Sedimentology of the Coal Measure Group

The Westphalian of the West Midlands comprises the Coal Measures Group of the southern Pennine Basin. This unit comprises cyclic sequences of sandstones, grey to black shales, clays, ironstones and coals. The Coal Measures Group is exposed at various localities throughout the West Midlands but the most extensive exposure is at the Saltwells Nature Reserve at Netherton near Dudley (SJ 934 872), where a succession 50 m thick is exposed (Fig. 2.2). The sedimentary succession exposed at the Saltwells includes the 'Ten Foot Measures' the horizon where the Coseley fossils were originally collected from. Detailed sedimentary logging was carried out there in order to constrain the environment of deposition of the Coseley Lagerstätte and five lithofacies were identified (Table 2.1).

Facies	**Lithology**	**Sedimentary structures**	**Interpretation**
A. Cross bedded coarse-medium grained sandstones	Erosively based with a pebble lag. Moderately sorted, angular sandstones rich in lithic clasts and feldspar	Normal grading Tabular cross bedding Trough cross bedding	Minor distributary channel
B. Interbedded fine grained sandstone and siltstone	Thinly bedded, carbonaceous sandstones rich in siderite and organic rich parallel laminated siltstones	Parallel laminated Partially developed sideritic concretions	Coarse-grained overbank deposits
C. Grey massive organic rich claystone	Grey, massive, fine grained claystone with a high proportion of organic detritus and fragmentary plant material	Massive	Fine-grained overbank deposits
D. Interbedded micaceous siltstone and coal	Finley interbedded, organic rich, micaceous siltstone and organic rich coal	Parallel laminated	Peat swamp deposits
E. Ripple laminated siltones and sandstones	Thinly bedded, organic rich, ripple laminated silstones with sideritic horizons and minor sandstone beds	Ripple laminated Siderite concretions Organic rich lenses	Lacustrine deposits

Table 2.1. Summary of the main characteristics for lithofacies A-E, which form the lacustrine delta complex.


35 m
Lithofacies D
Bottom of the 'Thick Coal'
Lithofacies B
15 m
50 m
Lithofacies C
Litho Facie E
Lithofacies A
Lithofacies D
'Heathen Coal'
'The Ten Foot Measure
Main fossils horizon
Lithofacies C
Lithofacies B
Lithofacies B
Missing Strata
Thick Coal Horizon
Lithofacies A
Lithofacies C
Muddy Siltstone
0 m

🟨 **Sandstone**

🟫 **Siltstone**

🟥 **Sideritic Siltstone**

▨ **Claystone**

⬛ **Coal and Claystone**

●●● **Siderite Nodules**

☰ **Planar Lamination**

⫽ **Cross Bedding**

⊥ **Ripple Lamination**

Key to Figure 2.2 Sedimentary log of the Coal Measures Group Saltwells Nature Reserve, Netherton, West Midlands.

Lithofacies A. Lithofacies A occurs at the base and top of the Saltwells section. Bed thickness varies from 25-350 cm, and at outcrop scale thickness can vary, giving the beds a lenticular or channel–shaped appearance. The bases of the beds are sharp and show an erosive relationship with the siltstones below. Lithologically this facies comprises pale grey, medium to coarse-grained sandstones that fine upwards from a pebbly base. The clasts at the bases of the beds vary from 0.5–4 cm are angular to sub-angular and are composed of quartz, feldspar and lithic fragments. These fine up into coarse and then medium-grained sandstone, both of which comprise angular to sub-angular clasts of quartz feldspar and lithics. The sandstones are quartz-rich, but with a sub-arkosic feldspathic component of about 15 per cent. This facies also shows occasional red-brown 'iron-rich' cemented horizons of fine grained sandstones that have developed a nodular appearance in places. Collectively the sandstones within this facies show well-developed tabular and trough cross-bedding.

Interpretation. The sandstones of Lithofacies A represent later stage flood flow deposits, where waning flows lead to the development of normal grading and bedform formation (Glover & O'Beirne 1994). The sediments of Lithofacies A fine upwards from the base, representing a decrease in energy levels. Deposition would have been too rapid and energy levels too high at the base of the lithofacies for bedforms to develop, so these occur higher up in the lithofacies where flow velocity and grain size would have been at the optimum levels for bedform development.

Lithofacies A represents a minor distributary river channel deposit. These minor channels formed by crevassing of larger major river channels during periods of flood. As the river banks of the major channel were breached, large volumes of rapidly moving water would have escaped cutting down into the surrounding flood plain sediments forming an incised channel. These developed into minor distributaries with the continued maintenance of the channel (Fielding 1986). The presence of a sharp erosive base to the sediments of Lithofacies A indicates that it would have formed from channel avulsion and incision into the surrounding softer overbank deposits.

Lithofacies B. This Lithofacies comprises fine sands and siltstones interbedded on a centimetre scale. The sediments are thinly bedded with a maximum bed thickness of 30 cm, and preserve well-developed parallel lamination. The sandstone beds are carbonaceous, some with a sideritic cement, and exhibit partially developed siderite nodules. The siltstones are organic rich and contain fragmentary plant material.

Interpretation. The coarser sand horizons were deposited by sheet flow over the channel banks during flood events (Fielding 1984) and the finer grained siltstones were deposited during intervening periods when fine grained sediment and plant debris settled out of suspension (Fielding 1986). The fine-grained sandstones and siltstones of Lithofacies B are overbank deposits that formed levee accumulations at the margins of the minor distributary channels (Fielding 1986). These coarse-grained overbank deposits in places pass up into the finer grained overbank deposits formed during successive flood events. The absence of plant rootlets indicates that the levee flanks were largely submerged and would have probably been subjected to periods of anoxia allowing the formation of diagenetic siderite.

Lithofacies C. Lithofacies C is composed of massive, grey clay that contains some fragmentary plant remains and organic detritus. It occurs above Lithofacies A, B and D. The clay is highly weathered and there are no longer any sedimentary structures preserved.

Interpretation. The claystones were formed by the rapid deposition of fine grained clay sized sediment as it settled out of suspension The clays of Lithofacies C are overbank deposits formed by sheet flow of sediment over the banks of the distributary channels during periods of flood (Fielding 1986).

Overbank sedimentation would have been common adjacent to an active river channel, due to frequent flooding that occurred as a result of the wet tropical climate, hence the presence of a thick clay horizon above Lithofacies A, the distributary channel. The clays do not show any reddening or palaeosol features indicating near-permanent submergence of the levee flanks and floodplains (Fielding 1986).

Lithofacies D. Lithofacies D comprises a fine-grained dark grey micaceous siltstone that is interbedded on a millimetre scale with a dark coal. The coal and the siltstone are both organic rich and fragmentary plant material is present within the siltstone. The siltstone shows well-developed parallel laminations. The beds of coal and siltstone reach a maximum thickness of one and a half metres and are found overlying Lithofacies B and C.

Interpretation. Lithofacies D represents the autochthonous deposits of peat swamps. These swamps developed through the rapid growth of hydrophytic vegetation such as lycopsids and *calamites* on the submerged flood basin floors, the vegetation acted as an efficient sediment filter allowing only background suspension deposition (Fielding 1984). However during periods of increased rates of subsidence or higher water levels clastic deposition occurred, forming the siltstone horizons. As the peat mires increased in size and mass they built up above the delta plain and clastic input was inhibited and coals formed (Guion *et al.* 2000) such as the Thick Coal horizon, which has subsequently been removed from the Saltwells section.

Lithofacies E. Lithofacies E comprises thinly bedded grey siltstones and minor fine-grained, yellow sandstone beds. The beds range in thickness from 30-40 cm and occur above the coals of Lithofacies D. The siltstones are ripple laminated and contain laminations of black organic material; they also exhibit well-developed nodular siderite horizons. The sandstones are also ripple laminated but do not contain any siderite nodules.

Interpretation. The ripple laminated siderite rich silts and sands of Lithofacies E formed within a lacustrine delta environment indicated by the presence of fresh water fossils such as fresh water bivalves and crustaceans and the absence of any marine indicators. Compaction of organic material to form coal within the peat mires led to subsidence of the delta plain; this allowed flooding from surrounding river channels onto the delta plain forming very large lakes. Clastic sediment was introduced repeatedly as successive flood events filled the lakes. Sand deposition occurred first followed by the deposition of siltstone out of suspension along with allochthonous organic matter. These silts were reworked during successive flood events forming ripple laminations. The accumulation of organic matter in the bottom of the lakes led to the development of strongly reducing bottom conditions conducive to the formation of early digenetic siderite (Fielding 1984).

2.1.3 Facies Organisation

The five sedimentary facies that are exposed at the Saltwells Nature Reserve are arranged vertically to form a lacustrine delta complex (Fig. 2.2), where distributary channel belts were separated by irregularly shaped interdistibutary areas in which lacustrine and fluvio-lacustrine sedimentation occurred. The absence of any evidence of marine or brackish conditions indicates that the interdistributary areas were enclosed freshwater lakes (Fielding 1984).

Lithofacies A represents a minor distributary channel complex which occurs at the bottom of the section and represents a minor meandering river channel. This sandstone has a sharp erosive contact with the muddier siltstones below representing channel avulsion. Lithofacies A is overlain by coarse grained overbank deposits of Lithofacies B followed by sandstones of Lithofacies A again which are then overlain by fine-grained overbank deposits of Lithofacies C which in turn are overlain by coarse grained overbank deposits of Lithofacies B. These overbank deposits were formed along with crevasse delta deposition from overtopping of the distributary channel banks during flood events (Fielding 1984). Organic rich siltstones and coal of Lithofacies D follow, which are in turn overlain by fine grained and coarse grained overbank deposits of lithofacies C and B both of which are overlain by coal of Lithofacies D. The first coal horizon is a minor clastic rich band called the 'Heathen Coal', which was formed from an unstable forest where rapid subsidence allowed flooding and clastic deposition and eventual drowning of the forest leading to the deposition of a sequence of overbank sediments. As the peat mires continued to grow and build up above the level of the flood basin enormous forests developed which in turn produced thick sequences of peat and then coal. These well established peat forests would have formed the Thick Coal horizon which is now absent from the Saltwells section.

A break in section, where the 'Thick Coal' horizon has been removed, is then followed by Lithofacies E or the 'Ten Foot Measures'; these ripple laminated silts and sands represent lacustrine deposits. The lakes would have developed on the delta plains from subsidence of the underlying peat mires, which would have allowed flooding from the distributary channels and drowning of the interdistributary areas. This horizon is important as it represents the equivalent of the horizon where the fossils were originally collected.

2.1.4 Palaeoenvironmental reconstruction

These typical Carboniferous Coal Measure Swamp conditions that had developed in the South Staffordshire Coalfield produced the ideal conditions for siderite concretion formation and fossil preservation. The swamp floors were near permanently waterlogged allowing the formation of large lakes within the flood basins, the rotting vegetation that accumulated in these lakes led to the development of anoxic bottom waters where siderite could be precipitated, these oxygen depleted bottom waters excluded scavengers so that plant organs and animal carcasses that fell in from the surrounding forest or sank from the water column above could remain intact long enough to become preserved in siderite.

The Interpretation of the palaeoenvironmental setting of the Coseley Lagerstätte as that of a lacustrine delta is supported by many strands of evidence. The Coseley fossils were widely collected for many years and the total number of known specimens exceeds several thousand. All of the collected specimens are of terrestrial and freshwater plants and animals. If the environment had been that of a tidally influenced setting and had a marine component it would be highly unusual for all marine fossils to be absent from the data set as they would have had a high preservation potential in a tidal environment. Also tidally influenced settings such as that represented in Mazon Creek are indicated by the presence of fine scale tidal laminations. There are no such fine scale cyclic pairings of silt and mud in the sedimentary succession in the Ten Foot Measures at the Saltwells Nature Reserve. Previous workers on the Westphalian Coal Measures of the British Midlands and other localities (Glover and O'Beirne 1994, Fielding 1984, 1986) concluded the dominance of lacustrine deltaic environments and not tidally influenced settings. Finally the oxygen isotope analysis of the Coseley siderite concretions indicates that the siderite precipitated from meteoric water and show δ O^{18} values in the range of –5 to –6 ‰ and do not indicate a marine influence.

The conclusion that the palaeoenviroment of the Coseley Lagerstätte was that of a lacustrine delta indicates that concretionary fossil preservation can occur in settings other than just tidal ones such as in Mazon Creek. It is perfectly feasible for extensive siderite formation to occur in a lacustrine setting. The low levels of dissolved sulphide inhibit sulphate reduction allowing extensive methanogenesis and siderite precipitation. The pore waters provide an iron source and biocarbonate will be produced from iron reduction and methanogenesis of more deeply buried organic matter excluding the need for a marine influence.

2.2 Palaeontology and biostratinomy of the Upper Carboniferous Coseley Lagerstätte

Introduction

The palaeoecological analysis of the Coseley Lagerstätte is based upon a dataset of over two thousand individual specimens from museums that include the Lapworth Museum of Geology, Dudley Museum of Geology, the Natural History Museum London, the Sedgwick Museum in Cambridge, Oxford Museum of Natural History, the National Museum of Scotland in Edinburgh and the Hunterian Museum, Glasgow. The large number of specimens available to study from this Lagerstätte enables a detailed palaeoecological investigation to be carried out. The Coseley Lagerstätte preserves a diverse assemblage of plants and animals from a variety of habitats and ecological guilds, but with careful analysis these can be disentangled and the palaeoecology of the Lagerstätte interpreted.

There are, however, some important constraints to take into consideration when analyzing the Coseley Biota. The fossils are only found in museum collections and not *in situ* in the field, therefore they are out of their original sedimentary context. The majority of the Coseley fossils held at the Lapworth Museum of Geology belong to the Holcroft Collection and were collected between 1877 and 1893 from Clay Croft open cast works (SO 9372 9297) at Coseley from the Ten Foot Ironstone. This is equivalent to the Ten Foot Measures at the Saltwells Nature Reserve therefore the environment of deposition of the 'Ten Foot Ironstone' and formation of the nodules can be deduced from analysis at the Saltwells locality.

2.2.1. The floral component of the Coseley Lagerstätte.

Introduction

The majority of the fossil specimens that comprise the Coseley Lagerstätte are plant fossils and include a diverse range of plant groups including lycopsids, sphenopsids, ferns and pteridosperms, all of which are typical of a plant assemblage growing within a Carboniferous Coal Measures swamp. The plant fossils are found as isolated fragments including stems, leaves, cones, seeds and pollen sacs (Table 2.2).

Lycopsids

The Coseley Lagerstätte includes 177 lycopsid specimens, assigned to five form genera: *Lepidodendron, Lycopodites, Sigillaria, Bothrodendron* and *Stigmaria* (Table 2.2). The lycopsids make up ten percent of the plant component of the Lagerstätte and eight percent of the total Lagerstätte. The different lycopsid species are representative of various plant organs for example, *Bothrodendron* represents stem specimens, *Lycopodites* comprises herbaceous shoots and *Stigmaria* the rooting organs and *Lepidodendron* by stem, cone, sporophyll and leaf specimens.

The biospecies *Lepidodendron* is the most common lycopsid found within the Coseley Lagerstätte, represented by 163 specimens (Fig. 2.3 b and c), with a total of only 14 specimens representing the other species of lycopsids. It is unlikely that this dominance is due to taphonomic bias as the specimens would have come from a similar environment and had similar preservation potential. It can therefore be assumed that *Lepidodendron* was the dominant lycopsid growing in the Coal Measures swamps.

Plants						
Group	**Biotaon**	**Form taxon**	**Plant Part**	**No. of Specimens**	**% of the plants**	**% of the biota**
Lycopsids	Lepidodendron	*Lepidodendron*	Stem	82	4.5	3.6
		Lepidostrobus	Cone	76	4.2	3.3
		Leidostrobphyllum	Sporophyll	3	0.16	0.13
		Lepidopholios	Stem	1	0.05	0.04
		Cyperites	Leaf	1	0.05	0.04
	Stigmaria		Rooting organ	1	0.05	0.04
	Lycopodites		Shoot	6	0.33	0.26
	Sigillaria		Stem	1	0.05	0.04
	Bothrodendron		Stem	4	0.22	0.17
Calamites	Calamite horestail	*Calamites*	Stem	50	2.75	2.2
		Annularia	Leaf	39	2.14	1.7
		Asterophyllites	Leaf	160	8.8	7.04
		Calamostachys	Cone	11	0.6	0.5
		Calamophloios	Cone	1	0.05	0.04
		Calamocladus	Cone	9	0.49	0.39
		Palaeostachys	Cone	10	0.55	0.44
Sphenophylls	*Sphenophyllum*		Leaf	6	0.33	0.26
Ferns	*Pecopteris*		Leaf	27	1.48	1.18
	Sphenopteris		Leaf	87	4.7	3.8
	Zeilleria		Leaf	2	0.11	0.08
	Cyathocarpus		Leaf	2	0.11	0.08
	Crossotheca		Leaf	35	1.92	1.54
Pteridosperms	*Alethopteris*		Leaf	123	6.7	5.4
	Callipteridium		Leaf	2	0.11	0.08
	Cyclopteris		Leaf	139	7.6	6.1
	Eusphenopteris		Leaf	1	0.05	0.04
	Fortopteris		Leaf	2	0.11	0.08
	Karinopteris		Leaf	1	0.05	0.04
	Laveinopteris		Leaf	61	3.3	2.6
	Macroneuropteris		Leaf	12	0.66	0.52
	Mariopteris		Leaf	17	0.93	0.74
	Neuralethopteris		Leaf	5	0.27	0.22
	Neuropteris		Leaf	1080	39.0	31.2
	Odontopteris		Leaf	8	0.44	0.35
	Pariipteris		Leaf	27	1.48	1.18
	Whittleseya		Pollen	17	0.93	0.74
	Rhabdocarpus		Seeds	6	0.33	0.26
	Trigonocarpus		Seeds	8	0.44	0.35
	Aulacotheca		Pollen	22	1.21	0.96
	Baulaya		Pollen	1	0.05	0.04
Cordaites	*Cardiopteridum*		Stem	3	0.16	0.13
	Cordaites		Stem	7	0.38	0.31
	Arista		Stem	2	0.11	0.08
				Total 2175	Total 100%	Total 100%

Table 2.2. Table of the plant taxa found within the Coseley Lagerstätte.

Sphenopsids

The Coseley sphenopsids are represented by calamite horsetails and the sphenophylls. The calamite horsetails are represented by one biogenus, *Calamites*, which is represented by *Calamites* stems, *Annularia* and *Asterophyllites* whorled leaves (Fig. 2.3 e) and by four species of cones; *Calamostachys, Calamophloios, Calamocladus* and *Palaeostachys*. There are in total 280 *Calamites* specimens in the Coseley Lagerstätte, which make up 15 percent of the plant component of the assemblage and 12 percent of the total Lagerstätte (Table 2.2). The sphenophylls are represented by one biogenus, *Sphenophyllum*, which is represented by six specimens and makes up less than one percent of the plant component. The sphenophylls were the second major lineage of sphenopsids found in the Late Carboniferous, and were a ground creeping plants that occupied clastic river levees (DiMichele & Philips 1994).

Ferns

Ferns are abundant in the Coseley Lagerstätte and comprise five species and a total of 153 specimens (Table 2.2), which makes up eight percent of the plant assemblage and just under seven percent of the total Lagerstätte. The most common fern genera are *Pecopteris, Sphenopteris* and *Crossotheca*. These species comprise the foliage of early marratialean ferns and were small ground creeping plants (DiMichele & Philips 1994).

Pteridosperms

The pteridosperms, are the most abundant plant group within the Lagerstätte and are represented by 18 species and 1164 specimens, which makes up 64 percent of the plant component and 51 percent of the total Lagerstätte (Table 2.2). The pteridosperms are dominantly composed of leaf specimens with some seed specimens, no other plant organs occur, the leaves occur as fronds and individual pinnules. The most abundant genus within the pteridosperms is *Neuropteris* (Fig. 2.3 a) which, is represented by 710 specimens comprising 39 percent of the plant assemblage and 31 percent of the total Lagerstätte. *Laveinopteris* is also an abundant plant genus within the assemblage and is represented by two leaf forms, the small *Laveinopteris* pinnules and the larger *Cyclopteris* (Fig. 2.3 d) leaves which, are represented by 61 and 139 specimens respectively.

Vegetational Habitats

According to the hypothesis of Cleal and Thomas (1994), plant fossils from the British Coal Measures can be divided into three major vegetational habitats: flood basin, river levee and areas surrounding open lakes. The plant fossils of the Coseley Lagerstätte can also be divided up using this model into the three main vegetational habitats.

The Flood Basin Environment. The coal swamps of the Carboniferous were dissected by meandering river channels, bounded by high levees with low-lying land between the levees forming the flood basins. These low lying flood basins were nearly permanently waterlogged and covered by swamp forest forming vegetation for the majority of the time (Cleal & Thomas 1994). The swamp forests were dominated by lycopsid trees, adapted to live on the waterlogged nutrient deficient peat soils of the flood basin (Cleal & Thomas 2001).

The various lycopsid species occupied different positions within the flood basin depending on their tolerance to waterlogged conditions. *Lepidodendron* and *Lepidophloios* were very similar in structure and both occupied similar habitats involving long periods submerged in standing water (DiMichele & Philips 1994). *Lepidodendron* was an opportunistic species that was well adapted to live in more clastic dominated substrates (Cleal & Thomas 1994), found near crevasse splays where micro-topographic relief was produced by better drained alluvial mud (Gastaldo 1987). Clastic sediment was introduced into the flood basin during flood events when channel fill breached the river banks.

In Contrast, *Lepidophloios* was a lycopsid that was tolerant of more waterlogged conditions and grew farther out in the flood basin (Gastaldo 1987). *Sigillaria* was adapted to live on drier substrates peripheral to mires such as channel margins or wet floodplain fringing channels (DiMichele & Philips 1994) and probably represents an intermediate stage between the flood basin and the levees of the river (Cleal & Thomas 1994). A distinct pattern of flood basin vegetation can therefore be seen along a transect through the flood basin swamp to the channel levee, and these are represented at Coseley. The deep swamp flood basin is dominated by water tolerant species of lycopsid such as *Lepidophloios*, followed by *Lepidodendron* near crevasse splays and then *Sigillaria* on drier substrates near the levees of the river (Cleal & Thomas 1994).

Open lake environment. An assemblage of plants that lived surrounding open lakes can also be identified from the Coseley Lagerstätte on the basis of the Cleal and Thomas (1994) model. Standing areas of open water were a common feature of coal measure swamps and were surrounded by thickets of *Calamites* horsetails. These plants were woody and rhizomatus with large sub-tree size aerial shoots enabling them to occupy the unstable clastic margins of lakes and streams (DiMichele & Philips 1994). They also had a shallow root system adapted for living on very waterlogged soils (Cleal & Thomas 1994). The Carboniferous forms were similar to living horsetails of today with regular branching stems, which bore leaves and cones.

River levee environment. The levees of the meandering river channels that dissected the flood basin swamps were raised above the level of the waterlogged swamp and provided a drier plant habitat (Cleal & Thomas 1994). The levees supported a diverse assemblage of plants including sphenophylls, ferns,

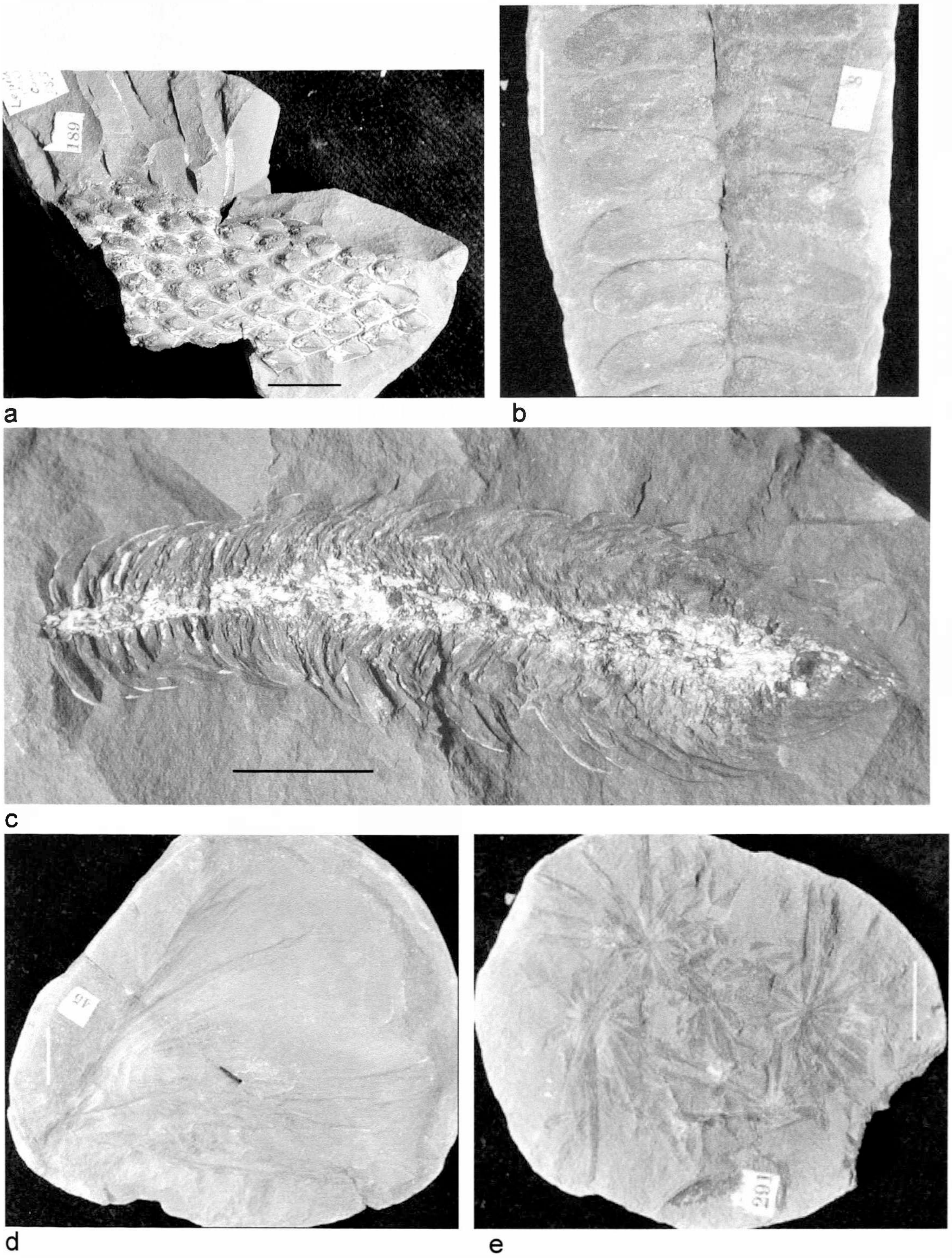


Fig. 2.3 Plant fossils from the Coseley Lagerstätte. a) *Lepidodendron* Sternberg, 1820. (BU 4443. b) *Neuropteris* Sternberg, 1825. (BU 4451. c) Leafy shoot (BU 4445). d) *Cyclopteris* Brongniart, 1828. (BU 4452). e) *Annularia* Sternberg, 1825. (scale bars = 1cm)

pteridosperms, and cordaites. These plants formed a mixed assemblage of trees, shrubs and ground creepers, which were adapted to a drier substrate. The Coseley plant assemblage contains specimens from all four of these groups with a total of 28 different form species (Table 2.2).

2.2.2 The faunal component of the Coseley Lagerstätte

Introduction

The animal component of the Coseley Lagerstätte comprises a diverse assemblage of arthropods along with molluscs and chordates. The animal component comprises 430 specimens, which make up 19 percent of the total Lagerstätte. The xiphosurans dominate the assemblage followed by the fish, bivalves, diplopods, crustaceans, the hexapods and finaly the arachnids (Table 2.3) and (Fig. 2.4).

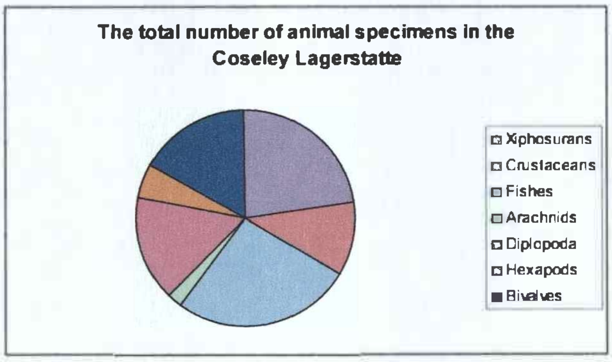


Fig. 2.4. Pie chart showing the relative proportions of the different animal groups within the Coseley Lagerstätte.

Phylum Mollusca

Class Bivalvia. The Coseley bivalves are represented by a small number of freshwater species, represented by 72 specimens, belonging to three genera:

Anthracosia, Carbonicola and *Naiadites*. *Carbonicola* is the dominant bivalve found in the Coseley Lagerstätte with 36 specimens, the next most abundant bivalve is *Anthracosia* represented by 18 specimens, with both of these bivalves belonging to the superfamily Anthracosiacea. The genus *Naiadites* is less common and in the Coseley Lagerstätte is represented by nine specimens.

Phylum Arthropoda

Order Xiphosura. The Xiphosura are represented in the Coseley Lagerstätte by three genera and six species. There are in total 98 xiphosuran specimens within the Lagerstätte, which make up 23 percent of the animal component but just four percent of the total assemblage. The most abundant species of horseshoe crabs within the Lagerstätte is *Euproops rotundatus* Woodward, 1918, (Fig. 2.5 e) which is represented by 51 specimens; a further 13 unidentified *Euproops* specimens are present. Other xiphosurans in the Lagerstätte include the genera *Bellulus* and *Liomesaspis*. The genus *Bellulus* is represented by four species and 33 specimens, the genus *Liomesaspis* is represented by one unidentified species.

Subclass Arachnida. The Coseley arachnids are a very diverse group represented by seven different orders, but low in abundance, with a total of ten arachnid specimens making up just under three percent of the animal component and less than one percent of the total assemblage. These include the scorpions which are represented by two genera *Eoscorpius* and *Anthracoscorpio*. The Thelyphonida or whip scorpions: the first British thelyphonids were described from Coseley, a specimen of the species *Gerlainura brittannica* Pocock, 1911. The final group of extant arachnids that are found in the Coseley Lagerstätte are the Amblypygida or tail-less whip scorpions and whip spiders. This group is closely related to the whip scorpions but they have a rounded carapace, flattened opisthosoma and long spinous front walking legs (Dunlop 1994). The remaining Coseley arachnids belong to the Phalangiotarbida, the Trigonotarbida, the Anthracomartida and the Haptopoda. The Phalanogiotarbida are an enigmatic group of arachnids that are found only in deposits that range from Westphalian A-D in age. They are known only from eight localities globally including Coseley (Dunlop & Horrocks 1997). The Coseley phalanogiotarbids include *Architarbus, Goniotarbus, Mesotarbus* and *Leptotarbus.* The Coseley trigonotarbids include the genera *Eophrynus* (Fig. 2.5 a) and *Trigonotarbus.* The Anthracomartids include the genera *Cryptomartus* and *Cleptomartus*, and the final group the Haptopoda is represented by the single species *Plesiosiro madeleyi* Pocock 1911, this species is unique to the Coal Measures deposits of Coseley.

Subphylum Crustacea. The crustaceans of the Coseley Lagerstätte are represented by 44 specimens that make up 10 percent of the animal component and two percent of the total assemblage. The Coseley Lagerstätte includes two species of Halicyna.The most abundant of which is *Cyclus johnsoni* Woodward, 1905 The Malacostraca also occur in the Coseley Lagerstätte and include the syncarid specimen *Palaeocaris retrastata* Meek and Worthern, 1865, and the pygocephalamorphid specimen *Pygocephalus cooperi* Huxley, 1857 (Fig. 2.5 b) and *Pygocephalus parkersi* Huxley, 1857.

Class Myriapoda. The Coseley myriapods include the Archipolypoda and the Arthropleurida, which together contribute a total of 68 specimens that make up 16 percent of the animal component and three percent of the total assemblage. The Archipolypoda are an extinct group of Palaeozoic myriapods and the Coseley fauna includes two species *Euphoberia ferox* Meek and Worthen 1868 (Fig. 2.5 d), and *Acantherpestes ferox* Meek and Worthen, 1868. The second group of Coseley myriapods are the arthropleurids which, are an extinct group of rare giant millipede-like arthropods.

Class Hexapoda. The final group of arthropods found in the Coseley Lagerstätte are the insects. There are 21 insect specimens in the assemblage making up five percent of the animal component and just under one percent of the total Lagerstätte. All of the insects within the Lagerstätte belong to the class

Pterygota; the winged insects. The Palaeoptera (mayflies and dragonflies) include three species represented by large wing specimens: *Brodia priscocincta* Scudder, 1885 (Fig. 2.5 c), *Oligotypus brittanius* Carpenter, 1931 and *Lamproptilia* sp Brongniart, 1885. The Neoptera include the insect division Blattoidea, (cockroaches) and the remaining Coseley insects belong to this group.

Phylum Chordata

Subphylum Vertebrata. The vertebrates from the Coseley Lagerstätte are represented only by fish specimens that belong to the Chondrichthyes and the Osteichthyes. The Chondrichthyans comprise the Holocephali or chimaeras and the Elasmobranchii or sharks and rays and are represented in the Lagerstätte by teeth specimens alone. The Coseley chimaeras include the species *Helodus simplex* Patterson, 1965, which was a medium sized fish about 30 cm in length. Xenacanthids which, were large shark-like fish that grew up to sizes of 70 cm or more (Zangerl 1981), are represented in the Coseley Lagerstätte by *Xenacanthus* Jaekel, 1899. The most common animal fossil within the Lagerstätte is that of *Palaeoxyris* Brongniart, 1828 (Fig. 2.5 f), these fossils are thought to be chondrichthyan egg cases and were probably produced by the shark like xenacanthids. Originally these unusual fossils were described by Brongniart in 1828 as plants, however later on in 1867 Schenk noticed that they closely resembled the egg cases of some fish and he advocated that they were indeed fish egg cases (Moysey 1910). The Coseley chondrichthyans also include petalodontids, a group of small ray-like fishes, specifically the taxon *Ctenoptychius apicalis* Jaekel, 1899.

The second group of fish that are found in the Coseley Lagerstätte are the Osteichthyans, which are represented only by specimens of sarcopterygian scales. The Coseley osteichthyans include members of the Osteolepiformes,

Phylum	Class	Taxon	No.of species	Trophic level	Life habit	Abundance
Arthropoda						
1	Xiphosura	*Euproops*	2	Carnivore / scavenger	Benthic	F
2		*Bellinulus*	5	Carnivore / scavenger	Necktobenthic	O
3		*Liomesopis*	1	Carnivore / scavenger	Necktobenthic	VR
4	Arachnida	Trigonotarbida	2	Carnivore	Terrestrial	R
5		Thelyphonida	1	Carnivore	Terrestrial	VR
6		amblypygids	1	Carnivore	Terrestrial	
7		Phalangiotarbida	4	Carnivore	Terrestrial	
8		Anthracomartida	2	Carnivore	Terrestrial	
9		Haptopoda	1	Carnivore	Terrestrial	
10		Scorpionida	3	Carnivore	Terrestrial	VR
11	Myriapoda	Arthroplura	1	Herbivore/ Detritus feeder	Terrestrial	R
12		Euphoberiida	2	Herbivore/ Detritus feeder	Terrestrial	O
13	Hexapoda	*Brodia*	1	Carnivore	Aerial/ terrestrial	R
		Indtr	3		Aerial/ terrestrial	VR
14		*Oligotypus*	1	Carnivore	Aerial/ terrestrial	VR
15		Blattoidea	4	Herbivore / detritus feeder	Aerial/ terrestrial	VR
16	Crustacea	Syncarida	1			VR
17		Pygocephalomorpha	3			O
18		Cycloid	3	Detritus feeder / scavenger	Necktobenthic	R
Chordata						
19	Chondrichthyes	Holocephali	1	Carnivore	Nektonic	VR
20		Xenacanthida	2	Carnivore	Nektonic	C
21		Petalondonitda	1	Carnivore	Nektonic	VR
22	Osteichthyes	Actinistia	1	Carnivore	Nektonic	VR
23		Osteleiformes	2	Carnivore	Nektonic	R
24		Dipnoi	1	Carnivore	Nektonic	R
		Indeterminate	5	Carnivore	Nektonic	R
Mollusca						
25	Bivalvia	*Anthracosia*	1	Filter feeder	Bysally attached	R
26		*Carbonicola*	1	Filter feeder	Bysally attached	O
27		*Naiadites*	1	Filter feeder	Bysally attached	R
28		*Myalina*	1	Filter feeder	Nektonic	Vr

Table 2.3 Animal Taxa present within the Coseley Lagerstätte
(abbreviations for abundance: A, abundant, > 200 specimens; C, Common, 100–200 specimens; F, Frequent, 50-100 specimens; O, Occur occasionally, 25-50 specimens; R, Rare, 5-25 specimens; VR, Very rare, < 5 specimens.)

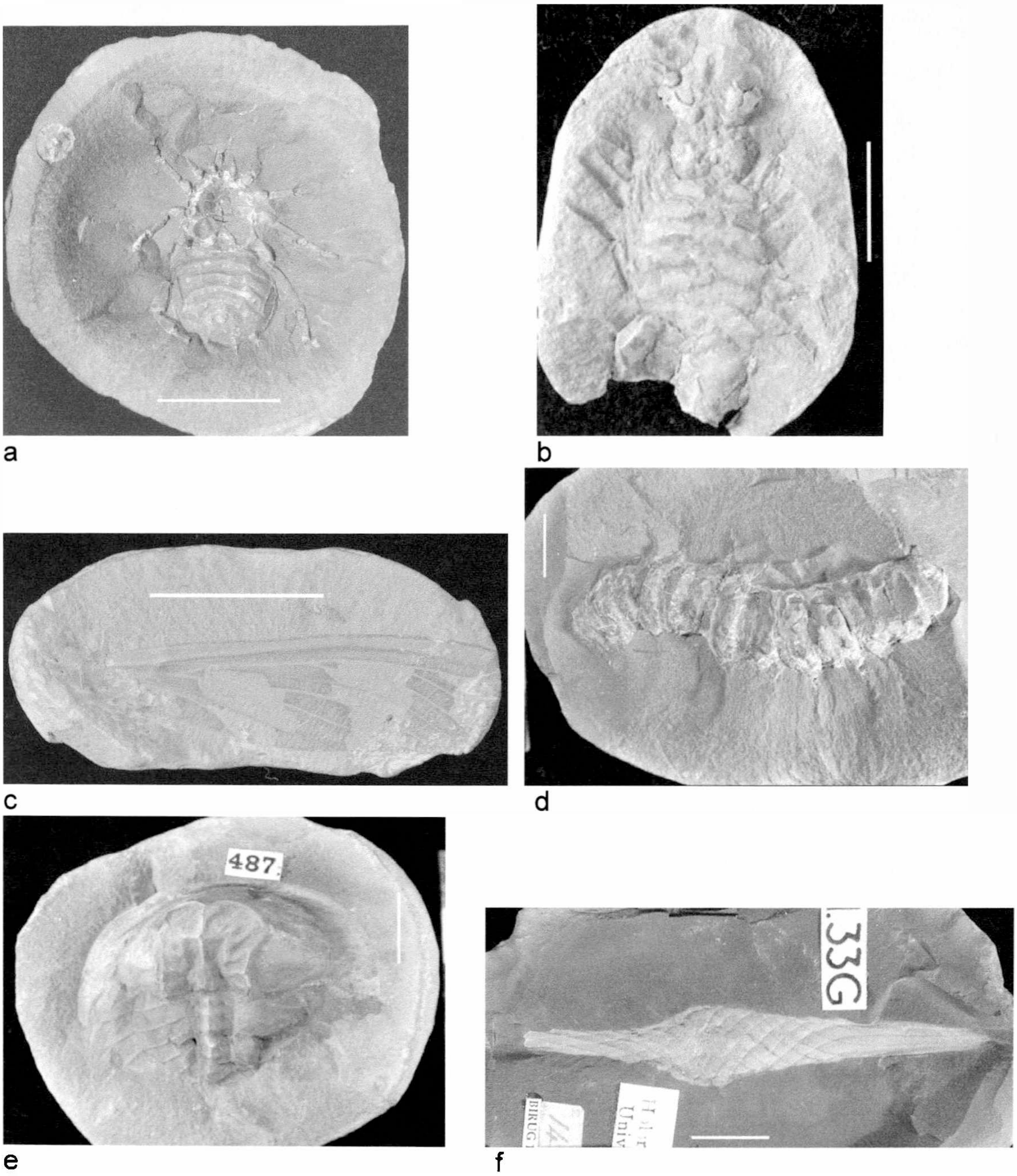


Fig 2.5 Animal fossils from the Coseley Lagerstätte. a) *Eophrynus prestvici* Buckland, 1871.(BU 699A). b) *Pygocephalus cooperi* Huxley, 1857. (BU 4453). c) *Brodia priscocincta* Scudder, 1881. (BU 686B). d) *Euphoberia* (BU 4455). e) *Euproops danae* Meek and Worthen, 1865. (BU 487). f) *Palaeoxyris* Brongniart, 1828 (BU4454).

Actinistia and Dipnoi. The Osteolepiformes are represented by two genera *Megalichthys* Jarvik, 1966 and *Rhizodopsis* Thomson and Hann, 1968. They were generally small fish but *Megalichthys* grew up to two metres in length (Nelson 1994).

A single coelacanth is found in the Lagerstätte. *Coelacanthus lepturus* Moy-Thomas, 1935, would have grown up to one and a half metres in length and occupied freshwater lakes on the swamp forest flood basin. The Coseley lungfishes include the genus *Ctenodus* that resembles the modern day Australian form *Neoceratodus*. *Ctenodus* would have inhabited the lakes of the Carboniferous swamp forest preying upon smaller fish and crustaceans.

2.2.3 Transportation, taphonomic bias and preservation potential of the biota.

In order to interpret the palaeoecology of the Coseley Lagerstätte, taphonomic bias must first be considered. The majority of the fossils in the Lagerstätte were collected from the lacustrine deposits. Therefore, the Coseley assemblage can be divided into a allochthonous component and an autochthonous component. The animals living within the lakes, including crustaceans, xiphosurans, bivalves and fish along with the calamite horsetails that grew around the edges of the lakes comprise an autochthonous component of organisms from the immediate surroundings. The hexapods, myriapods and arachnids were transported into the lake environment, along with the plants growing on the open flood basins, the lycopsids, and those growing on the river levees, the pteridosperms, ferns, cordaites and sphenophylls. The proportions of allochthonous and autochthonous fossils can be compared.

There is a greater proportion of transported plants than autochthonous ones in the assemblage (Fig. 2.6 a), this is because only the calamite horsetails grew around the edge of the lakes in the immediate preserving environment and these only make up a small proportion of the total plant component. This opposite is true when the number of transported to autochthonous animal fossils are compared (Fig. 2.6 b), there is a greater proportion of autochthonous animals present in the Lagerstätte. This is because there was a more diverse animal community occupying the lakes when compared to the plants that lived around the lakes. Also the animals that lived within the preserving environment would have had a higher preservation potential then those living elsewhere in the swamp forest. When the number of transported and autochthonous plants and animal fossils are combined (Fig. 2.6 c) there is a greater proportion of transported specimens; this reflects the large number of transported plants in the Lagerstätte.

When the total number of plant and animal specimens in the Lagerstätte are compared (Fig. 2.7 a) it is revealed that the Lagerstätte is dominated by plant fossils with a small animal component. This probably does reflect that plants would have been more abundant in the original biota then animals. But it probably also reflects that plants contain refractory tissues that can resist decay, and the fact that plants break down into many different organs and therefore produce more parts that can be preserved.

Plants from the levee community are far more abundant in the fossil assemblage then any other plant group (Fig. 2.7 b). This can be determined by analyzing the proportions of different plant organs and the proportions of the different plant groups within the assemblage (Fig. 2.7 c and d). This analysis reveals that pteridosperm leaves from the levee environment are the dominant component of the Lagerstätte. The abundance of pteridosperm leaves in the assemblage is considered to be due to a combination of factors including: the position the pteridosperms occupied within the forest, the preservation potential of the leaves and the method of transport. The pteridosperms grew on the levees of the rivers and were therefore ideally placed to be transported into the preserving environment. The pteridosperms would have hung over the levees enabling easy river transport into the lakes. In addition leaves had waxy coatings so could resist decay during transportation. The abundance of pteridosperms in the fossil assemblage does not reflect the original plant composition of the biota. The pteridosperms grew only on the river levees, which occupied only a small area of the total flood basin. They would therefore have been limited in their numbers by the amount of ground available. It is much more likely that lycopsids where the dominant plant of the Coal Measure swamps during the Carboniferous as they occupied the much larger flood basins.

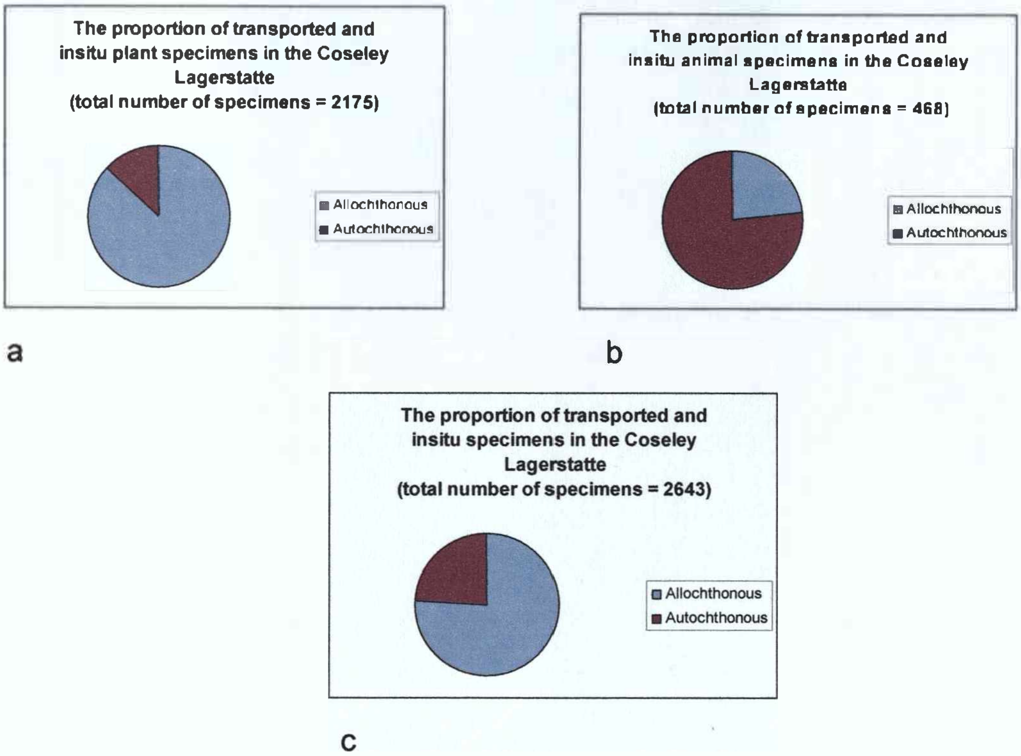


Fig 2.6. Pie charts comparing the proportions of transported and in situ plant and animal fossils in the Coseley Lagerstätte.

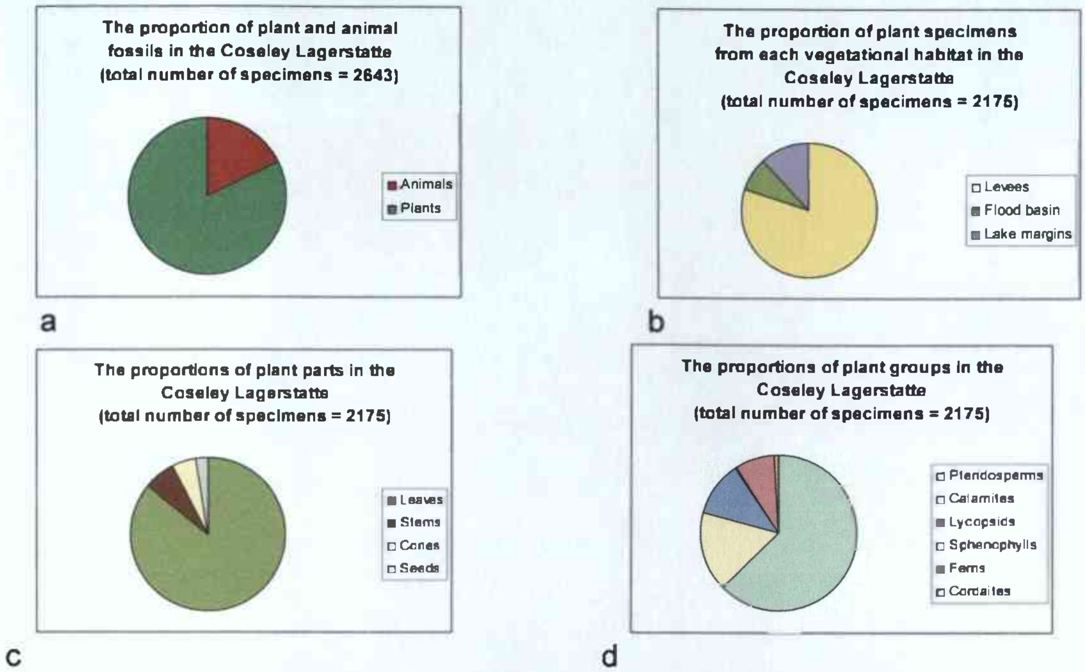


Fig 2.7. Analysis of the floral component of the Coseley Lagerstätte

2.3 Ecology, life strategies and trophic structure of the Coseley biota.

Introduction

As with any fossil assemblage, including those with exceptional preservation, it can be assumed that a significant percentage of the organisms will have left little or no fossil record (Martill *et al*. 1994). This is particularly true for the Coseley Lagerstätte, as the fossil occur inside siderite concretions where there is a size limitation on what will be preserved. The largest nodules are 25 cm therefore any large organisms will be excluded from preservation in its entirety. Also the Lagerstätte favours preservation of organisms living within the preserving environment (lakes) so the terrestrial component is somewhat reduced to organisms that have survived scavenging upon death and been washed into the preserving environment. For example, there would probably have been tetrapods living within the swamp forests but these large terrestrial organisms were not favoured by the fossilization processes and do not occur in the biota. Another significant problem associated with trying to asses the trophic structure of the Coseley Lagerstätte is the lack of information regarding the sedimentological context. The fossils were collected in the late 19th century from the 'Ten foot Ironstone' a sequence of lacustrine siltstones rich in siderite concretions that occurred above the regionally important 'Thick Coal'. This problem has been overcome by examining the 'Ten Foot Measures', a laterally equivalent horizon at the Saltwells Nature Reserve. However any body or trace fossils from the surrounding sediments have been lost making it difficult to decipher what other organisms existed in the original biota apart from those found preserved in the nodules. The preserving environment also produces some problems, as it was anoxic and excluded any infaunal benthic organisms which must have existed elsewhere in the flood basin environment.

However, even with the limited fossil information present it is possible to identify the mode of life of the organisms present, their trophic level and to come to some conclusions concerning trophic structure and predator-prey relationships that were present in the aquatic and terrestrial ecosystems (Figs. 2.8 and 2.9).

2.3.1 Aquatic biota

Epifaunal suspension feeders. The two most common bivalves found in the Coseley Lagerstätte include *Anthracosia* and *Carbonicola* which belong to the Anthracosiacea, which constitute a group of non-marine bivalves that had an average lenght of 45 mm. They inhabited paralic marshes (Moore 1969) and were common in the Westphalian swamps of Great Britain, which may have been the centre of their dispersal (Moore 1969). They commonly form widespread 'mussel bands' where thousands of individuals occurred packed together to form in many places stratal indicies (Moore 1969). *Naiadites* is the other common bivalve found in the Lagerstätte, it was a non-marine myalinid bivalve that occurred locally within the mussel bands in the British Coal Measures (Moore 1969). The bivalves of the Coseley Lagerstätte lived as epifaunal suspension feeders either bysally attached to hard substrates, *Anthracosia* and *Carbonicola*, or as nektonic free swimmers such as the myalinid forms.

Epifaunal scavengers/deposit feeders. The crustaceans of the Coseley Lagerstätte include the Halicyna, a group of small crustaceans with circular, flattened carapaces similar to modern day crabs, and the eumalacostraceans which include the shrimp-like syncarids and pygocephalamorphids. The crustaceans of Coseley had a benthic, epifaunal mode of life, crawling and swimming on and above the sediment surface, where they scavenged on dead organisms or removed food from the sediment (Schram *et al.* 1997).

Epifaunal scavengers/predators. The dominant xiphosuran in the Coseley Lagerstätte, *Euproops*, lived along the shallow margins of lakes, it was well adapted for a benthic mode of life, its streamlined body allowing it to move quickly through the water and its spines produced a large surface area allowing it to rest on soft substrates (Anderson 1994). The less common smaller form, *Bellnulus* may have been a swimming form occupying a wider lacustrine environment. The Carboniferous xiphosurans were scavengers or low level predators, they scavenged upon dead organisms and hunted for smaller invertebrates such as benthic crustaceans (Mikulic 1997).

Small carnivores. The small carnivores of the Coseley Lagerstätte are principally the small fish of the biota. These include the species *Helodus simplex*, a medium sized fish that grew to about 30 cm in size, it had a benthic mode of life (Martill *et al.* 1994) and hunted smaller crustaceans and bivalves which it crushed with the tooth plates in its mouth. Other cartilaginous fishes that also had tooth plates capable of crushing invertebrates included the petaladontids such as *Ctenoptychius apicalis*, a small ray–like fish and the osteolepiforme *Rhizodopsis* (Moy-Thomas & Miles 1971).

Large carnivores. The top predators of the aquatic food web were the large fish, which included the xenacanthids, which were shark-like organisms exceeding 70 cm in length (Zangerl 1981); the large osteolepiform *Megalichthys* which could reach up to 2 m in length (Nelson 1994), the coelacanth, *Coelacanthus lepturus,* which exceeded 1.5 m in length and the lungfish *Ctenodus.* These large fish would have had a necktonic mode of life, actively hunting smaller fish and invertebrates.

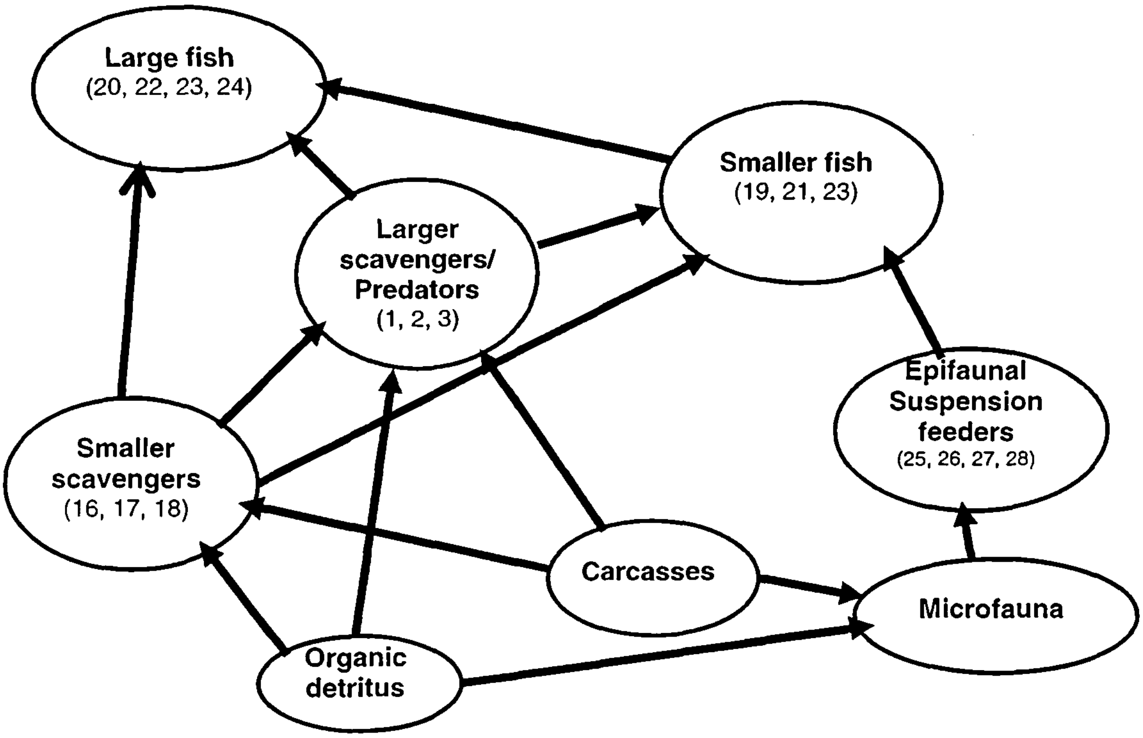


Fig 2.8 Food web for the aquatic organisms of the Coseley Lagerstätte (numbers refer to table 2.3, arrows represent flow of energy)

2.3.2 Terrestrial biota

Smaller detrivores. The small detrivores of the Coseley Lagerstätte included the euphoberrid myriapods and the blattoid hexapods. By comparison with extant biotas these small millipedes and cockroaches would have lived within the leaf litter on the forest floor consuming rotting vegetation (Duncan *et al.* 2003).

Larger detrivores. The large detrivores are represented by the arthropleurid myriapods. These gigantic millipedes also lived within the leaf litter of the forest floor consuming pteridosperm and fern detritus (Proctor 1998) but grew to such gigantic proportions they had few predators once fully grown.

Small predators. The small predators include five groups of small arachnids including the Trigonotarbida, Thelyphonida, Phalangiotarbida, Anthracomartida and the Haptopoda. All of which lived on the forest floor preying upon smaller arthropods such as the myriapods and hexapods. Trigonotarbid arachnids for example were unspecialized predators, they hunted smaller invertebrates and scavenged upon dead organisms. (Dunlop 1994). The trigonotarbid *Pleophrynus* preyed upon small invertebrates such as the hexapods catching them by grabbing their bodies using its cheliceral teeth, this would have left the wings intact and explains the abundance of insect wings in the Lagerstätte (Duncan *et al.* 2003). These arachnids were not top predators and exhibit adaptations to avoid predation, eophrynids for example were heavily tuberculated and were dorso-ventrally flattened enabling then to hide in small crevices (Dunlop 1994). The Haptopoda were also small predators, *Plesiosiro madeleyi* for example used tooth like projections on its legs to catch and immobilize prey, it too exhibits adaptations to avoid predators and hence was not a top carnivore (Dunlop 1999).

Aerial predators. These include the three species of 'dragonflies' found within the Lagerstätte, which probably preyed upon smaller insects. This can be interpreted from comparison with modern day forms, the fossil 'dragonflies' possess spiny legs and well developed mandibles which are associated with predation in extant forms. These 'dragonflies' grew to great sizes which may be explained by the lack of competition for food, as bats, birds and other large aerial predators had not evolved at this time and high levels of atmospheric oxygen (Jarzembowski 1987).

Larger predators. The top predators within the Coseley terrestrial biota were the large arachnids, the scorpions and amblypygids which preyed upon smaller arachnids such as the trigonotarbids and phalangiotarbids as well as other smaller invertebrates. Carboniferous amblypygids probably had a very similar mode of life to extant forms and would have been active predators. They would have preyed upon insects as well as smaller trigonotarbid and phlangiotarbid arachnids (Dunlop 1994).

It is conceivable that the top predators within the terrestrial food web would have been tetrapods, but as these are absent from the Lagerstätte they have been excluded from the analysis.

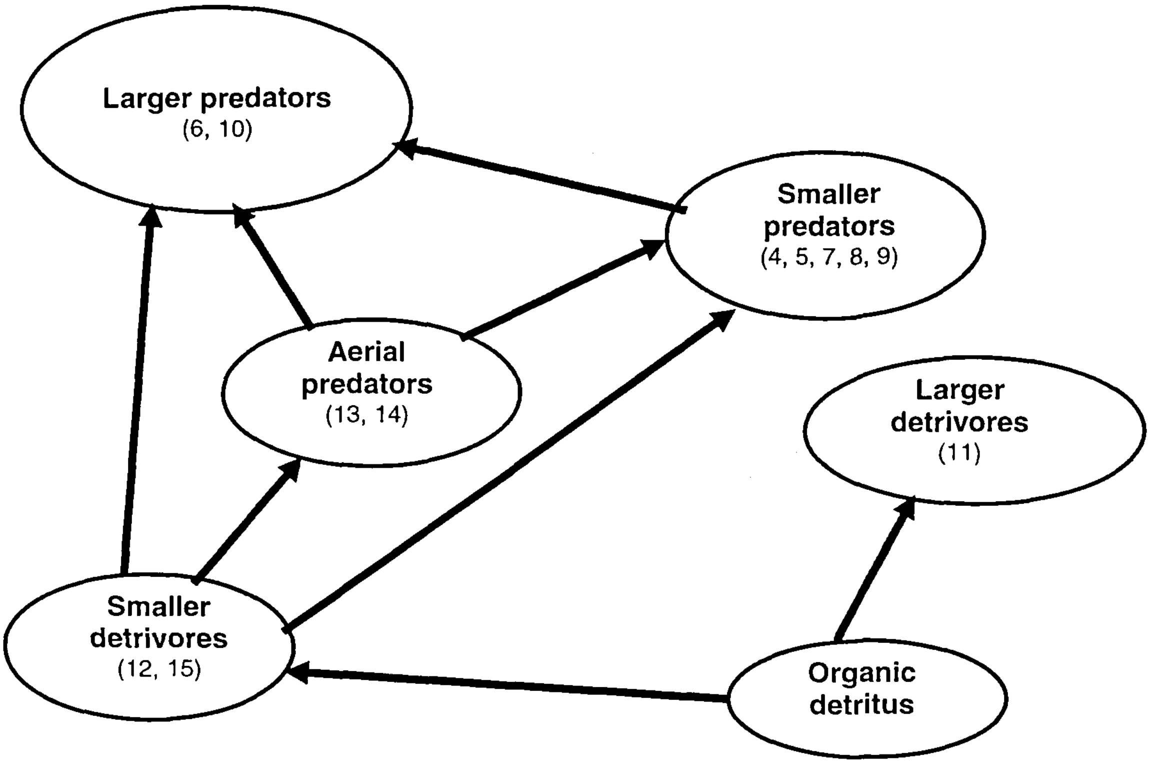


Fig 2.9 Food web for the terrestrial organisms of the Coseley Lagerstatte (numbers refer to table 2.3, arrows indicate flow of energy)

2.3.3 Comparison with a modern day analogue

Peat-forming tropical swamp forests occur at the present day in areas such as Sumatra, Southern Thailand, Malaya, Borneo and Western New Guinea. The ecology of these complex forest ecosystems has been studied in great detail, however after it is difficult to carry out a direct comparison between food webs from these ecosystems and the food webs produced for the Coseley Lagerstätte. The modern food webs available for such regions are much more complex and focus on higher taxonomic groups such as birds and primates therefore making it impossible to do a direct correlation.

3. Palaeoenvironment, palaeoecology and biostrationomy of the Upper Carboniferous Crock Hey Lagerstätte: a comparative study with the Coseley Lagerstätte.

Introduction

Outcrop of the Coal Measure Group sediments in the West Midlands is very limited as a majority of the coal exploitation occurred in the 19th century and in consequence, siderite nodules cannot be examined *in situ* in the field. To overcome this problem, sedimentological analysis was also carried out on Lower Coal Measure sediments (Westphalian A) in the Lancashire coalfield. An active open cast mine at Crock Hey (SJ 353 398) near St Helens exposes a succession of Lower Coal Measure sediments that are 84 m thick. The coal seams and more importantly the ironstone horizons, can be found *in situ,* so the relationships of the siderite nodules to the surrounding sediments can be determined. By examining the Coal Measure succession here and then comparing it with the Coseley sequence, it is possible to determine what sedimentary and palaeontological information is absent from the Coseley Lagerstätte.

Crock Hey open cast mine is situated close to the small village of Chadwick Green near St Helens, Merseyside. The mine occurs in the Lancashire coalfield which, as with Saltwells, is part of the Pennine Basin (Fig. 2.1). The Westphalian succession of the Lancashire coalfield is divided into the Coal Measures Group below and the Warwickshire Group above. Crock Hey open cast coalmine exposes three coal seams; the Wigan Nine-foot, Two-foot and Four-foot. Thick beds of sandstones, siltstones and nodular siltstones separate these seams. Study of these horizons has shown that the siderite nodules vary in size, shape, fossil content and fossil distribution.

3.1 Palaeoenvironment of the Crock Hey Lagerstätte.

3.1.1. Sedimentology of the Coal Measure sediments.

A 30 m section through the Coal Measure Group at Crock Hey exposes three coal seams, and four different sedimentary lithofacies that are the same as those lithofacies observed at the Saltwells Nature Reserve in the West Midlands. (Table 3.1 and Fig. 3.1).

The Coal Measure Group at Crock Hey exposes sediments that form a lacustrine delta complex, as at Saltwells. Only three of the five identified Lithofacies at Saltwells have been identified at Crock Hey: these are Lithofacies B, the coarse grained overbank deposits, Lithofacies D, the peat mire deposits; and Lithofacies E, the lacustrine deposits. Lithofacies A, the distributary channel deposits and lithofacies C, the fine grained overbank deposits are absent. Lithofacies B, the coarse grained overbank deposits at Crock Hey, has been divided into a coarse fraction and a finer fraction, representing different energy levels. The sedimentary log of the Coal Measure succession at Crock Hey (Fig. 3.1) reveals a cyclic succession of peat mire development, followed by flooding and clastic sediment deposition followed again by stabilization of the flood basin and peat mire development.

The Wigan Nine Foot Coal seam is exposed at the base of the section, followed by an interval of parallel laminated nodular siltstones, which in turn are overlain by the Wigan Two Foot Coal seam. This represents extensive peat mire development and vegetation accumulation interrupted by compaction of the peat allowing flooding onto the basin and temporary lacustrine development. The Wigan Two Foot Coal Seam is followed by an extensive nodule–bearing siltstone horizon. This horizon is the main fossil bearing horizon and is dominated by many closely packed small fossiliferous siderite concretions that bear plant, arthropod and vertebrate fossils. This thick siltstone horizon would also have formed due to subsidence of the underlying peat mire allowing flooding on to the basin floor, but this time forming a more extensive lacustrine feature that prevented recolonization of the swamp floor by vegetation.

The thick siltstone horizon is overlain by coarse grained overbank deposits that fine upwards from medium, cross-bedded sandstones that contain fossilised tree trunks to parallel-laminated, fine sandstones with plant roots, which are in turn overlain by the Wigan Four Foot Coal Seam. The coarse grained overbank deposits represent flooding form a nearby distributary channel, rapid flooding would explain the preservation of *in situ* tree trunks that would have been infilled with sand as flooding occurred. These sands fine upwards representing a decrease in energy levels as flooding waned. The presence of plant roots and the partial development of a seat earth at the top of the sandstone horizon indicates the end of clastic deposition and the recolonization of the swamp floor by vegetation eventually building up to form the overlying coal seam.

The absence of lithofacies A and C at Crock Hey indicates a more intermediate position on the flood basin with respect to the Saltwells succession. Crock Hey was more distant from any distributary channels, hence the lack of any coarse grained channelised sandstones but too close for the deposition of very fine grained overbank deposits such as mudstones. Overall, however the palaeoenvironment of the Lancashire Coalfield would have been very similar to that of the West Midlands during the Westphalian, with the subtle differences in sedimentary successions preserved at each locality explained by the position of the area within the ancient flood basin.

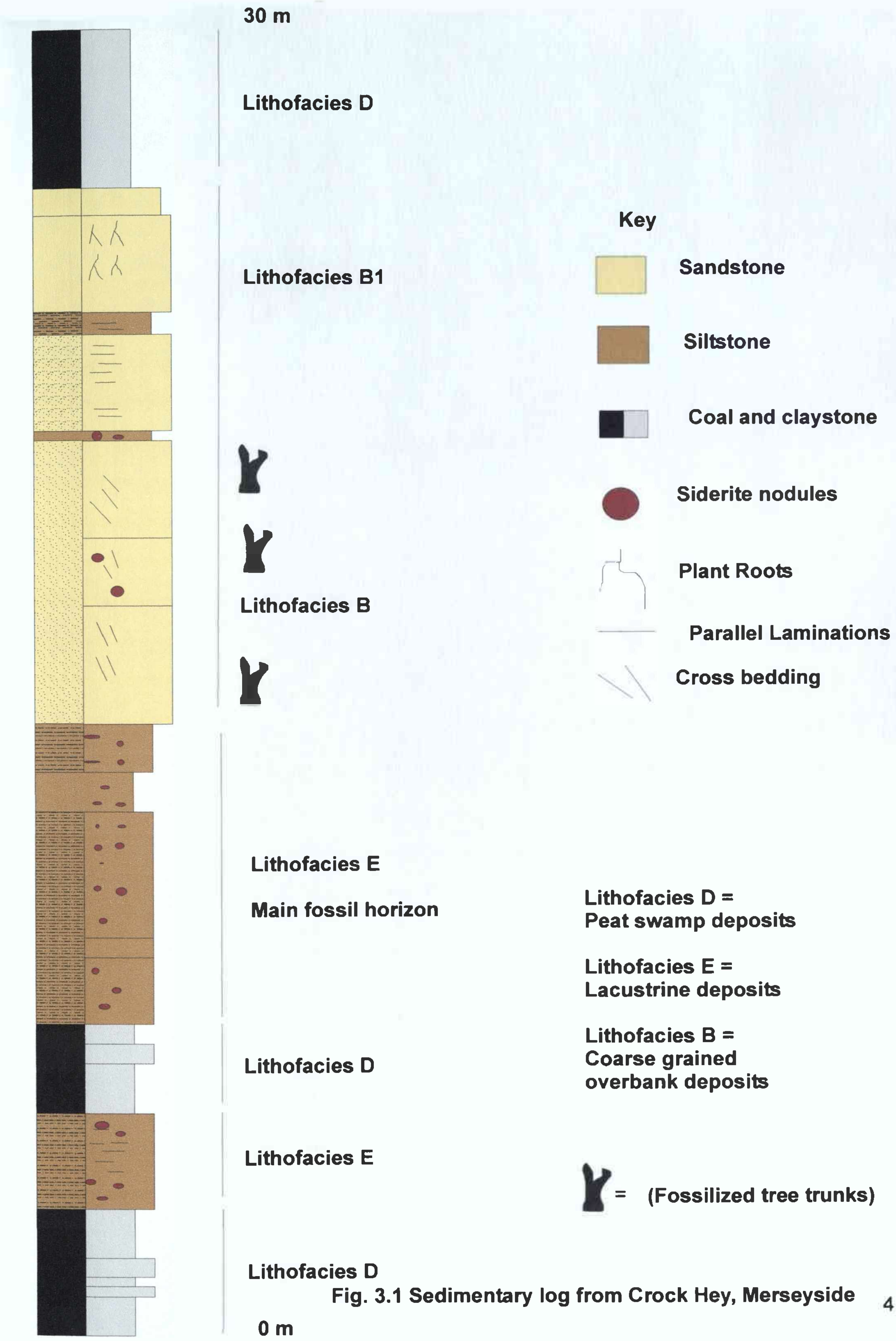


Fig. 3.1 Sedimentary log from Crock Hey, Merseyside

Lithofacies	Lithology	Sedimentary structures and fossils	Interpretation
B. Cross bedded fine grained sandstone	Sandstone beds with sharp contacts with the underlying units containing large fossilised trees, grading into lithofacies B1.	Cross beds and cross laminations and occasional large non-fossiliferous siderite nodules.	Coarse grained overbank deposits
B1. Parallel laminated fine grained sandstones with shale horizons	Tabular bedded sandstone with gradational bases and tops with organic rich shale horizons	Parallel laminations, fossil trees and plant roots	Coarse grained overbank deposits, (finer grained then lithofacies b)
D. Coal seams with shale horizons	Laterally continuous, tabular coal horizons	Parallel laminations in the shale horizons	Peat mire deposits
E. Siderite-bearing siltstones and mudstones	Siltstones and mudstones with abundant small siderite nodules.	Parallel laminations, fossil bearing siderite nodules	Lacustrine deposits

Table 3.1 Summary of the main characteristics for the Coal Measures lithofacies at Crock Hey, Merseyside.

3.2. Palaeoecology of the Upper Carboniferous Crock Hey Lagerstätte.

The palaeoecological analysis of the fossils from Crock Hey open cast mine in Lancashire is based entirely on specimens from a private collector, Mr L Cherry, and on specimens collected during fieldwork. The collection that the following results are based on contains about 1500 specimens; this is smaller than the 2000 specimens documented from the Coseley Lagerstätte but is large enough to be able to be statistically comparable with it. More importantly, the Crock Hey Lagerstätte provides information about the distribution of the fossils within the fossil bearing horizon and on fossils found within the surrounding sediment.

3.2.1. The floral component of the Crock Hey Lagerstätte.

The fossil plant assemblage from the Crock Hey Lagerstätte comprises a diverse assemblage of fragmentary plant fossils that includes leaves, stems, cones and seeds of lycopsids, sphenopsids, ferns and pteridosperms that would have formed a Coal Measures swamp forest similar to those of the West Midlands represented by the plant fossils of the Coseley Lagerstätte (Table 3.2). The nodular plant fossils of the Crock Hey Lagerstätte can also be divided up into the three major vegetational habitats suggested by the model proposed by Cleal and Thomas (1994) and show a very similar pattern to the Coseley plants.

Group	Biotaxa	Form taxa	Plant Part	no.of specimens	% of plants	% of the biota
Pteridosperms	*Neuropteris*		Leaf	822	58	46.75
	Alethopteris		Leaf	4	0.28	0.22
	Mariopteris		Leaf	8	0.56	0.45
	Cyclopteris		Leaf	32	2.24	1.82
	Macroneuropteris		Leaf	1	0.07	0.05
	Trigonocarpus		seed	295	21	16.78
Calamites	*Calamites*	*Calamites*	Stem	37	2.59	2.10
		Calamostachys	Cone	20	1.4	1.13
		Palaeostachys	Cone	5	0.35	0.28
		Asterophyllites	Leaf	46	3.22	2.61
		Annularia	Leaf	7	0.49	0.398
Lycopsids	*Lepidodendron*	*Lepidodendron*	Stem	10	0.7	0.56
	Sigillaria	*Sigillariostrobus*	Cone	94	6.6	5.34
Fern	*Aphlebia*		Leaf	2	0.14	0.11
Sphenophylls	*Sphenophyllum*		Leaf	6	0.42	0.34
			Total	1389	100	100

Table 3.2 The plant taxa found in the Crock Hay Lagerstätte

Lycopsids. The lycopsids of Crock Hey are represented by two species *Lepidodendron* and *Sigillaria*. There are a total of 104 lycopsid specimens in the assemblage, which represents seven per cent of the total plants and just under six percent of the total assemblage. The Crock Hey lycopsids are dominated by *Sigillaria* unlike Coseley which is dominated by *Lepidodendron*. *Sigillaria* was a plant adapted to live on drier more clastic–rich substrates indicating that either the flood basin plains of the Lancashire Coalfield had higher rates of clastic sediment influx then those further south in the South Staffordshire Coalfield or that the fossil assemblage at Crock Hey represents the remains of peripheral peat mires which would have been closer to active channel margins and exposed to clastic input.

Sphenopsids. Late Carboniferous sphenopsids are represented in the Crock Hey Lagerstätte by 115 specimens including stem, cone and leaf specimens of *Calamites.* Calamites specimens are dominated by the leaf taxon *Asterophyllites* and the stem taxon *Calamites.* The horsetails represent eight percent of the plant assemblage and just over six percent of the total assemblage.

Pteridosperms. The Crock Hey pteridosperms are the most dominant plant group in the Lagerstätte. There are 1162 specimens, which represent 82 percent of the plant biota and just over 69 percent of the total assemblage. The pteridosperms are dominated by the medullosan seed fern *Neuropteris* which is represented by a total of 822 specimens which makes up 58 percent of the plant biota and 46 percent of the total assemblage. These results show a similar pattern to the plants from the river levee environment in the Coseley Lagerstätte indicating that similar environmental conditions existed in both Lagerstätte resulting in similar ecological patterns.

Non-nodular plant fossils

At Crock Hey the siderite nodules are found *in situ* in a sedimentary lacustrine delta complex of siltstones, sandstones and coal. Therefore, important information about the plant fossils that occur within the surrounding sediment can also be obtained. A similar plant assemblage to the concretionary one occurs as impression fossils within the siltstone horizons and comprises pteridosperms, lycopsids and Calamites. This indicates that plants are being transported into the lakes and becoming preserved in the anoxic silts on the lakebed, this preservation will either occur as impression fossils or as siderite nodules. Stem specimens are a common feature in the shales around the nodules at Crock Hey and include abundant calamite and lycopsid stems. The rarity of stem specimens within the nodular plants may be due to taphonomic bias, the majority of nodular specimens are relatively small indicating that smaller organisms can easily be preserved within concretions, where as large specimens are rarely preserved in concretions, therefore large stem sections are less likely to become preserved in nodules. The siderite concretions also preserve a higher proportion of cone, pollen and seed organs then the compression flora in the surrounding shales, indicating that the siderite concretions preserve more labile tissues, suggesting earlier preservation then the compression flora where later preservation preserves only refractory plant tissues.

A common feature at Crock Hey is the presence of very large stem sections preserved within the sandstone horizons. These stems occur in life position, have been infilled with sand and have an average diameter of 50 cm. These fossil stem specimens occur across a quarry face that is 65 m in length and within three sandstone beds. There were about 15 fossil tree specimens visible along a transect through the Coal Measures forest. There is a change in the species of fossil trees across the transect, from sphenopsid (*Calamites*) dominant trees at one end of the section moving through to lycopsid (*Sigillaria*) dominant trees at the other end (Fig. 3.2). This transect therefore reveals a section through a swamp forest from the forest edge where there were calamite horsetails growing around standing bodies of water to the forest middle where lycopsids were growing on drier substrates (Fig. 3.3). The trees have been preserved by flooding events, during channel avulsion fast flows of water washed over the forest and broken the fossil tree trunks, these tree trunks have then been in-filled with sand and preserved. The flood waters died down and the plants recolonize the land and the process is repeated, this can be seen as the fossil trees occur in successive beds (Fig 3.3).

The presence of this transect through an ancient Carboniferous forest supports the model proposed by Cleal and Thomas (1994). They suggested that different plant groups grew at different localities within the swamp forest depending on

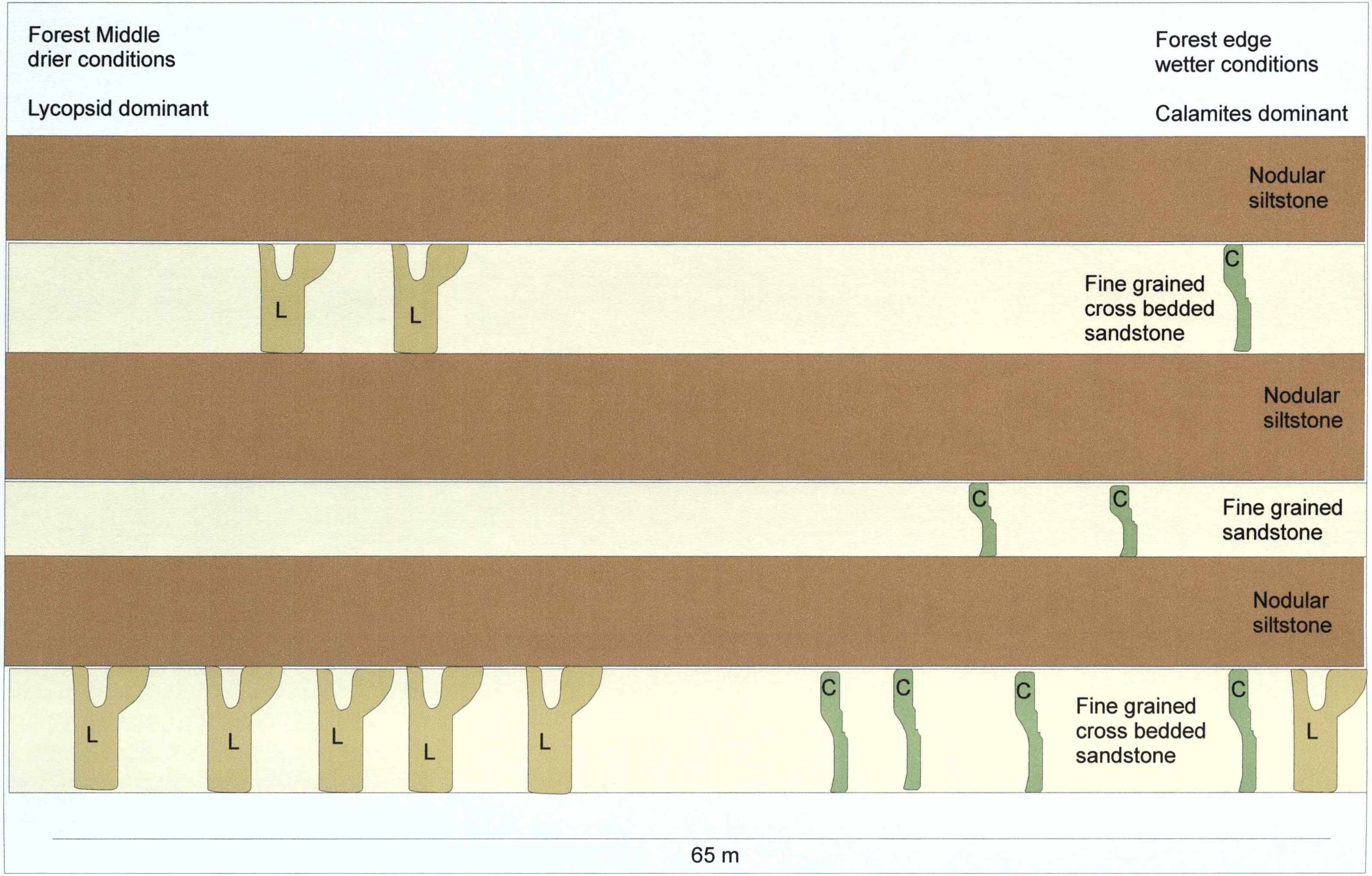


Fig. 3.3 Transect through a palaeoforest at Crock Hey open cast coal mine, Merseyside

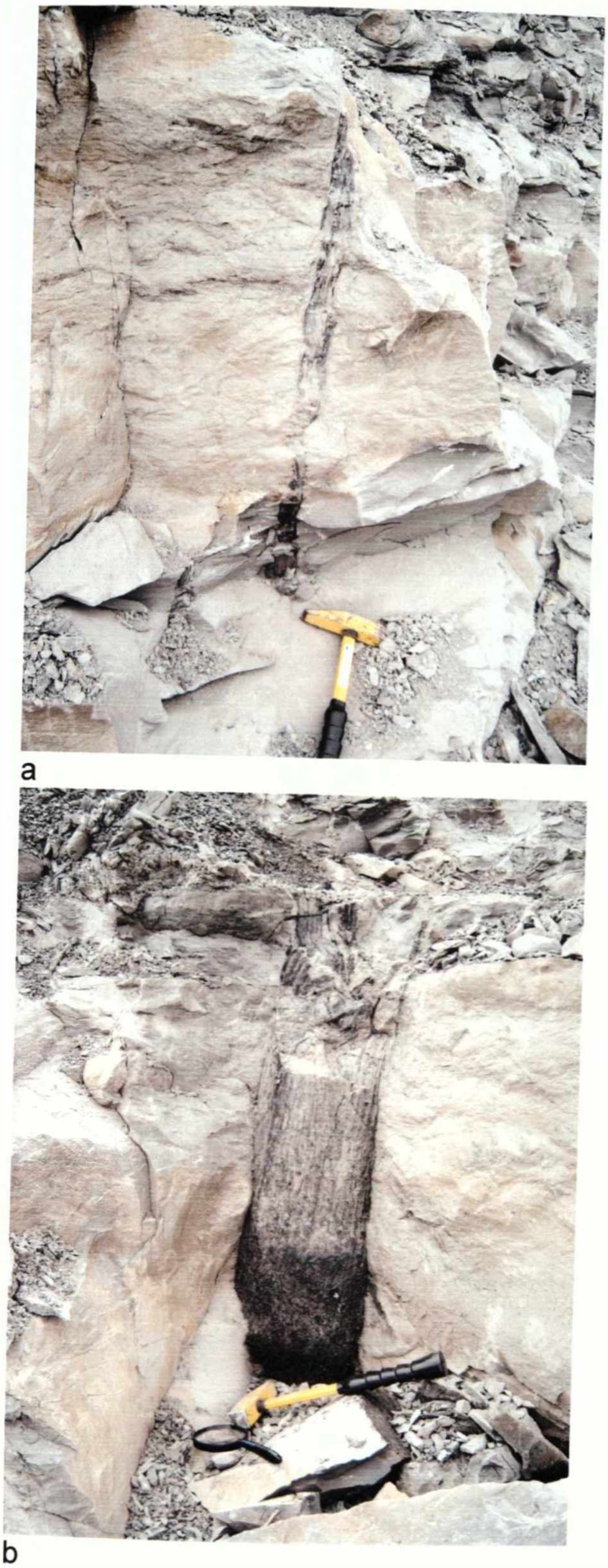


Fig. 3.2 Fossil trees preserved at Crock Hey open cast mine, a) calamite stem. b) lycopsid trunk (hammer 45 cm in length).

their tolerance to waterlogged conditions. This transect reveals that different Carboniferous plant groups did indeed grow at different localities, the lycopsids can be seen growing together and the *Calamites* seen growing away from these also clustered together. The presence of these fossil plants seen *in situ* also supports the division of the Coseley plant fossils into plant groups representing three different vegetational habitats. Crock Hey has therefore been an invaluable resource enabling nodular and non-nodular fossils to be observed *in situ* in the field and has provided unequivocal evidence to support theories drawn up about the Coseley museum specimens.

3.2.2. The faunal component of the Crock Hey Lagerstätte

The animal fossils from Crock Hey form a diverse assemblage of arthropods, molluscs and vertebrates that is very similar to the faunal component of the Coseley Lagerstätte (Table 3.3). The trophic structure of the Crock Hey biota would have also been similar to that of the trophic structure that existed in the Coseley biota and food webs constructed for the Coseley Lagerstätte can be applied to the Crock Hey faunal component.

Phylum	Class	Taxon	No. of species	Trophic level	Life Habitat	Abundance
Arthropoda	Xiphosura	*Euproops*	1	Carnivore/ scavenger	Benthic	A
		Bellinurus	1	Carnivore/ scavenger	Nektobenthic	R
	Arachnida	Trigonotarbida	1	Carnivore	Terrestrial	R
		Scorpionida	4	Carnivore	Terrestrial	R
	Crustacea	Syncarida	1	Deposit feeder/ scavenger	Benthic	R
		Pygocephalomorpha	1	Deposit feeder/ scavenger	Benthic	R
	Hexapoda	*Meganeura*	1	?	Aerial/ terrestrial	R
		Pruvostia	1	?	Aerial/ terrestrial	VR
		Unknown	?	?	Aerial/ terrestrial	VR
	Myriapoda	*Euphoberia*	1	Herbivore/ detritus feeder	Terrestrial	R
		Unkown	?	Herbivore/ detritus feeder	Terrestrial	R
Mollusca	Bivalvia	*Naiadites*	?	Suspension feeder	Bysally attatched	VR
		Anthracosia	?	Suspension feeder	Bysally attatched	VR
Chordata	Chondrichthyes	Xenacanthida	1	Carnivore	Nektonic	O
	Osteichthyes	Dipnoi	1	Carnivore	Nektonic	O

(abbreviations for abundance: A, abundant, > 200 specimens; C, Common, 100–200 specimens; F, Frequent, 50-100 specimens; O, Occur occasionally, 25-50 specimens; R, Rare, 5-25 specimens; VR, Very rare, < 5 specimens.)

Table 3.3. The animal taxa that occur in the Crock Hey Lagerstätte.

The composition of the Crock Hey nodular animal fossils does not really provide any additional information to what is known from the Coseley fossils. However as the fossils were collected *in situ* their exact stratigraphic position from within the nodular horizon is known, and this provides additional palaeoenvironmental information (Fig. 3.4). This log of the nodular bearing horizon shows that terrestrial fossils such as the arachnids and the myriapods were more abundant towards the bottom of the horizon with aquatic xiphosuran fossils becoming more abundant towards the top of the horizon, indicating that palaeoenvironment was becoming more aquatic up through the section i.e the lake was deepening. This supports the sedimentary information that indicates a terrestrial peat mire overlain by lake sediments that pass into more fluvial deposits.

3.3 Biostratinomy of the Upper Carboniferous Crock Hey Lagerstätte.

As with the Coseley Lagerstätte the fossil assemblage from Crock Hey can be analyzed to try to determine the original composition of the biota. The analysis has tried to take into account the effect of transportation, preservation potential and human interference to try to elucidate the original composition of the flora and fauna of the coal measure swamp forest of the Lancashire coalfield during the Late Carboniferous.

3.3.1. Transportation.

The fossils from Crock Hey were collected from a lacustrine siltstone horizon (Lithofacies E) above the Wigan Two Foot coal seam. This indicates that the lacustrine horizon represents the main preserving environment. The palaeoecology of the plants and animals from Crock Hey is well understood so it is therefore possible to divide the assemblage into a transported component and an *in situ* component. The aquatic faunal component includes the xiphosurans, crustaceans, bivalves and fish which along with the calamite horsetails which

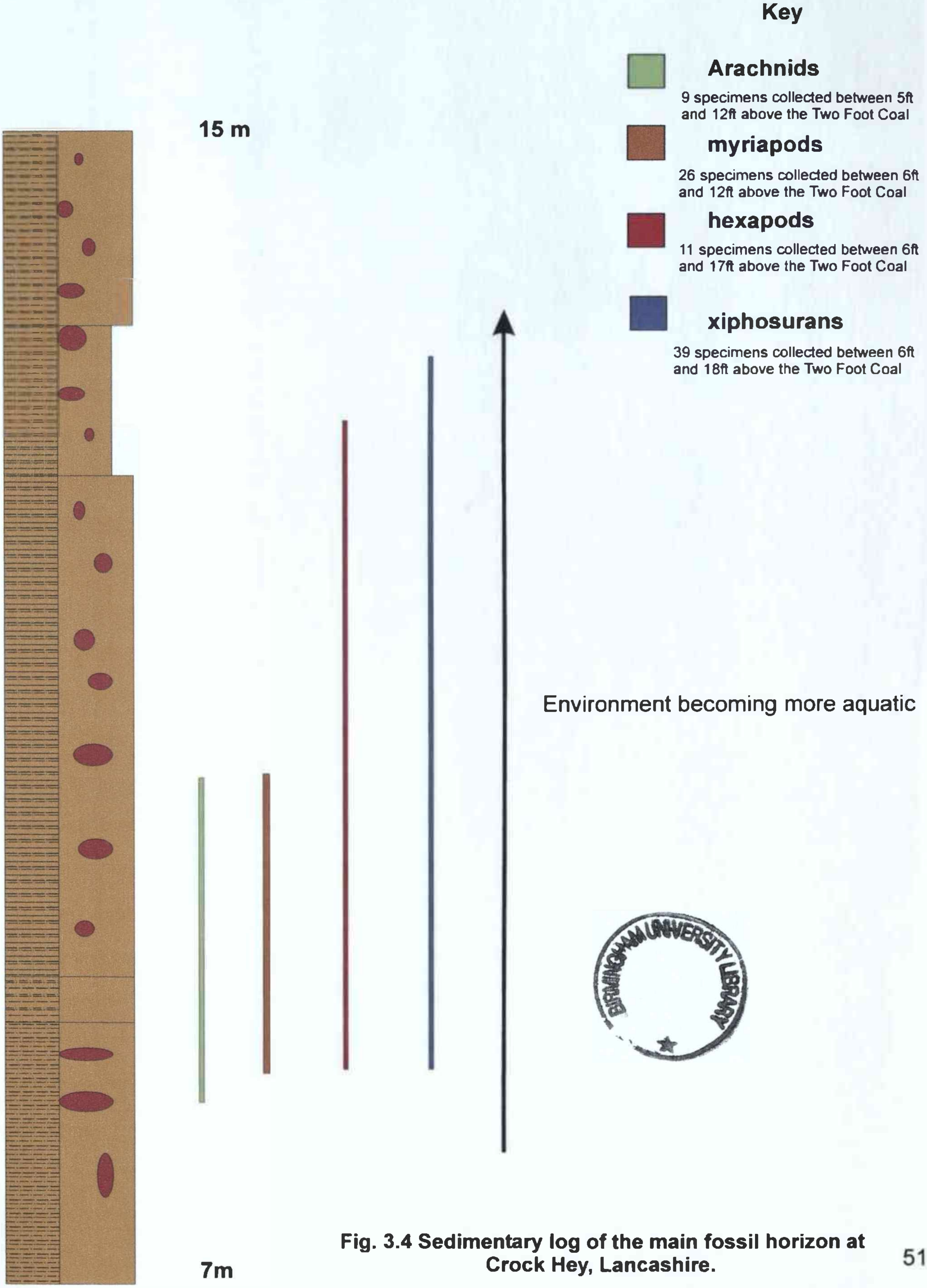


Fig. 3.4 Sedimentary log of the main fossil horizon at Crock Hey, Lancashire.

grew along the edges of the open lakes were being preserved in the immediate surrounding environment. Whereas the terrestrial animals which included the arachnids, hexapods and myriapods along with the plants from the flood basin environment, the lycoposids and the plants from the river levees the pteridosperms, ferns and sphenophylls were dying elsewhere and being brought into the preserving environment. The proportions of transported to autochthonous fossils can be compared (Figs. 3.5 a, b and c).

The animal component is dominated by autochthonous specimens as the carcasses of animals that had lived within the preserving environment would have had a greater preservation potential then those living elsewhere, since the bodies of terrestrial animals could have been easily decomposed or scavenged before they were transported into the preserving environment. The opposite pattern occurs in the plant component which is dominated by transported plants. This reflects the fact that a more diverse plant assemblage grew away from the lakes and that plants are much more resistant to bacterial decay than animals and are more likely to survive the transportation processes into the preserving environment.

When these results are compared with the Coseley transportation pie charts the results are strikingly similar. Both Lagerstätten are dominated by a transported component, the plant component is also dominated by transported fossils whilst the animal are dominated by autochthonous ones. This indicates that the preservational areas and methods of transport of the organic components were the same in both Lagerstätten.

3.3.2. The plant component.

Plants are more dominant in the fossil assemblage and this reflects that plants were more abundant and had a greater biomass than the animals in the original biota (Fig. 3.6 a): the same pattern occurs in the Coseley Lagerstätte. The different plant groups, the habitats that they occupied and the proportion of the different plant organs preserved can all be analyzed. These results show that the pteridosperms (Fig. 3. 7 a) are the dominant plant group present so the river levees were the dominant habitat (Fig. 3.7 b), and leaves are the dominant plant organ (Fig. 3.7 c). This pattern is identical to the pattern seen in the analysis of the Coseley plants.

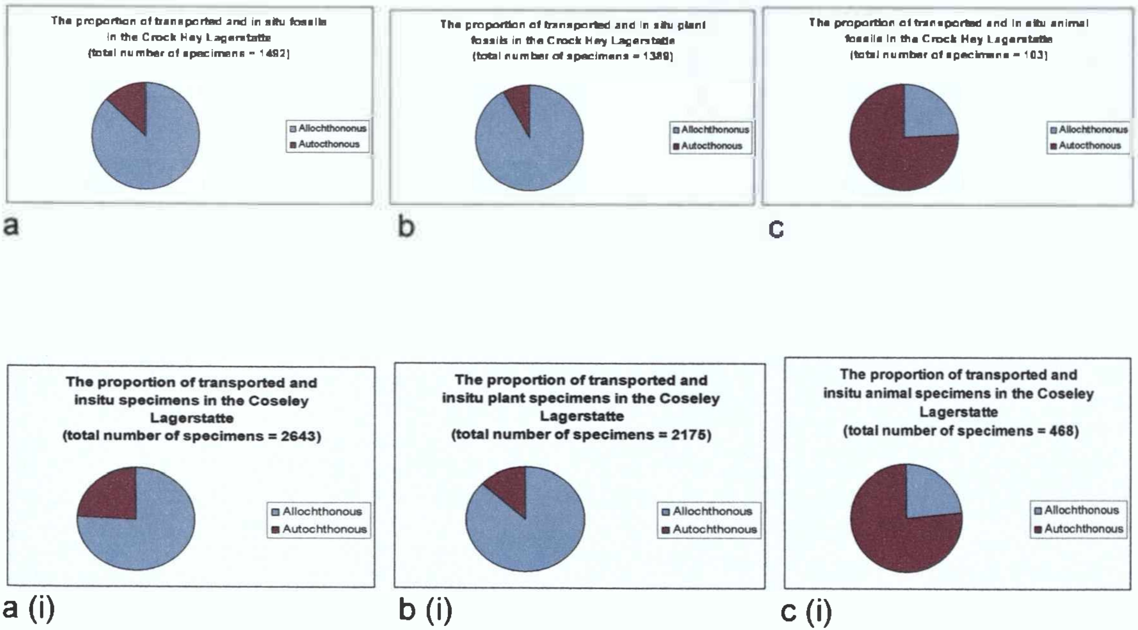
3.3.3. The animal component.

The different animal groups found within the assemblage and their habitats can be analyzed (Fig. 3.8 a). The results of this analysis show that aquatic animals are dominant in the assemblage due to the higher preservation potential compared with the terrestrial organisms (Fig. 3.8 b). The aquatic animals are disproportionately dominated by xiphosurans; this is because the majority of the specimens were fragmentary so the number does not reflect the number of original animals. Fish specimens are also common, but again the majority of the specimens are of individual scales and therefore do not give an indication of the number of individuals. The terrestrial animals comprise the arachnids and myriapods while the aerial component is comprised of only the hexapods.

When these results are compared to the proportions of different animal groups found in the Coseley Lagerstätte the results differ. The Crock Hey animal component is almost entirely dominated by xiphosuran specimens where as the Coseley animal component shows a more even distribution across all of the groups. It is unlikely that the original faunal component between the two areas differed to any great extent as this is not reflected in the plant component between the two Lagerstätten which is near identical. And is more likely to reflect collecting bias. The collectors at Crock Hey may have been specifically looking for xiphosuran specimens where as the collectors at Coseley were interested in all organisms

3.3.4. Collecting bias.

The fossil assemblage recovered from the Crock Hey Lagerstätte has been greatly influenced by the people who collected it. This is mostly reflected in the animal component where more 'interesting' specimens have been collected over other 'not so interesting' fossils, for example the arachnids, xiphosurans and fish specimens. The same is also true for the plant component which has a relatively high proportion of cone specimens. The majority of the lycopsids were monocarpic and only produced cones once in their life cycle so it would be expected that these would be rare in the fossil record, the high number of lycopsid cones in the assemblage reflects collecting bias. Analysis of the Crock Hey Lagerstätte reveals a very similar plant and animal assemblage to that of the Coseley Lagerstätte indicating that the original environments and biotas were similar and similar transportational and preservational processes operated in both Lagerstätte. The differences between the two Lagerstätte are likely to be a product of human interference during the collecting processes and not due to differences in the original biota.



a b c

a (i) b (i) c (i)

Fig. 3.5. Pie charts comparing the transported and *in situ* components of the Crock Hey and Coseley Lagerstätten.

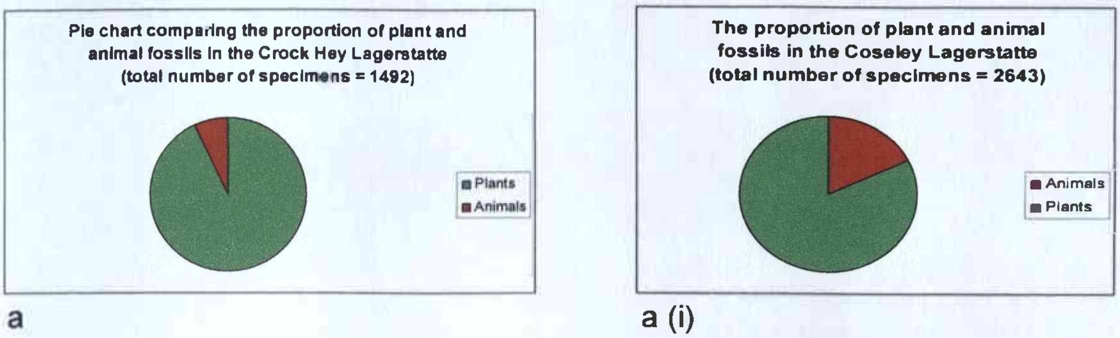


Fig 3.6. Pie charts comparing the proportion of animal and plant fossils between the Crock Hey and Coseley Lagerstätten.

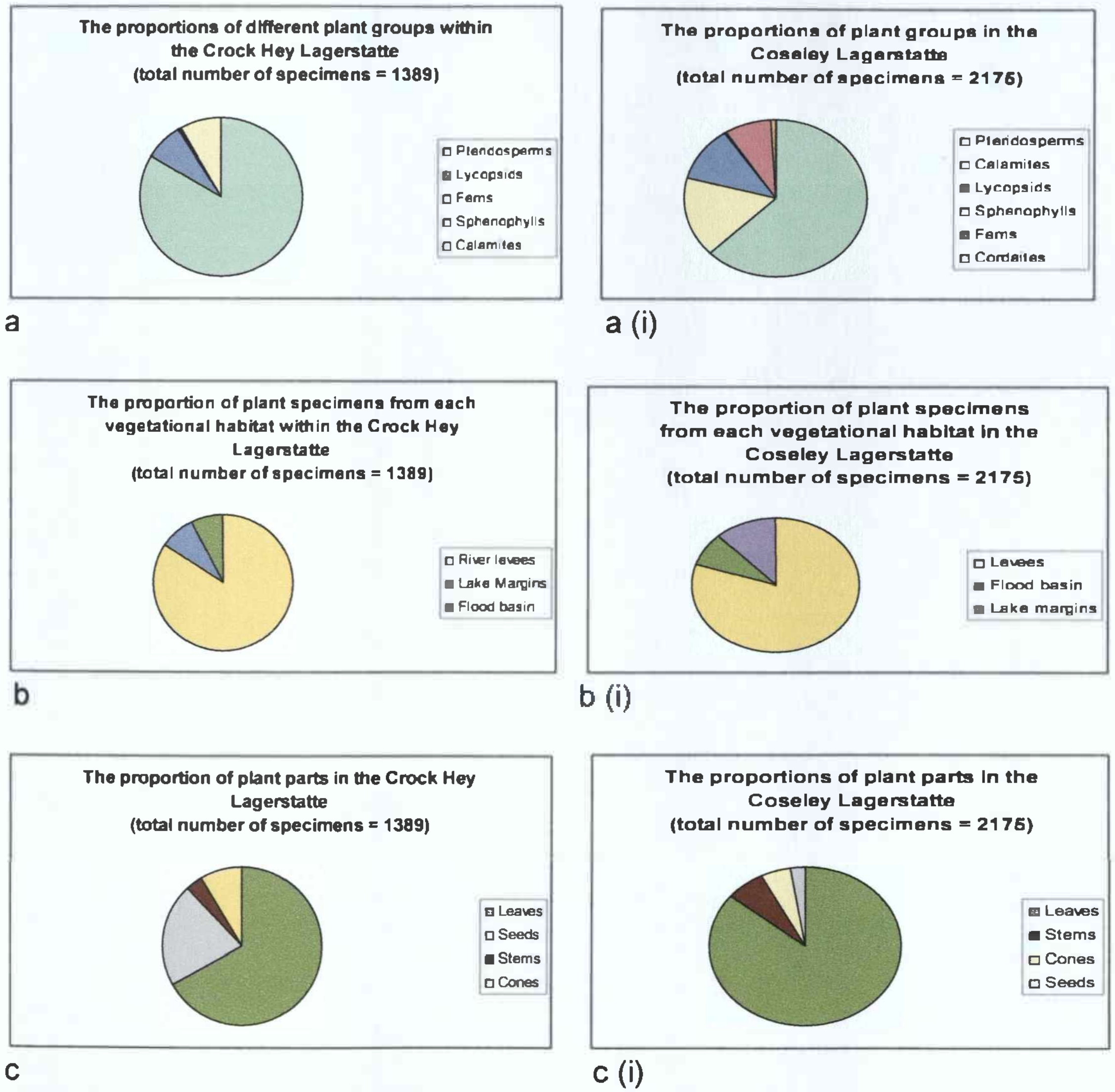


Fig. 3.7. Pie charts comparing the plant component of the Crock Hey Lagerstätte with that of the Coseley Lagerstätte.

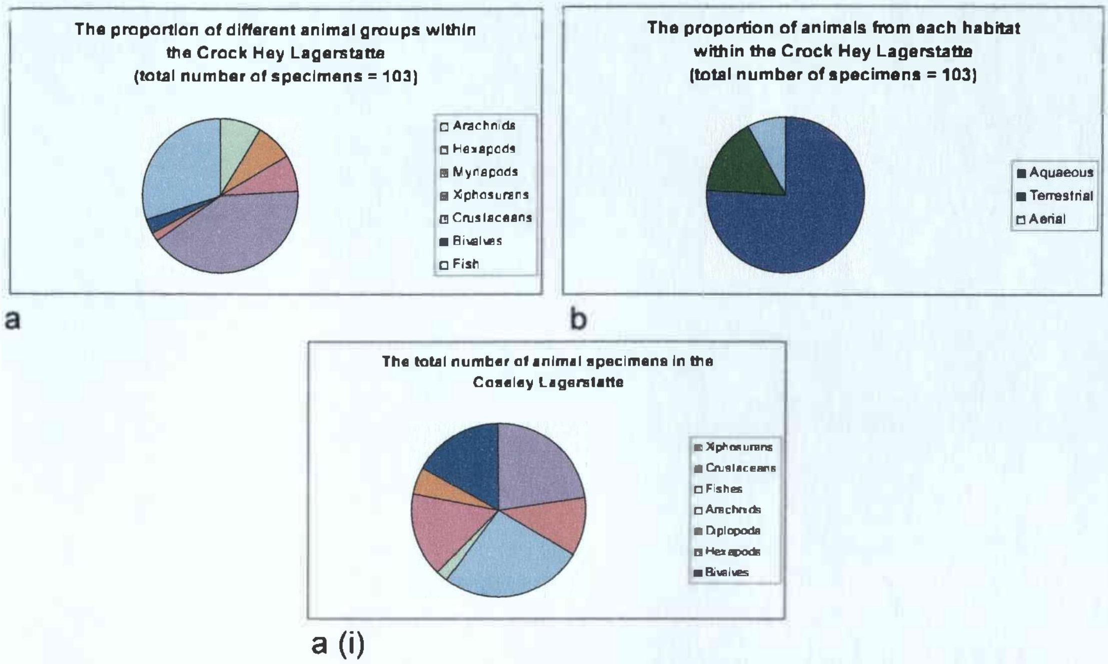


Fig 3.8. Pie charts comparing the animal component of the Crock Hey Lagerstätte with that of the Coseley Lagerstätte.

4. Palaeoenvironment and palaeoecology of the Upper Carboniferous Mazon Creek Lagerstätte.

Introduction

The Mazon Creek Lagerstätte is renowned worldwide for its diverse assemblage of plant and animal fossils preserved in siderite concretions (Baird *et al.* 1986). More than 200 species of plants and over 300 species of animals representing 11 animal phyla have been described from Mazon Creek (Baird *et al.* 1985). Mazon Creek is a small distributary of the Illinois River, situated about 150 km southwest of Chicago. The distributary has given its name to the fossil Lagerstätte collected from spoil heaps of strip mines in the surrounding area (Baird *et al.* 1985). The fossils of the Mazon Creek Lagerstätte are Westphalian D in age and over 280 million years old. They can be found within the northeastern part of the Illinois Basin in Will, Grundy, Kankakee, Laselle and Livingston counties (Baird 1997).

4.1 Palaeoenvironment of the Upper Carboniferous Mazon Creek Lagerstätte.

4.1.1 Stratigraphic setting and sedimentology

The Mazon Creek Lagerstätte occurs within the Middle Pennsylvanian (Westphalian D) Francis Creek Shale Member of the Carbondale Formation. The Francis Creek Shale is a regionally discontinuous unit composed of lenticular wedges of terriginous sediment that overlie the regionally extensive Colchester Coal (Baird *et al.* 1985). The Francis Creek Shale is composed of muddy siltstones with minor sandstone horizons, it has a very variable thickness with a maximum thickness of 25 m. (Baird 1997). It is muddy at the base and coarsens upwards with episodic appearances of rhymitic silt and clay laminations. Above this the shale exhibits cross-stratified muddy siltstones grading upward into coarser siltstones and sandstones (Baird *et al.* 1985). One notable feature of the Francis Creek shale is the cyclic pairing of clay and silt laminations which reveal cyclic sequences formed from the result of tidal processes (Kuecher *et al.* 1990). Siderite concretions occur only in the lower three to five metres of the Francis Creek Shale where it exceeds 15 m in thickness (Baird 1997) and contain a variety of terrestrial, fresh water and marginally marine fossils.

4.1.2 Mazon Creek palaeoenvironment

The palaeoenvironment of the Mazon Creek Lagerstätte was that of a river influenced estuarine coastal system. The Colchester Coal represents the Lower Carbondale Formation and would have formed from lycopsid dominant coal swamp forests that had developed in response to the warm tropical Carboniferous climate. Global sea rise then followed, leading to a marine transgression that inundated the Colchester Coal swamps and led to the deposition of the Francis Creek Shale. Due to its unique position, two different environmental habitats existed; the fresh water to minimally brackish water Braidwood Habitat and the brackish to marginally marine Essex Habitat, each with their own distinctive biotas. The Braidwood Habitat developed along the estuary margins and further inland in river channel waterways and coal swamps, whereas the brackish to marginally marine Essex Habitat occurred in the euryhaline prodeltaic setting of the semi-restricted estuary that had formed as the result of marine inundation of the delta dominated coast (Baird *et al.* 1985). The two distinct habitats are recognised by their different and distinct biotas, and the transition from one environment to the other is indicated with a sharp decline in taxonomic diversity from brackish water Essex environments to fresh water Braidwood environments (Baird 1997).

4.2 Palaeoecology of the Upper Carboniferous Mazon Creek Lagerstätte.

Introduction

The Mazon Creek Lagerstätte is very similar in many ways to the Coseley Lagerstätte, fossils from both are found within siderite concretions recovered from siltstones and shales of Coal Measure sequences. However there are some important differences. The Mazon Creek Lagerstätte is Westphalian D in age and is therefore slightly younger then the Coseley assemblage. The palaeoenvironmental setting was also different. The division of the Mazon Creek Lagerstätte into the freshwater and terrestrial Braidwood Biota and the brackish to marine Essex Biota is the most significant difference from Coseley, which does not have a marine component. The Coseley Lagerstätte is very similar in composition to the Braidwood Biota. The Essex Biota, in contrast, does not have any taxa in common with the Coseley Lagerstätte and represents a very different habitat. It is therefore convenient to discuss the two individual biotas of the Mazon Creek Lagerstätte separately. The analysis of the Mazon Creek Lagerstätte is based on first hand analysis of the Mazon Creek invertebrate collection at the Field Museum in Chicago, Illinois, which involved analysis of over 24,000 specimens.

4.2.1 Braidwood Biota

Over 250 species of plants and over 200 species of animals have been described from the Braidwood biota (Baird *et al.* 1985).

Plant Component

The Mazon Creek Braidwood biota is dominated by plants which comprise 83 percent of the biota and represent a typical Coal Measures flora (Baird *et al.* 1986). The nodules preserve a diverse assemblage comprising a fragmentary association of various plant organs including foliage, bark and stem fragments and fruiting organs. The plants found in the Braidwood biota include lycopsids such as *Lepidodendron* and *Lepidostrobus.* Sphenopsids represented by calamite horsetails such as *Calamites* and *Annularia.* The seed ferns or pteridosperms represented by the pinnule genera *Neuropteris, Cyclopteris* and *Alethopteris* and the corditales represented by mineralized trunks (Baird 1997).

This association of plants is very similar to the plant groups observed in the Coseley assemblage. It is therefore probable that the swamp forests in both Lagerstätte had similar environmental requirements and similar ecological processes operating within them. Like the Coseley plant assemblage the plant fossils of the Braidwood biota represent an allochthonous grouping of fragmentary plant material indicating that the plants have been transported from their original habitat to the preserving environment. The Braidwood flora like the Coseley flora is dominated by pteridosperm pinnules (Baird 1997) and not lycopsids, despite the fact that the latter were the dominant plants within the forests of the Colchester swamps (Baird 1997).

The allochthonous plant debris is thought to represent water transported material derived from an upstream setting. The pteridosperm dominated assemblage probably came from a very different habitat to that of the swamp forest such as river levees and areas surrounding distributary channels (Baird *et al.* 1986). Studies of similar modern day setting such as the Orinoco delta have shown that these inland settings are capable of releasing vast amounts of floating debris that contribute greatly to plant debris on the delta, in fact more so than the bounding swamp forests (Baird *et al.* 1986).

Animal component

The Braidwood fauna comprises a diverse assemblage of arthropods along with fish and tetrapods (Table 4.1). The arthropods are the most abundant and diverse group within the Braidwood animal component and comprise 60 different species that make up 70 percent of the animal specimens (Fig 4.1 a and b). The bivalves are the next most abundant group, followed by the fish and the tetrapods.

The Braidwood fresh water bivalves consist of two groups the myalinids and the unionaceans. The myalinids comprise the genera *Anthraconcaia*, *Naiadites*, *Cururirmula* and *Anthraconauta* and the unionaceans comprise the genera *Anthracosia* and *Carbonicola* (Bowman-Bailey & Sroka 1997).

The Braidwood freshwater arthropods are a large and diverse group comprising 2384 specimens in five main groups (Table 4.1). The crustaceans are dominant followed, in order of abundance, by the xiphosurans, myriopods, hexapods and arachnids (Fig. 4.1 c). The arthropods comprise 60 different species although interestingly the most abundant groups do not have the highest species diversity. The two least abundant groups have the highest species diversity; the hexapods are the most diverse group followed by the arachnids, the crustaceans, myriapods and finally the least diverse group the xiphosurans (Fig. 4.1 d).

Crustacea. The crustaceans are the dominant arthropod group in the Braidwood biota with 1250 specimens (Table 4.1) that belong to two main groups: the Syncarida and Pygocephalomorpha. The syncarids include the genera *Acanthotelson* and *Palaeocaris* (Fig. 4.2 e), both of which show similar abundance in the biota. The Pygocephalomorpha are less abundant in the biota than the syncarids (Fig 4.2 d) and are dominated by the genus *Anthracaris*.

Phylum	Class	Taxon	N.o of species	Trophic level	Life habit	Abunadance
Arthropoda						
1	Xiphosura	*Euproops*	1	Carnivore/ scavenger	Benthic	A
2		*Palaeolimulus*	1	Carnivore/ scavenger	Nektobenthic	O
3		*Liomesapis*	1	Carnivore/ scavenger	Nekotobentic	VR
4	Arachnida	Pjalangiotarbida	4	Carnivore	Terrestrial	F
5		Anthracomartida	1	Carnivore	Terrestrial	R
6		Trigonotarbida	2	Carnivore	Terrestrial	R
7		Uropygida	1	Carnivore	Terrestrial	VR
8		Amblypygida	1	Carnivore	Terrestrial	VR
9		Ricinuleida	2	Carnivore	Terrestrial	VR
10		Opilionida	1	Carnivore	Terrestrial	R
11		Scorpionida	?	Carnivore	Terrestrial	R
12	Myriapoda	Euphoberiida	5	Detritus feeder	Terrestrial	A
13		Arthropleuridea	2	Detritus feeder	Terrestrial	R
14	Hexapoda	Palaeodictyoptera	5	Carnivore	Aerial / terrestrial	R
15		Megasecoptera	1	Carnivore	Aerial / terrestrial	VR
16		Diaphanopterodea	1	Carnivore	Aerial / terrestrial	VR
17		Ephemeroptera	1	Carnivore	Aerial / terrestrial	VR
18		Protorthoptera	12	Carnivore	Aerial / terrestrial	F
19		Blattodea	2	Detritus feeder	Aerial / terrestrial	O
20		Un identified	14		Aerial / terrestrial	R
21	Crustacea	Syncarida	4	Detritus feeder/ scavenger	Nektobenthic	A
22		Pygocephalomorpha	2	Detritus feeder/ scavenger	Nektobenthic	F
23		Ostracoda	1	Detritus feeder/ scavenger	Nektobenthic	C
Mollusca						
24	Bivalvia	*Myalinid*	4	Suspension feeder	Nektonic	A
25		*Unionceas*	2	Suspension feeder	Benthic epifaunal	C

Table 4.1 Animal taxon present within the Mazon Creek Braidwood Biota.

(abbreviations for abundance: A, abundant, > 200 specimens; C, Common, 100–200 specimens; F, Frequent, 50-100 specimens; O, Occur occasionally, 25-50 specimens; R, Rare, 5-25 specimens; VR, Very rare, < 5 specimens.)

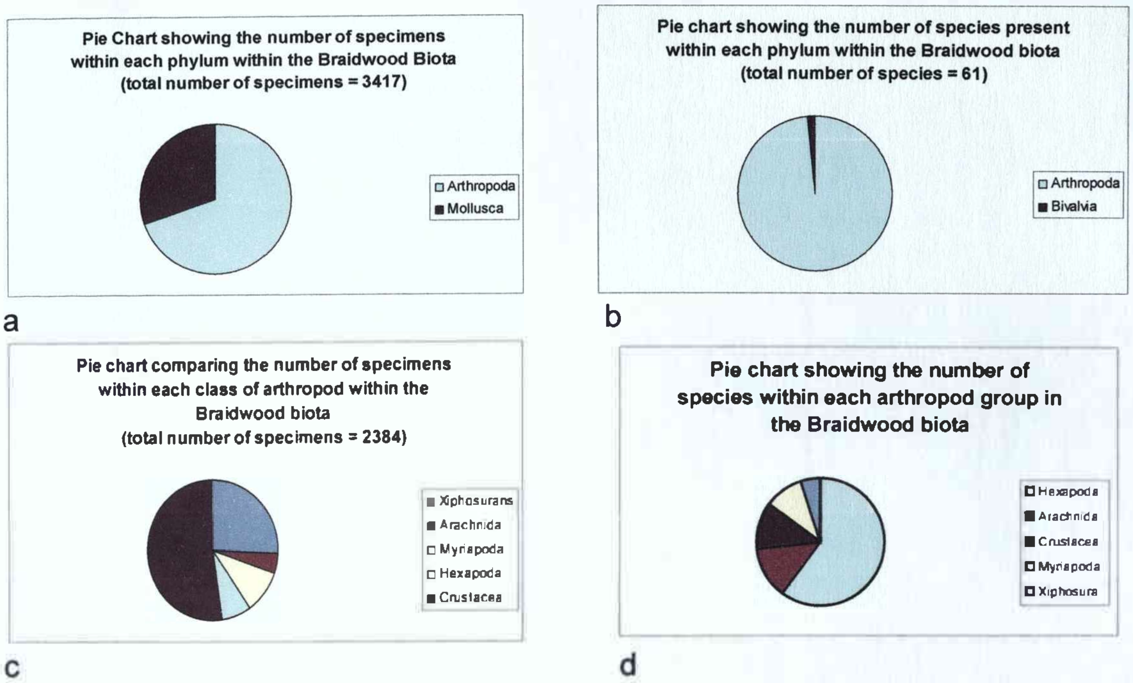


Fig 4.1. Analysis of the Mazon Creek Braidwood invertebrates from the Field Museum of Natural History, Chicago, Illinois.

Xiphosura. The xiphosurans comprise three principal genera the most common of which is *Euproops*, with 576 specimens recorded (Table 4.1) (Fig. 4.2 f).

Myriapoda. The Braidwood myriapods comprise 236 specimens and six different species from two classes; the extant Diplopoda (millipedes) and the extinct Arthropleuridea (Table 4.1). All of the Braidwood forms belong to the extinct order Euphoberiida, of which *Euphoberia* and *Xyloiulus* are the dominant forms (Fig. 4.2 c). The Arthropleuridea were a group of very large terrestrial millipedes that grew up to two metres in length and are represented in the Braidwood biota by isolated leg and plate fragments of *Arthropleura cristata* Richardson, 1956.

Hexapoda. The hexapods are the most diverse group in the Braidwood Biota and are represented 36 different species (Table 4.1). All of which belong to the subclass Pterygota, the winged insects, which in-turn can be divided into two infraclasses Palaeoptera and Neoptera. The Palaeoptera include the

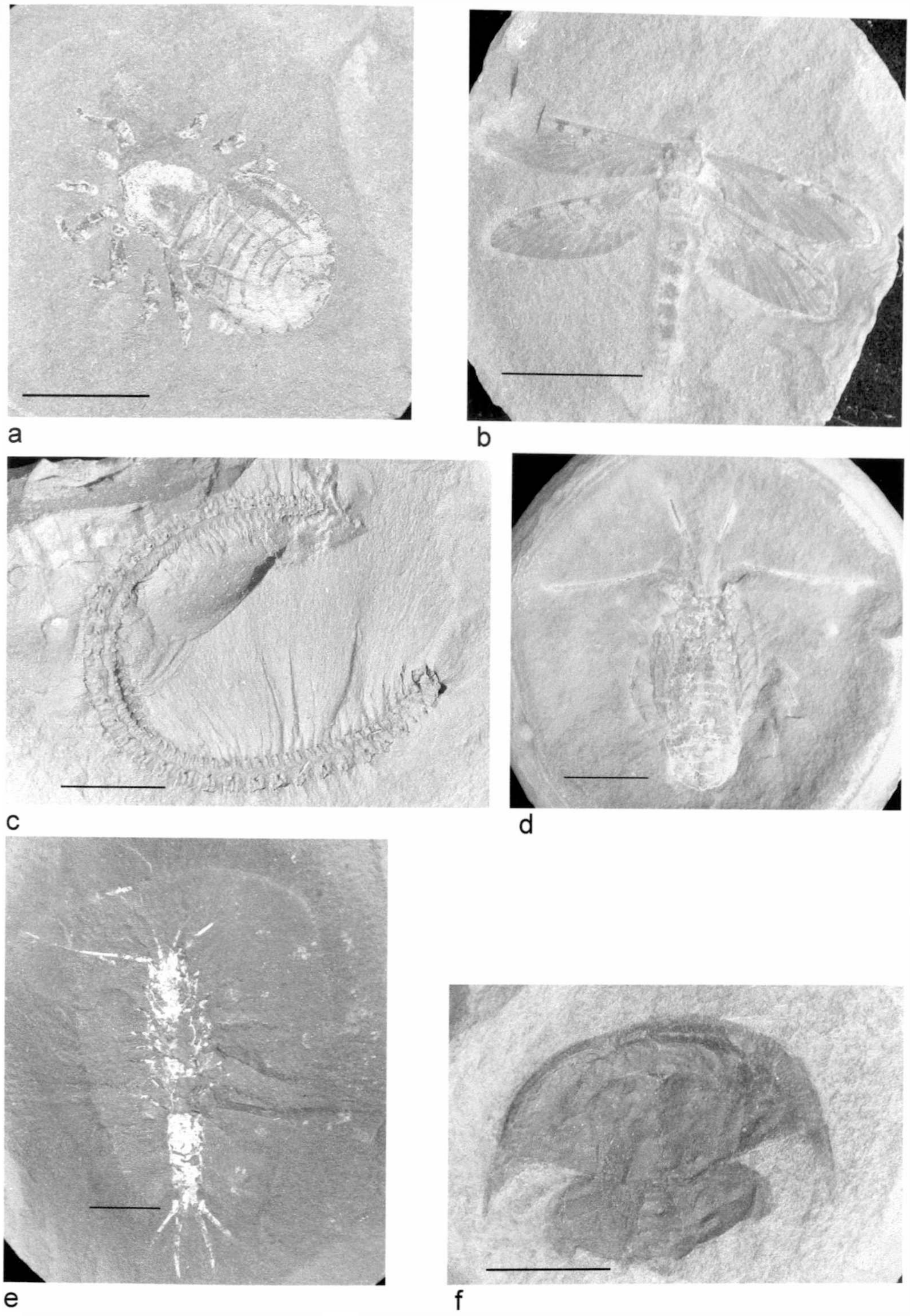


Fig. 4.2 Animal fossils from the Braidwood Biota of the Mazon Creek Lagersätte. a) Anthracomartid arachnid PE 9352. b) *Eubleptus danielsi* Handlirsch, 1906. PE 40223. c) *Euphoberia* PE22930. d) Pygocephalomorpha crustacean PE 36891. e) *Acanthotelson stimpsoni* Meek and Worthen, 1865. PE 45732. f) *Euproops danae* Meek and Worthen 1865. PE 29218. (scale bars = 1cm).

Palaeodictyoptera (Fig. 4.2 b) which were medium sized flying insects that displayed ornate patterned wings, the Megasecoptera, the Diaphanoptera and the Ephemeroptera.

The Neoptera include the Protorthoptera and the Blattoidea. The Protorthoptera were similar to modern day grasshoppers and are the largest known group of extinct insects comprising some 50 families of which twelve are known from Mazon Creek (Carpenter 1931). The most common protorthopteran is the genus *Gerarus* which includes 46 specimens. The final group of Braidwood insects are the Blattoidea, which comprise 46 specimens.

Arachnida. The final group of arthropods found in the Braidwood biota are the arachnids, which are highly diverse and represented by eight different orders (Table 4.1). The most diverse and abundant of these are the Phalangiotarbida. This is a group of extinct terrestrial arachnids that were abundant during the Upper Carboniferous. In the Braidwood biota there are 59 indeterminate specimens and six identified specimens comprising three different genera, including *Phalangiotarbus* and *Architarbus.* Two other extinct arachnid orders are present in the biota including the Anthracomartida (Fig. 4.2 a) and the Trigonotarbida. Five orders of living arachnids also occur in the biota including the Uropygida (whip scorpions), Amblypygida (whip spiders), Ricinuleida, Opilionida (harvestmen) and the Scorpionida.

Vertebrates. The Braidwood vertebrates include both fish and tetrapods. The fish are a low abundance high diversity group of organisms with over 30 known species that make up less than 0.1 percent of the biota (Baradack 1997). The fish are divided up into the agnathans, Chondrichthyes and Osteichthyes. The agnathans include one species of hagfish and several species of lampreys. The chondrichthyans are represented by a rare but diverse fauna of mainly juvenile organisms comprising five orders and 12 different species. The most common of these are the xenacanthids, which probably also produced the fossil egg case

Palaeoxyris. The osteichthyans are also a diverse group represented by 15 genera that range from brackish to fresh water forms. Coelacanths and lungfish also occur in the Braidwood biota, the same species of lungfish, *Ctenodus*, occurs in both the Mazon Creek and Coseley Lagerstätten.

Tetrapod specimens are very rare in the Mazon Creek Lagerstätte and commonly occur as isolated fragments of juvenile specimens (Baird 1997). There are 23 published amphibian specimens, representing six orders, and one reptile specimen.

4.2.2 Essex Biota

The Essex Biota is characterized by an abundant high diversity assemblage of marginal marine organisms, many of which are soft bodied. The biota also includes a washed in freshwater and terrestrial component (Baird 1997). The majority of Essex organisms lived at or near their site of burial. It is therefore difficult to determine the size and character of the larger nektonic organisms that existed at the time as these would have been able to escape the obrution that led to preservation of the smaller, planktonic and sessile organisms (Baird *et al.* 1986). It is however possible to analyze the benthic and planktonic component of cnidarians, bivalves, crustaceans, polycheate worms, holothurians and other such organisms (Fig. 4.3) (Baird *et al.*1985).

The Essex Biota comprises 24018 specimens, representing nine different groups (Table 4.2). The molluscs are the most abundant followed in descending order by the arthropods, cnidarians, annelids, the problematic species *Tullimonstrum gregarium* Richardson, 1966, echinoderms, non-annelid worms, brachiopods and the hemichordates (Fig. 4.4 a). The Essex Biota is a diverse assemblage comprising 76 different species; the arthropods are the most diverse group followed by molluscs, annelids, cnidarians and non-annelid worms. The

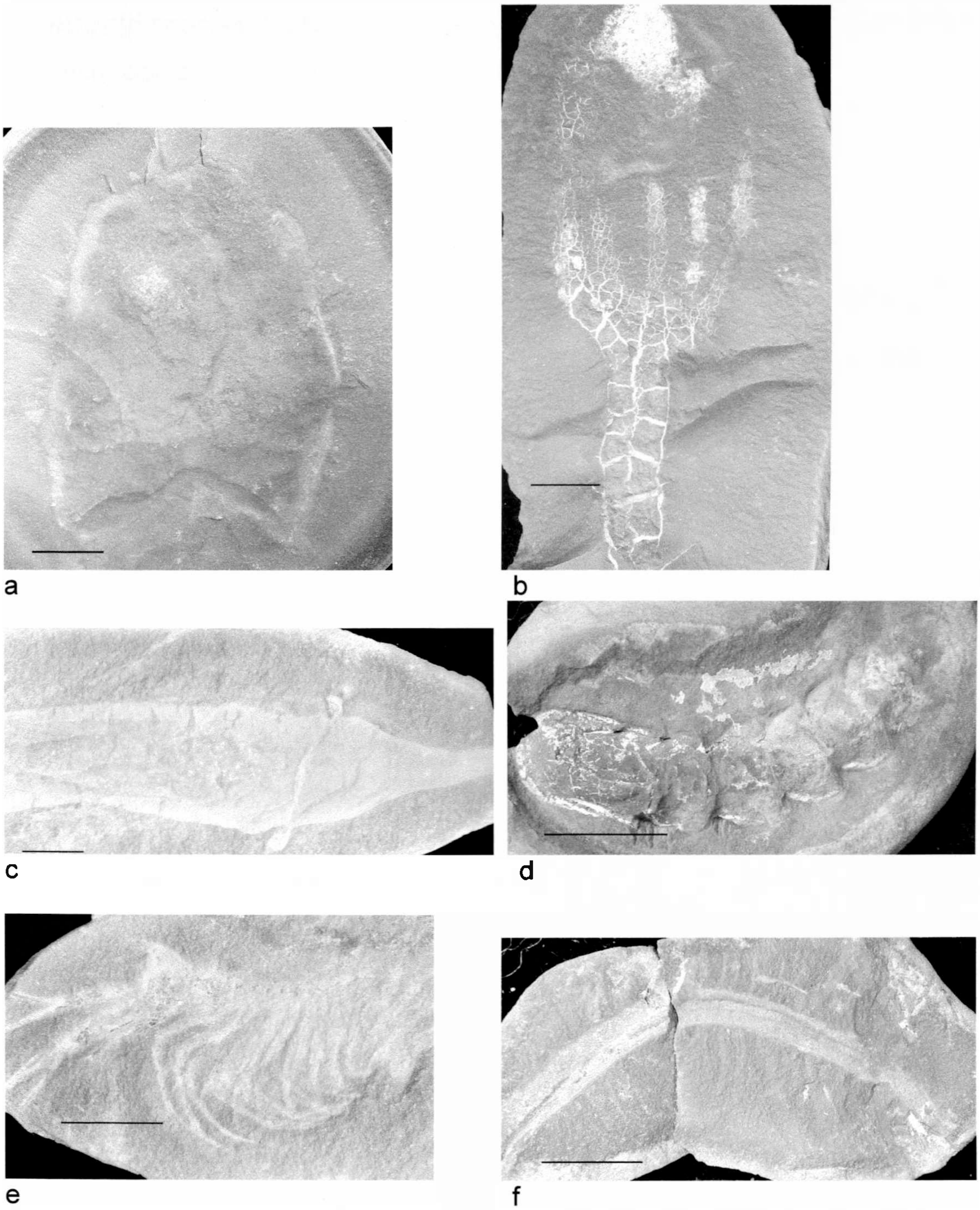


Fig 4.3. Animal fossils from the Essex Biota of the Mazon Creek Lagerstätte. a) *Essexella asherae* Foster, 1979. PE 47546. b) *Achistrum* Etheridge, 1881. PE 56607. c) *Tullimonstrum gregarium* Richardson, 1966. PE 40121. d) *Glaphurochiton concinnus* (Richardson). PE 31886. e) *Belotelson magister* Packard, 1886. PE 37387. f) *Nemavermes mackeei* Schram, 1973. PE 23045. Scale bars = 1cm.

problematic species *Tullimonstrum gregarium,* echinoderms and hemichordates are each represented by only one species (Fig 4.4 b).

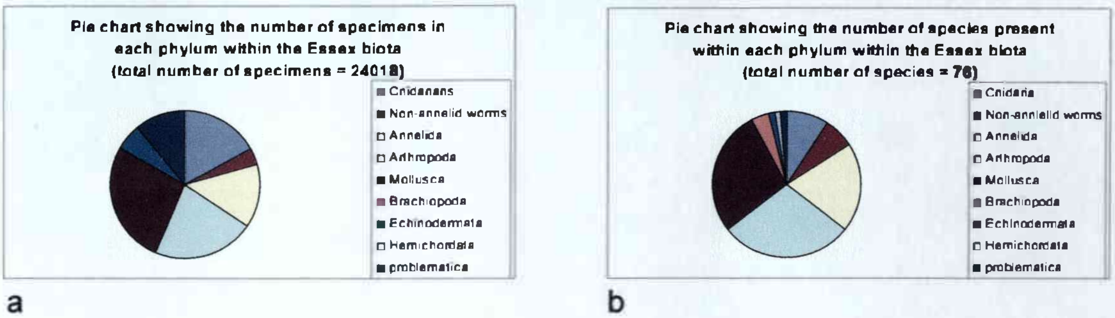
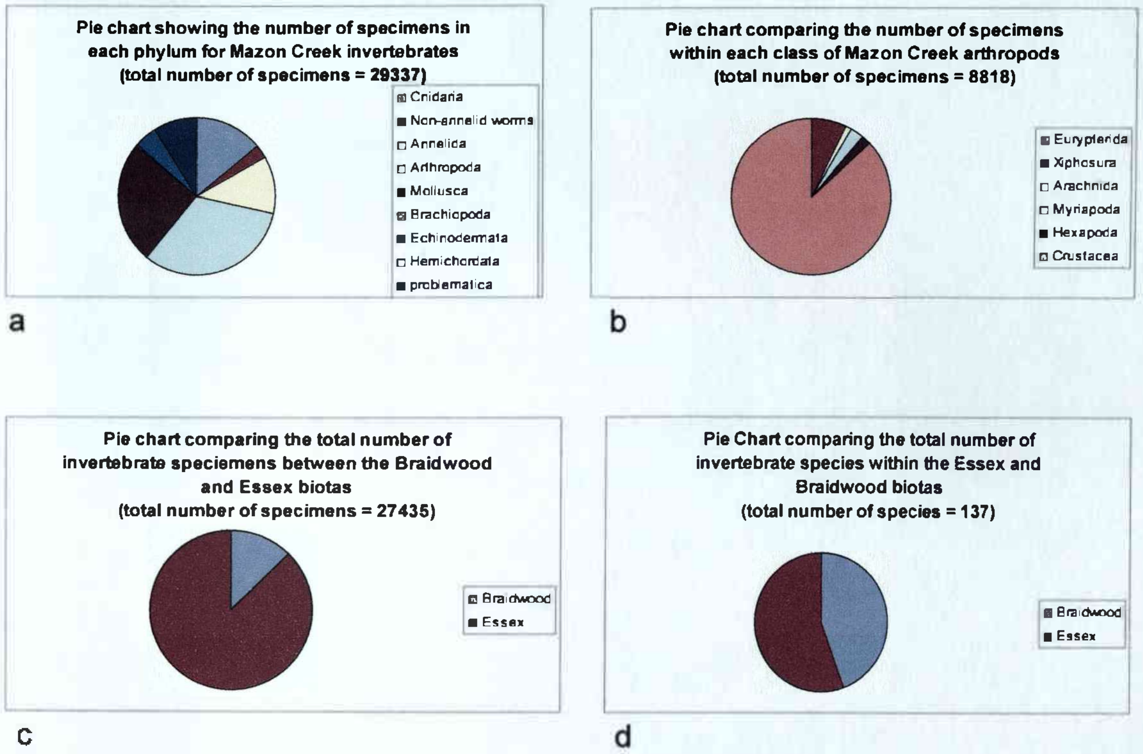


Fig 4.4. Analysis of the Mazon Creek Essex invertebrates from the Field Museum of Natural History, Chicago, Illinois.

4.2.3 Combined analysis

The Braidwood and Essex biotas can be analyzed as one to give a summary of phylum abundance for the Mazon Creek invertebrates (Fig. 4.5 a). This reveals that the arthropods are the dominant phylum followed in descending order by the molluscs, cnidarians, annelids, problematic forms, echinoderms, non-annelid worms, brachiopods and finally the hemichordates. The arthropods are the most diverse group within the Mazon Creek invertebrates (Fig. 4.5 b) the crustaceans are the most abundant arthropod followed by the xiphosurans, myriapods, hexapods, arachnids and finally the eurypterids. The abundance and diversity of the Braidwood and Essex biotas can also be compared (Figs. 4.5 c and d): the Essex biota is more abundant and diverse then the Braidwood Biota.



Pie chart showing the number of specimens in each phylum for Mazon Creek invertebrates (total number of specimens = 29337)

Pie chart comparing the number of specimens within each class of Mazon Creek arthropods (total number of specimens = 8818)

Pie chart comparing the total number of invertebrate speciemens between the Braidwood and Essex biotas (total number of specimens = 27435)

Pie Chart comparing the total number of invertebrate species within the Essex and Braidwood biotas (total number of species = 137)

Fig 4.5 Analysis of the Mazon Creek invertebrates from the Field Museum of Natural History, Chicago, Illinois.

Phylum	**Class**	**Taxon**	**N.o of species**	**Trophic level**	**Life habit**	**Abundance**
Cnidaria						
1		Cubozoa	1	Carnivore	Planktonic	O
2		Scyphozoa	4	Carnivore	Planktonic	A
3		Hydrozoa	2	Suspension feeder	Benthic	R
Non-annelid worms						
4		Nemertea	1	Carnivore	Benthic epifaunal	O
5		Nematoda	1	Parasitic?	n/a	R
6		Priapulida	1	Carnivore	Benthic epifaunal	O
7		Cheatognatha	1	Carnivore	Planktonic	O
8		Echiura	1	Detritus feeder	Benthic burrower	A
Annelida						
9		Eunicida	1	Carnivore	Benthic epifaunal	A
10		Phyllodocida	8	Carnivore	Benthic epifaunal	A
11		Sabellida	1	Carnivore	Benthic epifaunal	A
12		Indtr	5	n/a		A
Arthropoda						
13	Chelicertata	Eurypterida	1	Carnivore	Nektonic	R
14	Crustacea	*Cryptocaris*	1	?	?	VR
15		*Kallidecthes*	1	Scavenger/ deposit feeder	Nektobenthic	O
16		*Tyrannophontes*	1	Carnivore	Benthic	O
17		Belotelsonidea	3	Scavenger/ deposit feeder	Benthic	A
18		Pygocephalomorpha	1	Scavenger/ deposit feeder	Benthic	O
19		Lophogastrida	3	Scavenger/ deposit feeder	Benthic	C
20		*Eucryptocaris*	1	Scavenger/ deposit feeder	Benthic	VR
21		*Hesslerella*	!	Scavenger/ deposit feeder	Benthic	VR
22		*Dithyrocaris*	1	Scavenger/ deposit feeder	Benthic	R
23		*Kellibrooksia*	1	Carnivore	Benthic	F
		Leaia	1	?	?	VR
24		Ostracoda	?	Scavenger/ deposit feeder	Nektobenthic	O
25		Halicyna	3	Scavenger/ deposit feeder	Benthic	A
		Concavicarida	2	?	?	A
Mollusca						
26	Polyplacophora	*Glaphurochition*	1	Grazer	Benthic	C
27	Gastropoda	*Euphemites*	1	Grazer	Benthic	C
28		*Hypselentoma*	1	Grazer	Benthic	VR
29		*Straparollus*	1	Grazer	Benthic	VR
30		*Naticopsis*	1	Grazer	Benthic	VR
31		Strobeus	1	Scavenger	Benthic	C
32	Bivalvia	Solemyoida	1	Symbiotic	Epifaunal burrower	F
33		*Myalinid*	1	Suspension feeder	Nektonic	A
34		Pectinoida	3	Suspension feeder	Nektonic/ bysally attatched	A
35		Limoida	1	Suspension feeder	Epifaunal nestlers	R
		Modiomorphoida	1	?	?	F
		Venerioda	1	?	?	O
36		Trigonioida	1	Suspension feeder	Benthic infaunal	O
37		Pholadomyoida	1	Suspension feeder	Benthic infaunal	R
38		indeterminate	?	n/a	n/a	A
39	Cephalopoda	Nautiloidea	1	Carnivore	Nektonic	VR
40		Teuthoidea	1	Carnivore	Nektonic	VR
Brachiopoda						
41	Inarticulata	Lingula	2	Suspension feeder	Benthic infaunal	C
Echinodermata	Holothuroidea	*Achistrum*	1	?	?	A
Hemichordata	Enteropneusta	*Mazoglossus*	1	?	?	C
Uncertain		*Tullimonstrum*	1	?	?	A

Table 4.2 Taxon present within the Mazon Creek Essex biota.

(abbreviations for abundance: A, abundant, > 200 specimens; C, Common, 100–200 specimens; F, Frequent, 50-100 specimens; O, Occur occasionally, 25-50 specimens; R, Rare, 5-25 specimens; VR, Very rare, < 5 specimens.)

4.3 Ecology, life strategies and trophic structure of the Mazon Creek Biota

Introduction

It is possible to determine the trophic level and life habit of the individual organisms present within the Mazon Creek Biota and from this to reconstruct food webs and predator prey relationships that would have existed in the original biota. It is convenient to discuss the trophic structure of the Braidwood and Essex biotas separately.

4.3.1 Trophic structure of the Braidwood Biota.

Aquatic biota

Epifaunal suspension feeders. The bivalves of the Braidwood Biota included nektonic free swimming forms, such as *Naiadites,* and three other myalinid genera. Other bivalves such as *Anthracosia* and *Carbonicola* lived bysally attached to hard substrates commonly forming widespread 'mussel bands' where thousands of individuals occurred packed together (Moore 1969). All of the Braidwood bivalves lived as epifaunal suspension feeders living on the microfauna found in the water column.

Epifaunal scavengers / deposit feeders. The crustaceans of the Braidwood biota include the Halicyna, a group of small crustaceans with circular, flattened carapaces similar to modern day crabs, the Ostracoda and the eumalacostraceans (higher crustaceans) which include the shrimp-like syncarids and pygocephalamorphids. The crustaceans of Braidwood biota all had a benthic, epifaunal mode of life, crawling and swimming on and above the sediment surface, where they scavenged on dead organisms or removed food from the sediment (Schram *et al.* 1997).

Epifaunal scavengers / predators. The dominant xiphosuran in the Braidwood biota, *Euproops*, lived along the shallow margins of lakes, it was well adapted for a benthic mode of life, its streamlined body allowed it to move quickly through the water and its spines produced a large surface area allowing it to rest on soft substrates (Anderson 1994). The Carboniferous xiphosurans were scavengers or low level benthic predators that scavenged upon dead organisms and hunted for smaller invertebrates such as benthic crustaceans (Mikulic 1997).

Small carnivores. The small carnivores of the Braidwood biota comprised small fish that hunted smaller crustaceans and other invertebrates. The small fish of the Braidwood Biota comprise species that are similar to those found in the Coseley Biota such as the chimaeras.

Large carnivores. The top predators of the aquatic food web were large fish and comprise similar groups to what are present in the Coseley biota including the xenacanthids, the large osteolepiform *Megalicthys* which could reach up to 2 m in length (Nelson 1994), the coelacanths, which exceeded 1.5 m in length and the lungfishes which are still noted as formidable predators at the present day. These large fish would have had a nekctonic mode of life, actively hunting smaller fish and invertebrates.

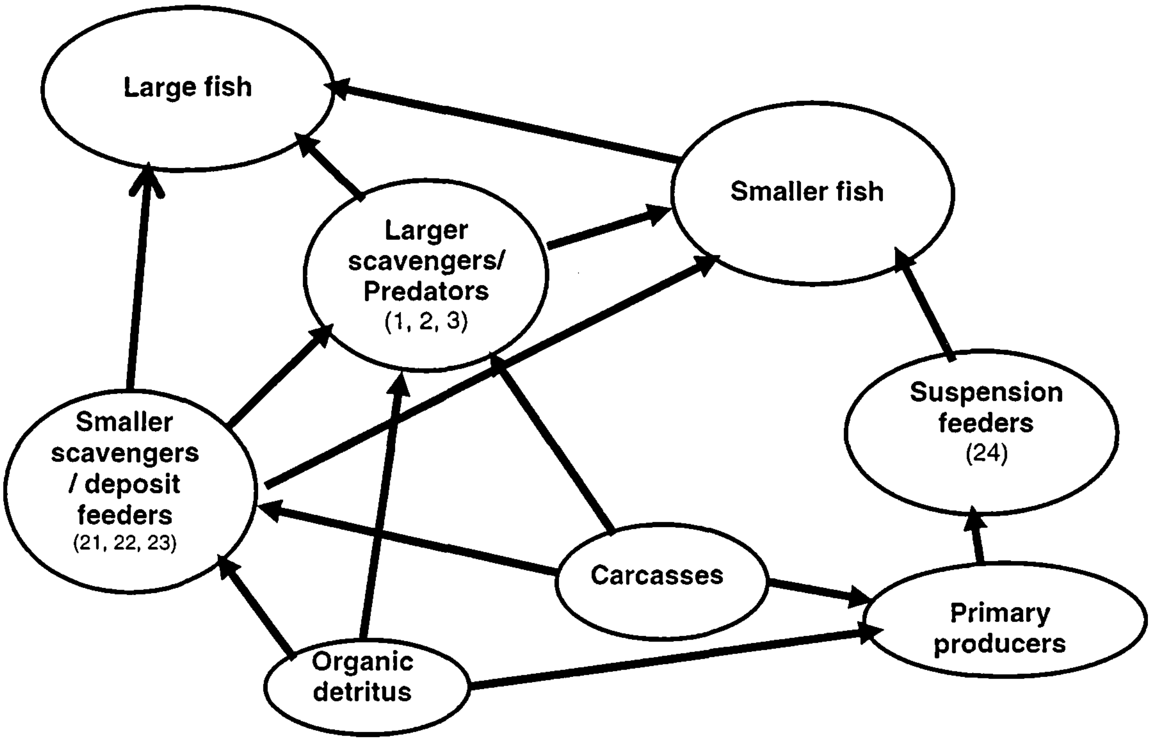


Fig 4.6 Food web for the aquatic organisms of the Braidwood biota of the Mazon Creek Lagerstatte (numbers refer to table 4.1, arrows indicate flow of energy).

Terrestrial biota

Smaller detrivores. The small detrivores of the Braidwood Biota included the Euphoberiid myriapods and the Blattoidea hexapods. Both these small millipedes and cockroaches lived within the leaf litter on the forest floor consuming rotting vegetation (Duncan *et al.* 2003).

Larger detrivores. The large detrivores are represented by the arthropleuriid myriapods. These gigantic millipedes also lived within the leaf litter of the forest floor consuming pteridosperm and fern detritus (Proctor 1998) but grew to such gigantic proportions they had few predators once fully grown.

Small predators. The small predators include six groups of small arachnids including the Trigonotarbida, Uropygida, Phalangiotarbida, Anthracomartida, Ricinuleida and the Opilionida. All of which lived on the forest floor preying upon smaller arthropods such as the myriapods and hexapods or scavenging upon dead organisms. (Dunlop 1994, 1997, 1999).

Aerial predators. These include the three genera of dragonflies found within the Lagerstätte, and probably acted as present day forms preying upon smaller insects.

Larger predators. The top predators within the Braidwood biota were the large arachnids, the scorpions and amblypygids which preyed upon smaller arachnids such as the trigonotarbids and phalangiotarbids as well as other smaller invertebrates such as blattoid hexapods (Dunlop 1994).

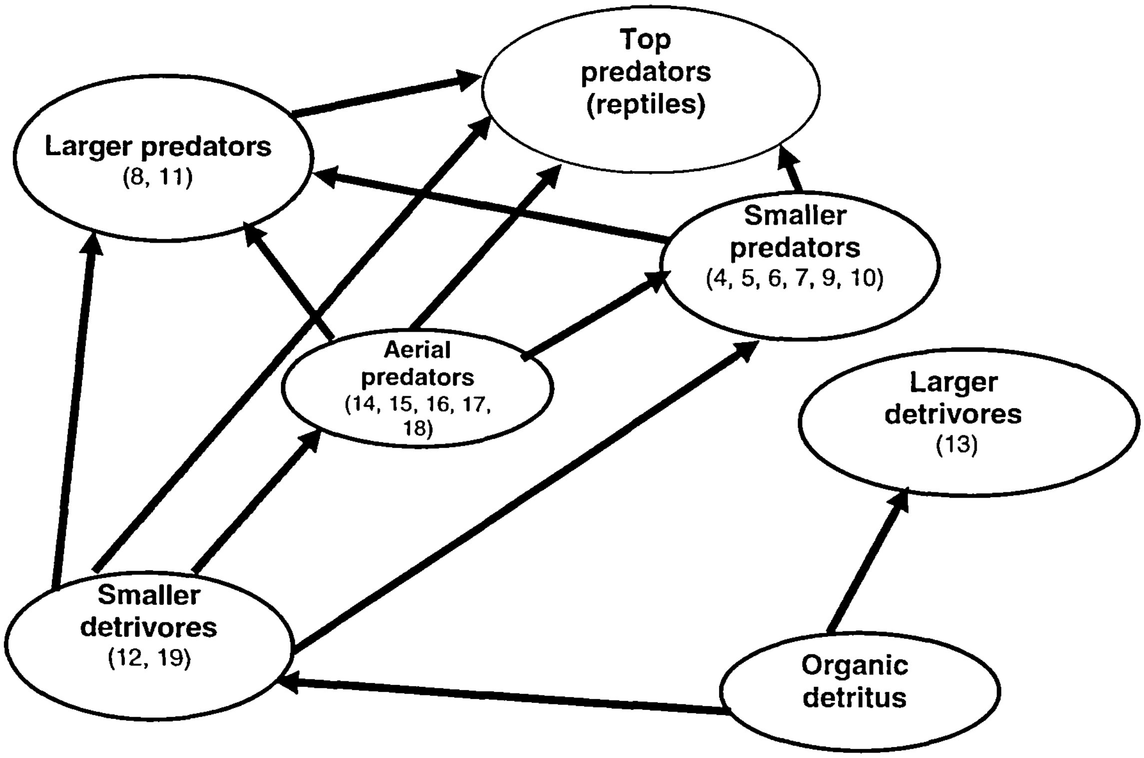


Fig 4.7 Food web for the terrestrial organisms of the Braidwood biota of the Mazon Creek Lagerstatte (numbers refer to table 4.1, arrows indicate flow of energy).

4.3.2 Trophic structure of the Essex biota

Grazers. The Essex grazers include two groups of molluscs the Polyplacophora and the Gastropoda. The Polyplacophora includes the single chition genus *Glaphurochition* and the Gastropoda includes four species of Prosobranchia including *Euphemites richardsoni* Schindel and Yochelson, 1979. These molluscs used their radula to scrape algae from hard surfaces (Kleussendorf 1997).

Infaunal detritus feeders. The only infaunal detritus feeder found within the Essex biota is that of the non-annelid worm *Echiura.* These organisms buried into the sediment where their proboscis extended over the sediment surface collecting sediment particles which were then conveyed to the mouth (Fitzhugh & Sroka 1997).

Scavangers / deposit feeders. These animals include the majority of the crustaceans and the gastropod *Strobeus.* The crustaceans had a nektobenthic mode of life scavenging upon dead organisms or forging for food within the sediment. The gastropod *Strobeus* scavenged upon dead soft bodied organisms and is commonly found clustered together in association with the jelly fish fossil species *Essexella asherae* Foster, 1979 (Kleussendorf 1997).

Infaunal suspension feeders. The inafunal suspension feeders include the burrowing bivalve, *Schizodus* and the burrowing brachiopod, *Lingula.* The bivalve *Schizodus* was one of the largest Essex forms and was an active burrower (Bowman-Bailey & Sroka 1997). The brachiopod *Lingula* lived in deep vertical burrows which can be found preserved at the present day (Hay 1997).

Epifaunal suspension feeders. This group includes one species of the cnidarian class Hydrozoa, *Drevotella proteana* Nitecki and Richardson, 1972, which was a colonial benthic organism (Sroka 1997) and many species of bivalves including bysally attatched, nestling and free swimming forms.

Benthic epifaunal carnivores. This group includes the only two species of carnivorous crustacean, including the mantis–shrimp–like *Tyrannophontes theridion* Schram, 1969 and *Kellibrooksia macrogaster* Schram, 1973. The non-annelid worms Nemertea and Priapulida and several species of annelid worms. These benthic carnivores would have preyed upon smaller benthic invertebrates such as crustaceans and worm like organisms (Schram *et al.*1997).

Planktonic carnivores. The planktonic carnivores comprise the cnidarian classes cubozoa and scyphozoa including the most common fossil of the biota *Essexella asherae.* These were jellyfish like organisms that caught prey using their stinging tentacles (Sroka 1997). This group also includes the non-annelid worm group cheatognatha which preyed upon crustaceans, small fish and others of the same species (Fitzhugh & Sroka 1997).

Nektonic carnivores. The top predators of the Essex biota are the cephalopods: these free swimming animals were efficient active predators that preyed upon crustaceans and other invertebrates and included the ammonoids and nautiloids (Kluessendorf 1997).

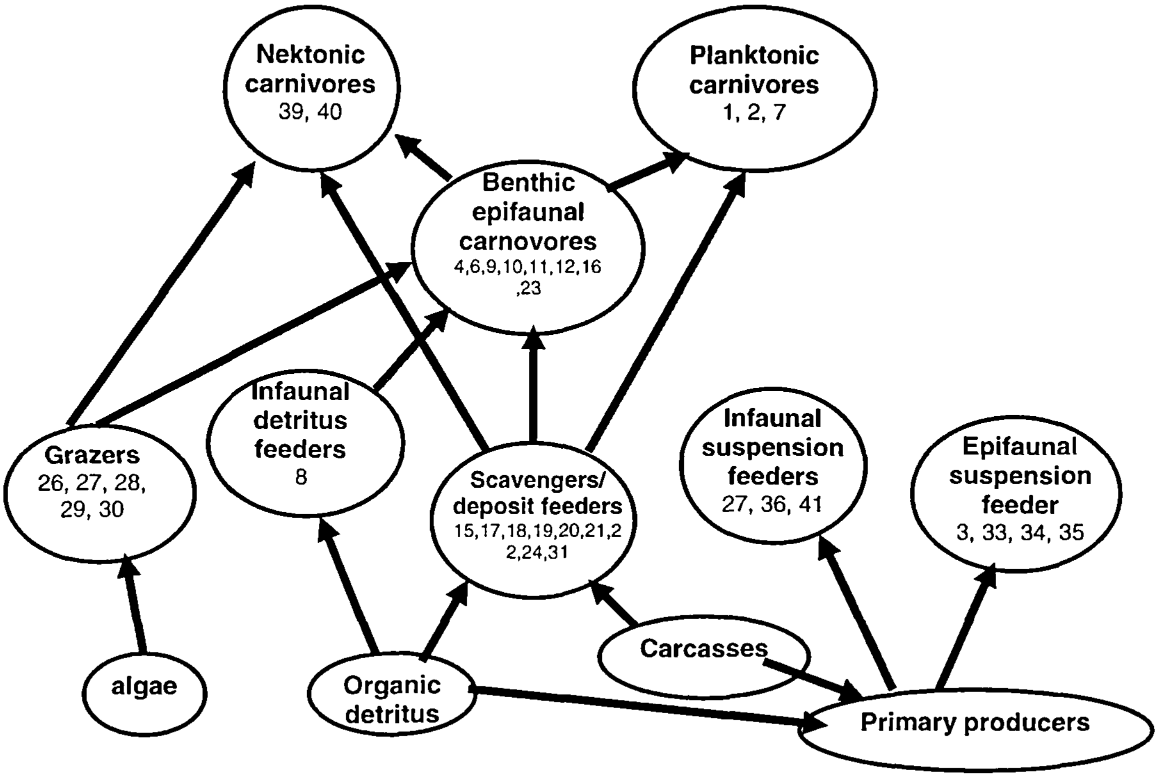


Fig 4.8 Food web for the Mazon Creek Essex Biota (numbers refer to table 4.2, arrows indicate flow of energy).

4.4 Summary and comparison

It is possible to compare the faunal and floral compositions of the Mazon Creek Biota's with that of the British equivalents, Coseley and Crock Hey. It is clear that the Mazon Creek Braidwood Biota is more similar to the Coseley and Crock Hey Biota's then the Essex Biota which is completely different. The Braidwood, Coseley and Crock Hey Biota's show a similar floral component and are comprised of the same main plant groups the lycopsids, pteridosperms, calamites, ferns, sphenophylls and cordaites. The Coseley and Crock Hey floral components can be compared further and show similar group abundance and are both dominated by the pteridosperm genera *Neuropteris*. For both assemblages the calamites are the next most abundant group followed by the lycopsids. However there are some differences the Coseley floral component shows a higher species diversity and higher abundance than the Crock Hey floral component. Overall the similarity in the plant groups between the three assemblages would indicate the development of a broadly similar environment between them.

The Invertebrate faunal component can also be compared between the Braidwood, Coseley and Crock Hey Biota's. All three assemblages are comprised of the same major invertebrate groups, the xiphosurans, arachnids, hexapods, crustaceans, myriapods and molluscs, but the similarity between the three assemblages decreases at generic and species level. The Braidwood Biota in particular shows a greater species abundance and diversity than either of the British assemblages. The hexapods and arachnids in particular are much more diverse an abundant in the Braidwood biota then the Coseley or Crock Hey assemblages and share very few common species between them.

Statistical analysis can be used to compare the similarity of species abundance between these three assemblages. The Chi-square test has been used to statistically compare the distributions of plant and invertebrate groups between the Coseley, Crock Hey and Braidwood Biota's. The Chi-square test will show if the animal and plant group compositions (abundances) between the samples are different.

Null Hypothesis = The data are drawn from populations with the same distributions.

The results (Fig 4.9) of the Chi-square test disprove the null hypothesis and prove that the plant and invertebrate group distributions between the three assemblages are statistically different. However as the samples were collected by different people at different times using different methods this may have influenced the total numbers of fossils collected and the Chi-square test results.

Chi-square analysis could not be done below group level due to the number of species with less than five representative specimens.

Coseley vs. Crock Hey (invertebrate comparison)
One Constraint
N1: 278
N2: 156
Deg. Freedom: 5
Chi^2: 62.003
P (same): 4.6833E-12

Braidwood vs. Crock Hey (invertebrate comparison)
One Constraint
N1: 156
N2: 3017
Deg. Freedom: 5
Chi^2: 207.13
P (same): 0

Coseley vs. Braidwood (invertebrate comparison)
One Constraint
N1: 278
N2: 3017
Deg. Freedom: 5
Chi^2: 81.87
P (same): 3.407E-16

Coseley vs. Crock Hey (plant comparison)

One Constraint

N1: 2140

N2: 1397

Deg. Freedom: 4

Chi^2: 109.42

P (same): 9.671E-23

Fig 4.9 Chi-square analysis of abundance data between the Coseley, Crock Hey and Braidwood Biota's.

5. Exceptional fossil preservation and mineral paragenesis in siderite–hosted Lagerstätten

5.1 Taphonomy and mineral paragenesis of the Upper Carboniferous Coseley Lagerstätte.

Introduction

The fossils of the Coseley Lagerstätte occur as refractory hard parts and mineralized soft tissues with various degrees of lability, sealed within siderite concretions. The Lagerstätte preserves a diverse assemblage of plant and animal fossils including several major plant groups, including the sphenopsids and lycopsids, along with a diverse arthropod fauna and several fish species. The diverse nature of the biota is reflected in the diversity and manner of the biomolecules that have been preserved. This has led to a complex preservational history involving several phases of preservation and a variety of minerals, which differ between fossil groups and between species of organisms within the same group. The preservation of these organisms was not simply controlled by the decay of their tissues but involved a complex relationship between the decaying carcass, the surrounding sedimentary environment and the alteration of chemical conditions within them both. Detailed analysis of the Coseley fossils will help to understand how these organisms came to be preserved and unravel the complex diagenetic and chemical processes that have led to high fidelity soft tissue preservation, and may serve as a model for other siderite-hosted Lagerstätten.

5.1.1 Preservation style

The fossils of the Coseley Lagerstätte occur within siderite concretions; the concretions vary in size from 15 mm to 250 mm and are spherical to oval in shape. In general the shape and size of the nodule is proportional to the shape and size of the fossil, no nodules are found larger than 250 mm. The fossils occur as moulds or impressions within the nodules and usually consist of a part and counterpart. The fossils occur as grey to white or dark brown films within the nodules and some display a complex range of void-filling carbonate and sulphide minerals.

Three main groups of fossils occur in the Coseley Lagerstätte; plants, arthropods and fish. These three groups represent a wide range of original biomolecules and resulting preservational style. The preservation style of each of the three groups of organisms will be discussed individually, since the biomolecular composition to a degree determines the ensuing taphonomic pathway.

Preservation style of the plant fossils

Three main preservational styles occur within the plant component of the Lagerstätte; three-dimensional moulds, external moulds and impression fossils. The three different preservational styles occur in different plant groups (Table 5.1) the lycopsids are represented by occasional three-dimensional moulds of stem fragments and more commonly by external moulds of stems and cones with varying degrees of relief. The sphenopsids are represented by external moulds of cones and stems, and leaf impressions. The ferns and pteridosperms are represented by impression fossils of leaves.

The lycopsid stems show surface relief and leaf cushions can be seen on the surfaces of the stems, the leaf cushions are diamond shaped and preserved as dark brown to black organic films with an intervening white mineral between the leaf cushions. Branching organs, possibly roots, can also be seen radiating away from the main trunk; these are also preserved as black and white films for example, specimen (BU 4443) (Fig. 5.1 a). Three-dimensional stems are also preserved and exhibit leaf cushions on the external surface of the stem and vascular tissue on the internal surface, for example specimen, (BU 4444) (Fig. 5.1 b). Lycopsid leafy shoots are also preserved dominantly as a white mineral film with some dark organic material, the morphological detail preserved is very high with individual shoots seen radiating away from the main body of the shoot for example specimen (BU 4445) (Fig. 5.1 c). Another key difference in the mode of preservation of the lycopsids to the other plant groups is the degree of mineralization that they exhibit. The lycopsid cones and stems exhibit varying degrees of relief and had a high proportion of void space that became infilled by a wide range of sulphide and carbonate minerals including sphalerite, galena and calcite.

The impression fossils of the sphenopsids, together with the pteridosperm and fern leaves, preserve detailed external morphology of the plant organ but do not retain any internal cellular detail, they occur as dark brown to black organic rich films along with a white mineral on the surface of the nodule, they do not exhibit any sulphide or carbonate mineralization (Fig. 5.1 d).

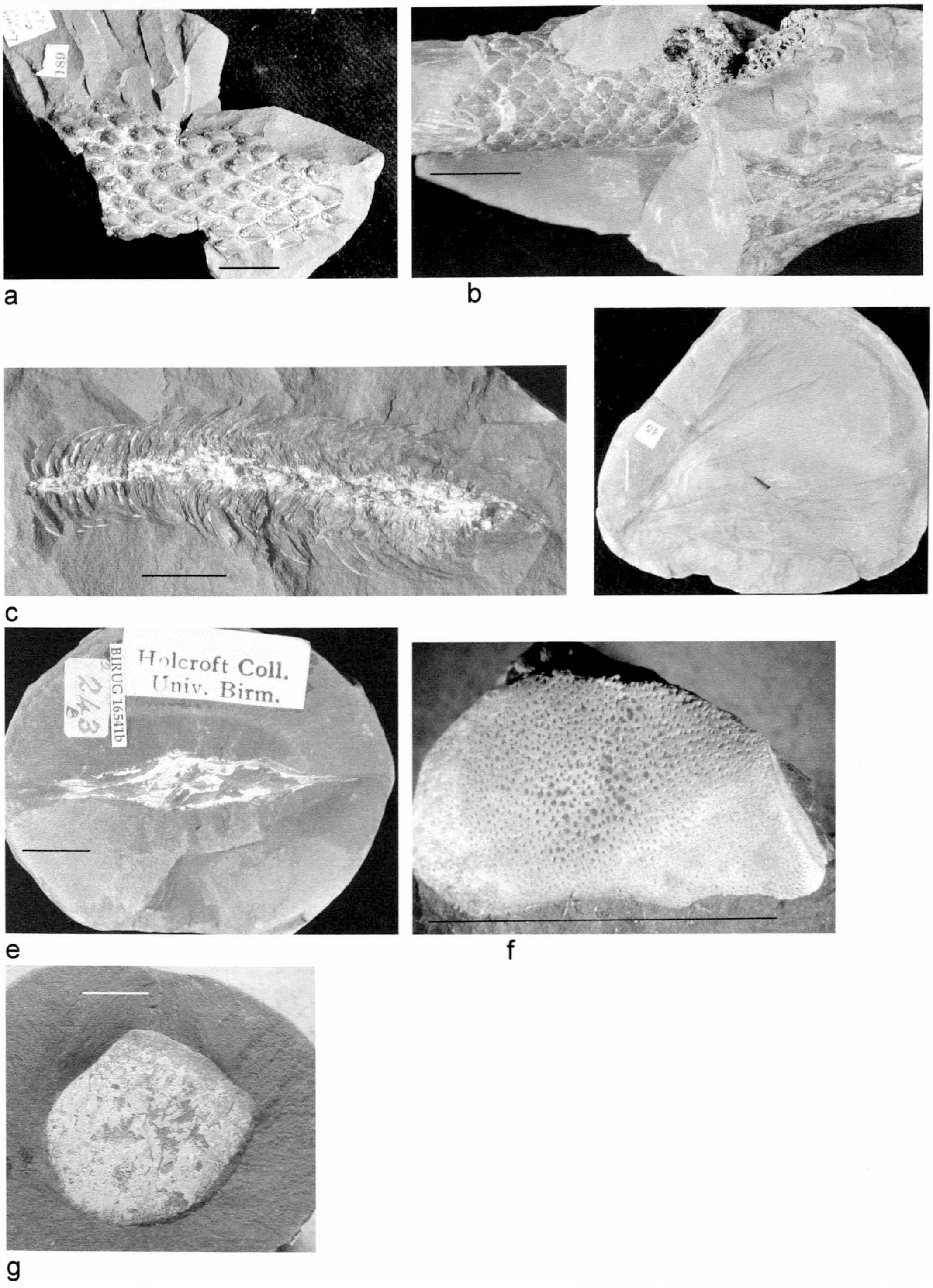


Fig. 5.1 Hand specimen photographs of the Coseley fossils. a) (BU 4443) *Lepidodendron.* b) (BU 4444) *Lepidodendron* c) (BU 4445) Lycopsid leafy shoot d) (BU 4452) *Cyclopteris* e) (BU 4450) *Palaeoxyris* f) (BU 1784) *Helodus* g) (BU 4447) *Ctenodus* (scale bars = 1 cm).

Plant Group	Plant Organ	Original composition	Composition now	Additional minerals	Type of preservation
Lycopsids	stem	Cuticle of cutin and cutan	Kaolinite and Organic carbon	Ti mineral, sphalerite, galena, pyrite, pyrite framboids, calcite	Mould with 3D surface relief
	cone	Cuticle of cutin and cutan	Kaolinite and organic carbon	Sphalerite, galena, Ti mineral, pyrite, pyrite framboids, calcite	Mould with 3D surface relief
Sphenopsids	cone	Cuticle of cutin and cutan	Kaolinite and organic carbon	No	External mould
	leaves	Cuticle of cutin and cutan	Kaolinite and organic carbon	No	Impression of a leaf
	stem	Cuticle of cutin and cutan	Kaolinite and organic carbon	No	External mould
Ferns	leaves	Cuticle of cutin and cutan	Kaolinite and organic carbon	No	Impression of a leaf
Pteridosperms	leaves	Cuticle of cutin and cutan	Kaolinite and organic carbon	No	Impression of a leaf

Table 5.1 showing for each plant group the organs preserved, their original composition (Van Bergen *et al.* 1995) and present composition and type of preservation.

Preservation style of the animal fossils.

Arthropod preservation style. The Coseley arthropod fauna is diverse and includes xiphosurans, crustaceans, millipedes and arachnids preserved as external moulds and hexapods preserved as impression fossils (Table 5.2). The arthropod fossils preserve detailed external morphological features, including appendages, but do not preserve any internal morphological or cellular detail. The hexapods are dominantly represented by wing specimens that occur as impressions on the nodule surface, and preserve very detailed morphological features including venation patterns and colour banding indicating some mineralization in addition to the siderite. The arthropod external moulds occur as dark brown films on the surface of the nodule and in thin section they occur as carbonate layers with or without clay minerals.

The abundance of insect wings within concretionary fossil Lagerstätte has been investigated by Duncan *et al.* 2003. They conducted decay experiments upon two genera of cockroaches to determine if selective preservation led to the high number of wing specimens in the fossil record. They found that the more heavily sclerotized forewings dominate many Carboniferous Lagerstätte and that in decay experiments the forewings did survive the longest (Duncan *et al.* 2003). However the fossil wings are commonly found broken across veins and this is similar to damage observed during breakage of dry wings during experiments. They concluded that the condition and preponderance of isolated cockroaches wings is consistent with the activity of arachnid predation, and not with drowning of the insects and selective preservation of the wings whilst the rest of the carcass decayed (Duncan *et al.* 2003).

Arthropod class	Arthropod organ	Original composition	Composition now	Additional minerals	Type of preservation
Xiphosuran	Cuticle of the head and body	Lipids, tanned proteins, chitin, resilin and sulphur	Cuticle occurs as a layer of rhombic dolomite crystals	Occasional pyrite crystals, kaolinite	External mould
Crustacean	Cuticle of head, body and appendages	Lipids, tanned proteins, chitin, resilin, calcium carbonate	Cuticle occurs as layers of siderite crystals	Kaolinite	External Mould
Millipedes	Cuticle of the body	Lipids, tanned proteins, chitin, resilin, calcium carbonate and calcium phosphate	Cuticle occurs as a layer of rhombic carbonate crystals	Kaolinite	External Mould
Arachnids	Cuticle of head, thorax, abdomen and appendages	Lipids, tanned proteins, chitin, resilin,	?	Kaolinite	External Mould
Hexapods	Cuticle of the wings	Lipids, tanned proteins, chitin, resilin,	?	No	Impression of the wing

Table 5.2 Table showing for each arthropod class the arthropod organ preserved, its original (Briggs 1999) and present composition and type of preservation.

Preservation style of the fish specimens. The chondrichthyans are represented in the assemblage by teeth specimens (Fig. 5.1 f) that occur as three dimensional fossils which still have a similar composition to the original teeth. An unusual aspect of the chondrichthyan fish fossils is the presence of exceptionally well preserved egg capsules, (Fig. 5.1 e). The osteichthyans are represented by scale specimens, which would have originally been composed of hydroxyapatite similar to that of teeth specimens; scales occur as moulds and preserve external morphological detail (Fig. 5.1 g). In thin section the scale of the sarcopterygian *Ctenodus* shows well-preserved internal detail and is composed of laminated dermal bone, composed of apatite.

Fish Class	Fish Group	Fish organ	Original composition	Composition now	Additional minerals	Type of preservation
Chondrichthyans	Holocephali	Teeth	Hydroxyapatite	apatite	No	3D tooth
	Elasmobranchii	Teeth, egg capsules	Hydroxyapatite, keratin	kaolinite	No, galena	3D tooth, mould
	Petalodontids	Teeth	Hydroxyapatite	apatite	No	3D tooth
Osteichthyans	Sarcopterygians	scales	Hydroxyapatite	Apatite as laminated dermal bone	Kaolinite, pyrite	Mould

Table 5.3 Table showing for each fish group the organs preserved, their original and present composition and type of preservation.

5.1.2 Timing of fossil preservation.

The rate and timing of decay of biomolecules has been well studied and documented, (Logan *et al.* 1991). By identifying which biomolecules decay rapidly, and those that are more resistant to decay, it is possible to work out the relative timing of decay and preservation of a fossil assemblage. Figure 5.2 shows the relative timing of decay for certain biomolecules. The most labile of these decay very early on and include starch, albumin and glycogen and nucleic acids; no tissues comprising these very labile biomolecules occur in the Coseley fossil assemblage, therefore the Coseley fossils do not represent extremely early preservation. The presence of some plant cellular tissue within several plant specimens indicates the presence of cellulose, the preservation of both insect wing structure and pigment also indicates early preservation as they were composed of non-mineralized cuticle. The presence of these tissues indicated relatively early preservation following the decay of the most labile tissues. The style of preservation can also help to elucidate the timing of preservation of the fossils (Fig. 5.3). The Coseley fossils preserve tissue outlines and refractory tissues but the majority of internal soft tissues have decayed before preservation occurred. This indicates that mineralization was delayed until more labile tissues had decayed (Allison and Briggs 1991).

Very Early Decay

Plant	Animals	Both
starch cellulose glycolypids resins sopropollenin lignin, cutan, suberan	albumin, glycogen collagen, keratin osteocalcin, skeletal glycoproteins, chitin	nucleic acids, amino acids

Very Late Decay

Fig 5.2 Timetable for the decay of biomolecules (adapted from Allison and Briggs 1991)

Very Early Decay

Degree of decay	Preservation style
Inhibited decay	Carbonized volatile soft tissues.
Inhibited decay along with mineralization	Three dimensional soft tissue preservation.
Mineralization delayed and continued decay	Destruction of internal soft tissues but preservation of tissue outlines and refractory tissues (Coseley).
Further decay	Complete destruction of volatile soft tissues, only complex macro molecules remain
Unabated decay	Organic carbon completely destroyed only mineralized hard parts remain such as shell and bone.

Very Late Decay

Fig 5.3 Timetable for decay and resulting preservation style (adapted from Allison and Briggs 1991)

5.1.3. Comparison of the preservational style of the plant and animal fossils of the Coseley Lagerstätte.

The preservational style and the mineral phases present in the plant and animal fossils of the Coseley Lagerstätte can be compared (Table 5.4 and 5.5). The Plant fossils occur as impression fossils particularly the leaf specimens and as three dimensional moulds. Original plant tissues occur as degraded organic carbon. The concretions that surround the plant fossils are comprised of crystalline siderite, the other mineral phases found in the plant fossils include void filling kaolinite, an unusual titanium oxide enrichment and a wide range of void filling sulphides including sphalerite, galena and pyrite. The animal fossils of the Coseley Lagerstätte mainly occur as external moulds except for the insects wings which occur as impression fossils. The only original tissues that remain are biomineralized apatite from the fish teeth and scales. The Siderite that surrounds the animals is comprised of an early microbial phase and a latter void filling crystalline phase. Late void filling sulphide mineralization is limited to a few specimens which exhibit galena crystals. Both the plant and animal fossils however show a similar detrital mineral component within the matrix of the nodules, comprising quartz and chlorite and smectite clay grains within the same sedimentary medium.

FOSSIL STYLE	PLANT	ANIMAL
Impression fossil	Yes	Yes
External mould	No	Yes
3D external mould	Yes	No

Table 5.4. A comparison of the preservational style of the plant and animal fossils in the Coseley Lagerstätte.

MINERAL PHASE	PLANT	ANIMAL
Organic carbon	Yes	No
Early kaolinite	Yes	Yes
Microbial siderite	No	Yes
Rhombic siderite	Yes	Yes
Pyrite framboids	Yes	Yes
Quartz overgrowths	Yes	No
Ti enrichment	Yes	No
Void filling kaolinite	Yes	Yes
Void filling sulphides	Yes	Yes
Void filling carbonates	Yes	No
Detrital minerals	Yes	Yes

Table 5.5. A comparison of the mineral phases present within the plant and animal fossil of the Coseley Lagerstätte.

5.2 Material and Methods

The Coseley Lagerstätte includes over two thousand specimens from several different museums in the UK. The specimens analyzed for the taphonomical study were selected from the collection held at the Lapworth Museum of Geology, University of Birmingham. Just under 1000 Coseley specimens were studied in hand specimen and the mode of preservation, the degree of compaction, the fidelity of soft tissue preservation and the presence or absence of hard parts, soft tissues and biominerals was observed. This has produced an overview of the preservational style and the degree of preservation of the fossils as well as highlighting any differences in preservational style between the different fossil groups. The hard parts and soft tissues along with the concretions that surround the fossils were analyzed separately to determine their composition and mineralogy. Twenty fossils were then selected for further analysis, 14 plant fossils and six animal fossils. Plants are much more abundant in the assemblage and hence make up the majority of the specimens chosen for destructive analysis, a variety of different plant organs that represented all of the major plant groups were chosen for analysis; the plants chosen also showed a variety in the degree and style of preservation and the degree of mineralization. The plants varied from impression fossils of leaves that showed no biomineralization to three-dimensionally preserved stem and cone specimens that exhibited a variety of different minerals.

The number of animal fossils available for destructive analysis was limited as many specimens were type or figured specimens and other taxa were represented by only one or two specimens. This was particularly true for the arachnids and hexapods, hence these were not utilised in the analysis. The animal fossils chosen were from groups where numerous specimens were available such as xiphosurans, crustaceans and millipede arthropods and sarcopterigian fishes.

Specimen preparation. The fossils were vacuum resin impregnated using a 10:1 mixture of Araldite M7778 and hardener H7951 to prevent the specimen disintegrating when it was sectioned, then sectioned and mounted upon a two by one inch glass slide and ground and polished using a diamond based polishing medium. The thin sections were left uncovered for chemical analysis. All of the specimens were first analyzed using transmitted light microscopy using a Zeiss Axioskop and then under cathodoluminescence using Nikon optiphot. This analysis identified several mineral phases within the siderite nodule and the presence of several different sulphides along with the extent of the clay mineralization in the fossil.

Scanning electron microscopy. The next step was to analyze the different mineral phases in detail using scanning electron microscopy. The thin sections were first coated either in gold using a Polaron SC7 640 sputter coater, platinum using an emscope SC500 sputter coater or in carbon. The gold coated plant and animal specimens were analyzed at Metallurgy and Material sciences at the University of Birmingham using a JEOL 5410, JEOL 6060 and a Philips XL-30

FEG environmental SEM. Element mapping was also carried out on specimens analyzed by the JEOL 6060 and the Philips XL-30 FEG using the Oxford Inca 300 EDS system. Carbon coated specimens were analyzed at The University of Leicester and at The University of Liverpool using a Phillips XL series 30 SEM, here energy dispersive x-ray (EDX) analysis was also carried out to give qualitative chemical analysis of some of the mineral phases.

Electron microprobe analysis. Electron microprobe analysis was carried out on several specimens do identify different mineral phases particularly the clay mineral phases. As electron microprobe analysis is quantitative, cation proportions could be calculated allowing the determination of mineral species (Gabbott 1998).

5.3 Environment of deposition.

During the Late Carboniferous, Coseley formed part of the European Paralic Coal Basin, which ran from the British Isles to Poland (Cleal and Thomas 1994), and lay within the tropics a few degrees north of the equator producing a humid and tropical ever wet to seasonally wet palaeoclimate (Cleal and Thomas 1994). The sedimentary environment would have been that of a lacustrine delta complex (see Chapter two) where lycopsid rich vegetation accumulated in vast thicknesses in rheotrophic swamps to form peat and in turn coal. These typical Carboniferous Coal Measures swamps produced the ideal conditions for siderite concretion formation and fossil preservation. The swamp floors were near permanently waterlogged allowing the formation of large lakes within the flood basins, the rotting vegetation that accumulated in these lakes led to the development of anoxic bottom waters where siderite could be precipitated. These oxygen depleted bottom waters excluded scavengers so that plant organs and animal carcasses that fell in from the surrounding forest or sank from the water column above could remain intact long enough to become preserved in siderite. The Upper Carboniferous, Westphalian, of the West Midlands comprises the Coal Measures Group of the Southern Pennine Basin. This unit comprises cyclic sequences of sandstones, grey to black shales, clays, ironstones and coals.

The fossils of the Coseley Lagerstätte were not smothered alive, the organisms died either in the lakes or within the forests and were the transported to then preserving environment, the lake bottoms. This is an important observation as it indicates that obrution or smothering does not have to occur to lead to exceptional preservation.

The original sedimentary medium in which the fossils were preserved and from which the siderite concretions grew can be inferred by examining the detrital sedimentary minerals that occur within the matrix of the siderite concretions. The detrital minerals found within the matrix of the siderite concretion include clays, micas, feldspars and quartz, that range in grain size from 5-50 μm indicating a silt sized sedimentary medium. This would have been permeable allowing ion exchange and fluid flow through the sediment. The quartz clasts range in size from 20-50 μm and are angular to sub-angular in shape (Fig. 5.4 a). The clays that dominate the concretion matrix are thin, elongate grains that range in size from 20-30 μm (Fig. 5.4 b), and analyses show a composition consistent with illite / smectite (Fig. 5.4 c). Other detrital minerals include sheet silicates such as biotite and chlorite, and feldspars which, in places have decayed into kaolinite.

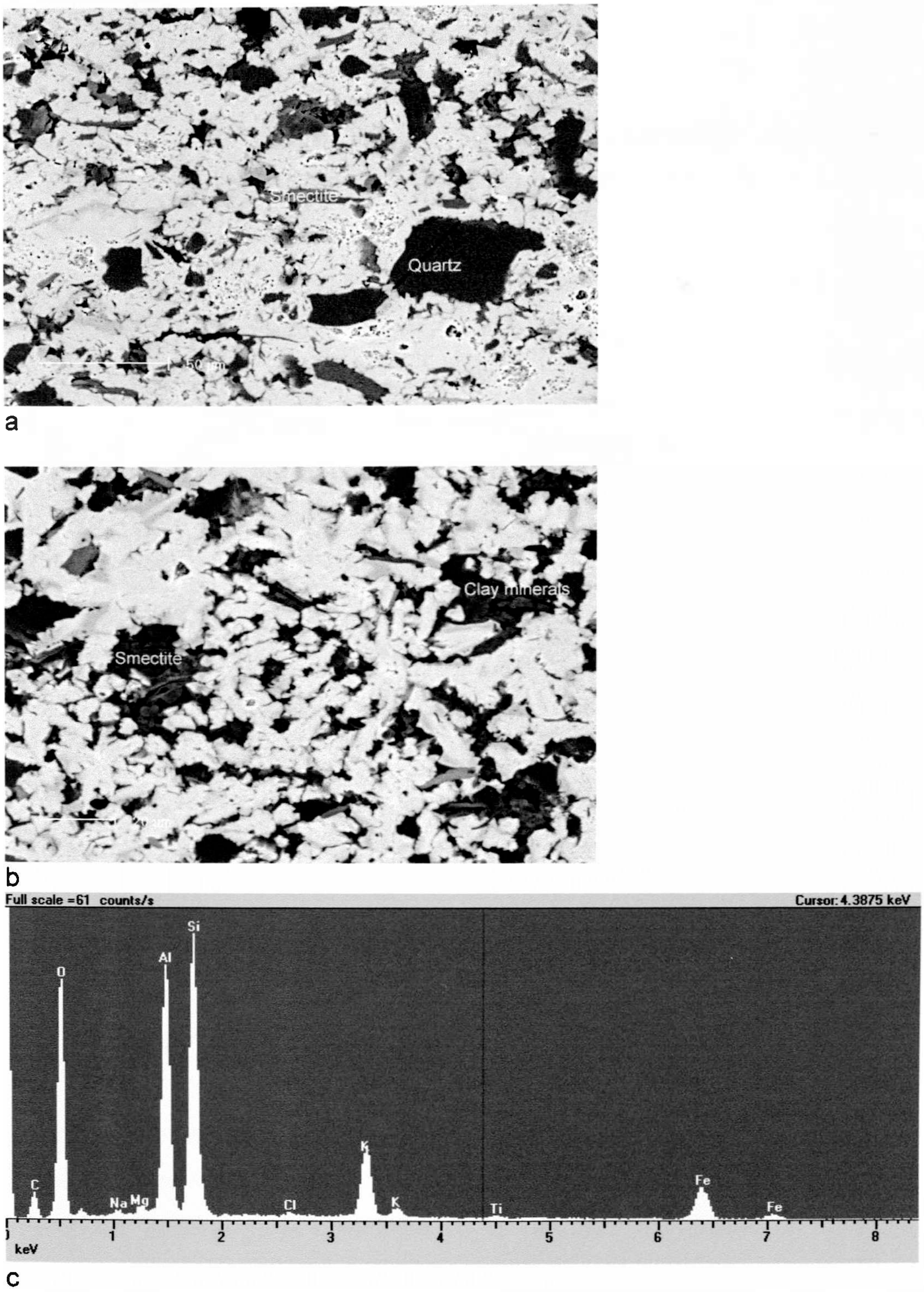


Fig. 5.4 Detrital minerals that occur within the siderite nodules of the Coseley Lagerstätte. a) BU 4447 *Ctenodus*, detrital clay and quartz minerals. b) and c) BU 4443 *Lepidodendron*, detrital clay minerals and analysis of the clay minerals.

5.4 Stages of preservation of the fossils of the Coseley Lagerstätte.

5.4.1. Burial and initiation of decay

The plant and animal fossils of the Coseley Lagerstätte comprise soft tissue outlines and refractory tissues only, indicating that decay of the very soft tissues occurred prior to mineralization. The organic remains received from the swamp forest were buried in silt within lakes where soft tissues decayed and mineralization commenced.

Refractory plant tissues. In the plant fossils some refractory plant tissues still remain as organic carbon and occur either as fine particles or larger fractured blocks. The fine-grained carbon occurs as small particles with an average size of 10-15 µm interspersed with the loosely packed kaolinite particles and larger sulphide crystals, and can be seen using back scattered scanning electron microscopy. The organic carbon also preserves plant vascular tissue for example specimen *Lepidodendron* (BU 4444) and *Lepidostrobus* (BU 4446) (Fig. 5.6 a).

Biomineralized animal tissues. The majority of the animal tissues have decayed leaving only biomineralized tissues including fish scales and teeth. These are composed of apatite and the scale of the sarcopterigian fish *Ctenodus* still exhibits the laminated dermal bone (Fig. 5.7 a).

5.4.2. Early pyrite formation

Pyrite has been found in association with plant fossils and is common in the three-dimensionally preserved lycopsid specimens. The pyrite occurs as framboids that range in size from 10-15 µm and are formed of cubic crystallites that have an average size of 2 µm. The crystallites occur as well organized, equally spaced cubes that form spherical framboids. The framboids occur within the siderite of the nodule and within the fossil (Figs. 5.5 a and b). Fine grained disseminated pyrite can also be seen throughout the siderite concretions (Fig. 5.5 c) and as polyhedral crystals within plant vascular tissue (Fig. 5.5 d).

The main mechanism for sulphide production at low temperatures (<100°C) in anoxic sediments is by bacterially mediated sulphate reduction (Fortin & Beveridge 1997). Pyrite formation requires a source of organic carbon, iron and sulphate and begins to form in the sulphate reduction zone within a few metres of the sediment surface. In freshwater environments, the concentration of sulphate ions is low and the sulphate reduction zone will be somewhat reduced compared to that of a marine setting (Postma 1982). However in freshwater siderite bearing sediments, sulphate is found in the uppermost porewaters. The source of this sulphate is the oxidation of iron sulphide or organic sulphur which will in turn result in the production of sedimentary sulphide (Postma 1982). Pyrite is only stable in anoxic conditions in the presence of dissolved sulphide ions. This would have been achieved in the lake bottoms by the rapid accumulation of organic matter and its rapid metabolism by bacteria consuming all available oxygen which in turn would have been replaced by dissolved sulphide (Berner 1970).

There are three stages in the formation of sedimentary pyrite formation; bacterial sulphate reduction, reaction of H_2S with ion minerals and the transformation of iron monosulphides to pyrite (Berner 1970). During low temperature diagenesis (<100°C) bacteria contribute to the formation of crystalline metal residues by accelerating the formation of authigenic mineral phases. Iron sulphide is the most common metal deposit attributed to biogenic activity. Bacteria play a vital role in sedimentary pyrite formation as bacterially formed pyrite exceeds the levels and rates of abiotically produced pyrite (Donald & Southam 1999). Sulphate reducing bacteria utilize sulphate as an energy source while reducing it to H_2S. The H_2S is then available to react with divalent metal cations to form iron monosulphides such as mackinawite and greigite (Berner 1970). The conversion of these intermediate phases to pyrite in fresh water settings occurs by the subtraction of iron (Berner 1970).

Both framboidal and polyhedral pyrite occur within the Coseley fossils, these textures depend on the chemical factors that influence the extent to which the iron monosulphides greigite and mackinawite are involved in pyrite formation (Raiswell 1982). Separate reaction pathways lead to framboidal and euhedral pyrite formation, depending on the formation of metastable iron sulphides (Raiswell 1982). Framboidal textures start to develop in the earliest stages of diagenesis as soon as sulphate reduction begins by the re-crystallization of iron monosulphides. The spherical shape of the framboids is associated with the transformation of mackinawite to gregite and cubic microcrysts develop as gregite is transformed to pyrite (Canfield *et al.* 1992). Euhedral pyrite develops either from direct precipitation of pyrite when the iron monosulphides are undersaturated and prevented from forming, or by the reaction between mackinawite and elemental sulphur (Raiswell 1982). The two different pyrite textures in Coseley therefore represent changes in ion mobility through the sediment. Framboidal pyrite would have formed first utilizing ions available within the adjacent sedimentary horizon, whilst euhedral pyrite would have developed later once this source had been consumed by the diffusion and transportation of iron in from the surrounding sediment (Raiswell 1982).

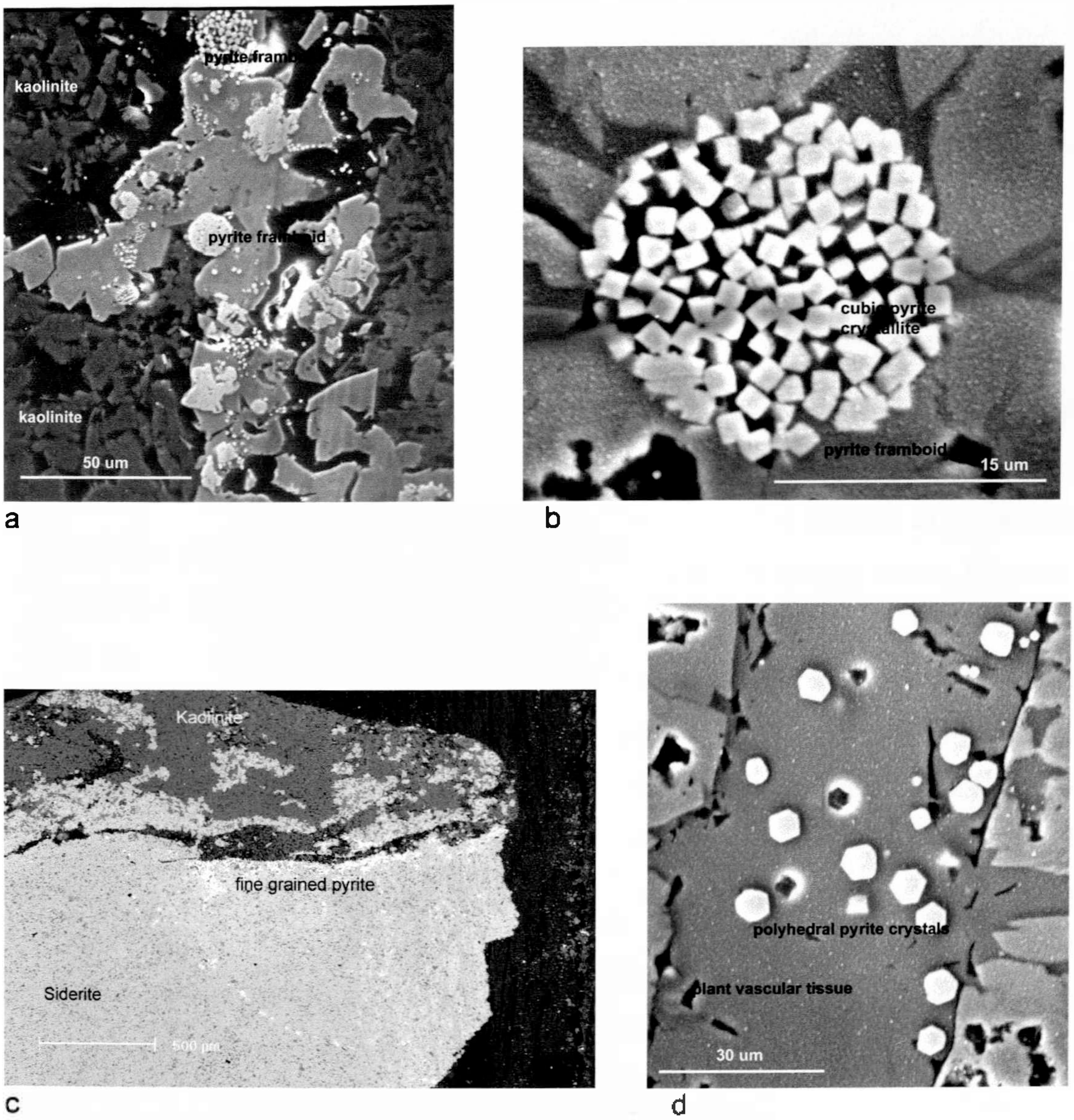


Fig. 5.5 Pyrite mineral textures observed within the fossils of the Coseley Lagerstätte. a) BU 4445 *Lepidostrobus*, pyrite framboids. b) BU 4444 *Lepidodendron*, pyrite framboids. c) BU 4445 *Lepidostrobus*, fine grained pyrite. d) BU 4443 *Lepidodendron*, euhedral pyrite crystals.

5.4.3. Early microcrystalline and microbial siderite

Methanogenesis commences below the sulphate reduction zone and any remaining organic material is degraded to methane. It is here that carbonate precipitation begins and siderite is generated (Raiswell 1988). The siderite develops around the decaying carcass forming an external mould in the developing concretion.

Early microcrystalline siderite in plant fossils. The siderite enclosing the plant fossils is composed of a fine-grained, equigranular, mosaic of siderite crystallites that are densely packed and uniformly distributed across the nodule. The siderite has been identified using EDX analysis (Fig. 5.6 b). The siderite crystals have in places been replaced by dark brown to black amorphous iron oxide, limonite due to weathering, particularly around the edge of the nodules. The siderite crystallites show non-concentric zoning, where compositional zones occur on individual crystal faces and not, as is usually the case, on radial crystal growth zones. The zoning shows magnesium enriched zones and magnesium depleted zones (Figs. 5.6 c and d). The siderite crystallites are euhedral in shape where they have grown into pore spaces, and more irregular in shape where the siderite has replaced detrital quartz grains. The siderite crystallites also show a variation in packing, the crystallites are more closely packed near to the fossil (i.e. towards the centre of the nodule) and more loosely packed away from the fossil towards the edge of the nodule.

Early microbial siderite in animal fossils. The early siderite that forms around the animal carcasses develops as a microbialite, and shows a very different texture to the siderite encasing the plant fossils. The siderite does not occur as a series of well developed rhombic crystallites, as with the plant remains, but as an unstructured, chaotic assemblage of poorly developed siderite crystals with a high percentage of detrital quartz and clay minerals. The siderite exhibits a high porosity with many large holes that are crossed by a network of thin strands of siderite. The texture of the siderite appears to be microbial, where an algal mat or bacterial coating on and around the decaying carcass has been converted to siderite. This bacterial texture is prominent adjacent to the fossil and becomes less defined towards the nodule edge (Figs. 5.7 b, c and d).

Early crystalline and microbial siderites are commonly affected by brittle shrinkage cracks and can be seen in the plant and animal fossils. In the plant specimens sigmoidal shaped fractures that are in-filled with clay and sulphide, are present in the nodule matrix, for example *Lepidostrobus* (BU 4443) (Fig. 5.7 e). Brittle cracks can also be seen in the animal specimens as vertical cracks running through the fossils, for example *Ctenodus* (BU 4447) (Fig 5.7 f).

5.4.4. Early non-microbial siderite in animal fossils

In the animal fossils, for example specimens *Ctenodus* (BU 4447) and *Pygocephalus* (BU 4448) a non-microbial early siderite phase occurs. The siderite occurs as a fine-grained Mg depleted phase that has formed between the microbialite and the biomineralized tissues indicating that it precipitated after the formation of the micobialite. This phase must have precipitated after brittle failure as it can be seen developing cubic crystal faces as it precipitates into the brittle voids (Fig. 5.7 f). Dolomite is also present in the animal fossils for example it occurs between the siderite and kaolinite particles in the specimen *Euproops* (BU 4449). This mineral phase indicates a change in the chemical conditions that lead to siderite formation around the carcass.

In freshwater environments such as the floodplain lakes of the South Staffordshire Coalfield during the Westphalian, low sulphate concentrations produced only small amounts of pyrite for a limited period of time (Postma 1982). Once sulphate reduction had ceased other microbial oxidation processes such as methanogenesis commenced (Raiswell 1988). Earlier sulphate reduction generated an excess of Fe^{2+} stripping out any HS^- in the sediment. With low HS^-

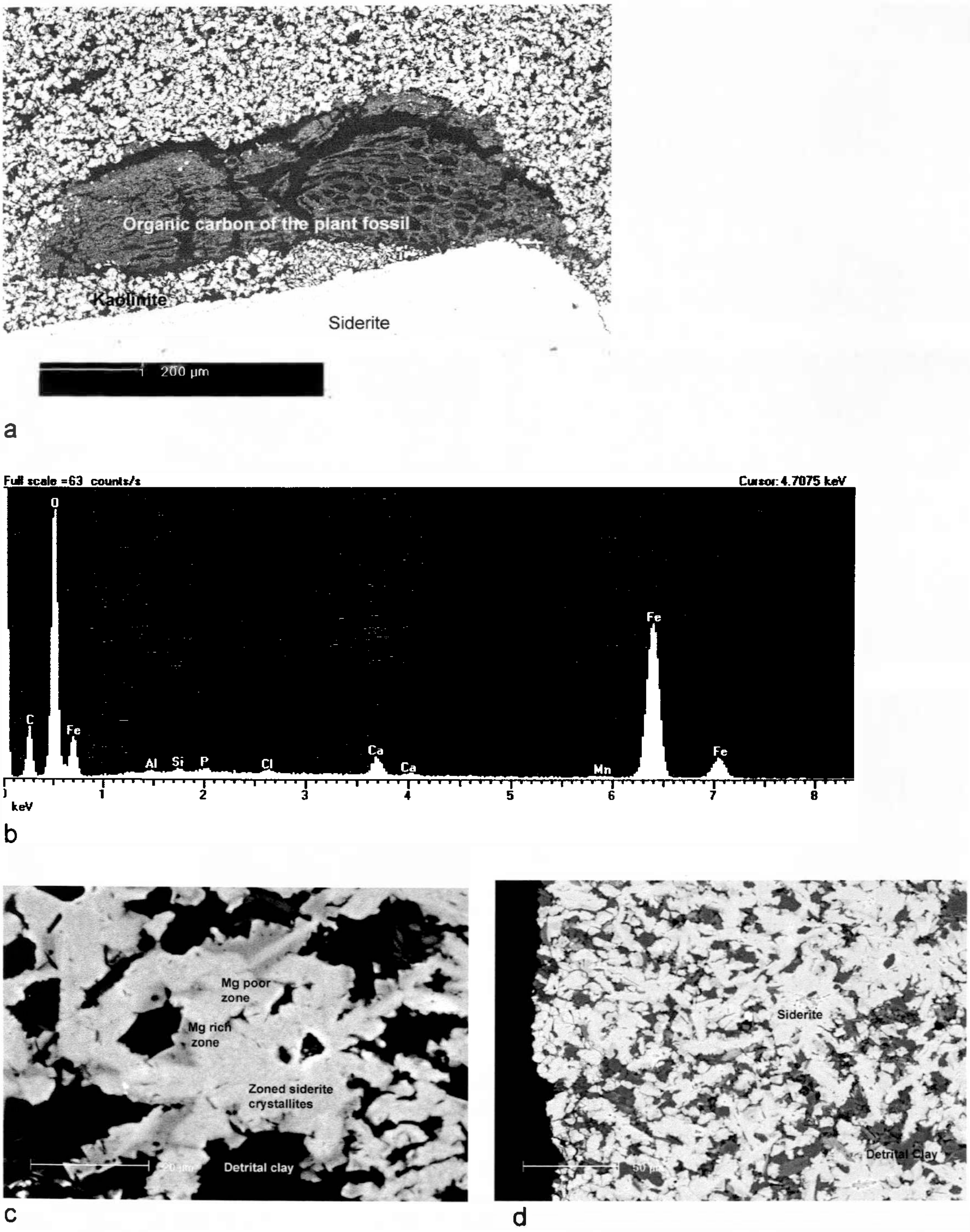


Fig. 5.6. Refractory plant tissues and early siderite textures observed in the plant fossils of the Coseley Lagerstätte. a) BU 4446 *Lepidostrobus*, refractory plant tissues preserving vascular structures. b), c) and d) BU 4443 *Lepidodendron*, analysis of the siderite and zoned siderite textures.

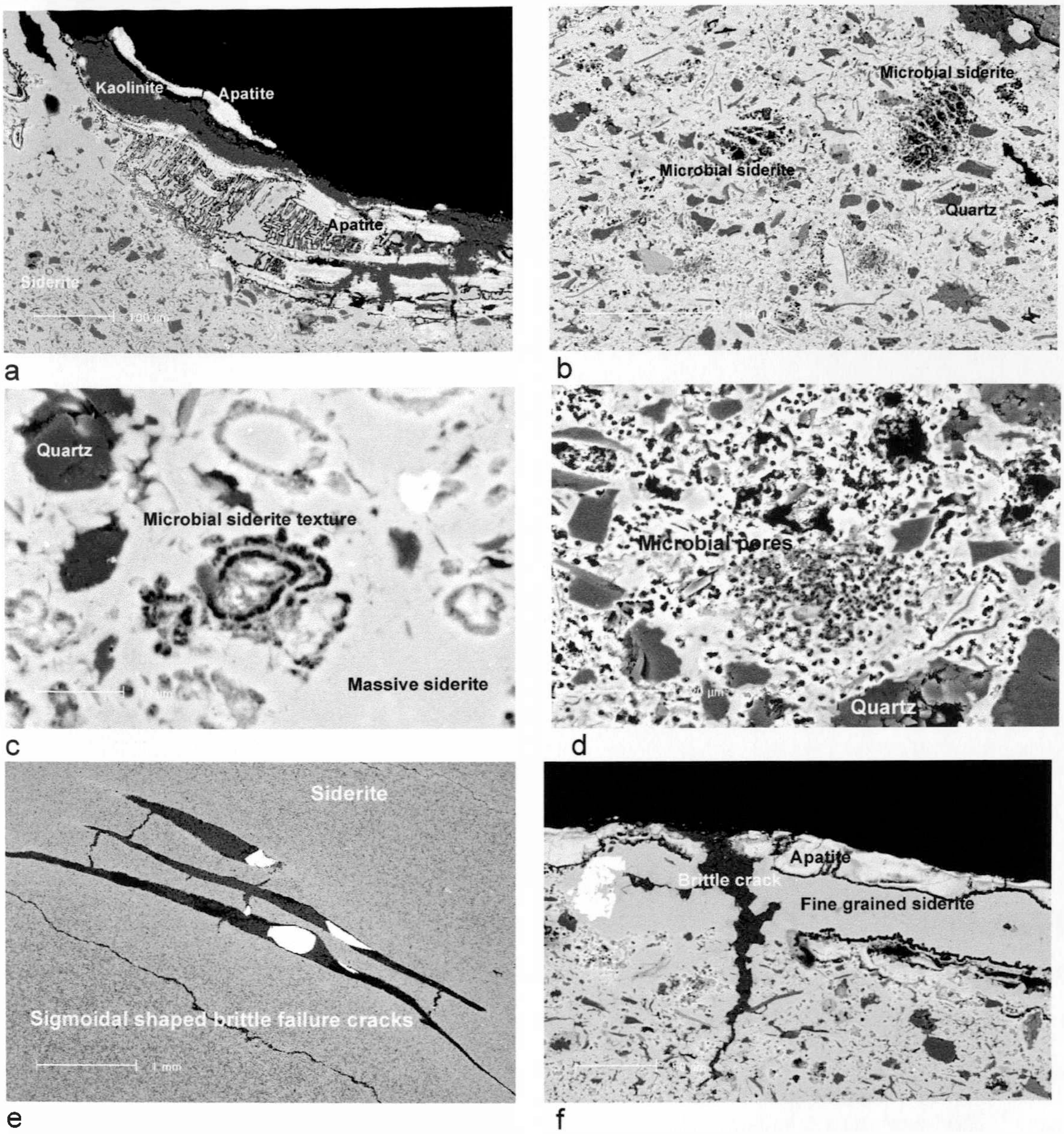


Fig. 5.7 Biomineralized animal tissues and early microbial siderite observed in the animal fossils of the Coseley Lagerstätte. a) BU 4447 *Ctenodus*, apatite of the original scale. b) BU 4449 *Euproops*, Microbial siderite textures. c) BU 4447 *Ctenodus*, Microbial siderite textures. d) BU 4448 *Pygocephalus*, Micro-pores in the siderite possibly bacterial borings. e) BU 4443 *Lepidodendron*, sigmoidal shaped brittle cracks in the siderite. f) BU 4447 *Ctenodus*, brittle crack in the scale filled with kaolinite.

levels, anoxia, high iron concentrations and increased HCO_3^- activity siderite precipitation occurred (Al-Agha *et al.* 1995). Siderite formation therefore commenced close to the sediment-water interface within the zone of methanogenesis (Raiswell & Fisher 2000).

The initial siderite precipitation occurred around decaying plant organs leaving voids in the siderite that formed external moulds of the original plants. Only very refractory plant tissues remained preserved within the concretions. Back scattered electron microscopy has revealed that the Coseley concretions are composed of a series of zoned crystallites. This texture is indicative of pervasive growth (Raiswell and Fisher 2000). The concretion initially formed by the simultaneous nucleation and precipitation of isolated siderite crystallites within the enclosing sediment around the fossil (Raiswell & Fisher 2000). These crystallites grew until they made contact with each other forming a framework which allowed plasticity during shallow burial but was rigid enough to prevent compaction, preserving the fossil, and undergo brittle failure forming tensile cracks in the nodule (Raiswell & Fisher 2000). This initial pulse of pervasive growth left substantial unfilled porosity in the nodule (Raiswell & Fisher 2000).

Carbon and oxygen isotopes were analyzed from three concretions the isotopes were taken along a transect across each concretion (Fig. 5.8). For concretion one the δO^{18} values range from -6.0 to -6.5 and show little variation across the concretion. The δC^{13} values range form +6.34 to +6.48 and show a slight decrease in the centre of the concretion. For concretion two the δO^{18} values range from -5.5 to -6.7 and are slightly higher at the edge of the concretion and the δC^{13} values range from +6.50 to +7.44 and are slightly lower in the center of the concretion. Finally for concretion three the δO^{18} values range from -5.7 to -6.6 and are slightly lower at the concretion edge and the δC^{13} values range from +6.18 to +6.76 and are again slightly depressed in the centre of the concretion. Overall the δO^{18} isotope values range from -5.5 to -6.7 and do not show any distinct pattern across the concretions. The δC^{13} isotope values range from +6.18 to +7.44 and are slightly depressed at the centre of the concretions.

The δC^{13} isotope values indicate a weighted function of all carbon sources with methanogenesis providing an isotopically and distinct major component, as stated by Curtis *et al.* (1986) that methanogenic reactions produce positive δC^{13} values whereas thermal decarboxylation produces negative δC^{13} isotope values. The oxygen isotope data also indicates the precipitation of the siderites from meteoric water as the δO^{18} values fall in the range between -5 to -6 ‰.

Sample	**δC^{13} values**	**δO^{18} values**
Concretion no. 1		
1	+ 6.48	- 6.0
2	+ 6.41	- 6.5
3	+ 6.34	- 6.3
4	+ 6.45	- 6.0
5	+ 6.37	- 6.0
Concretion no. 2		
6	+ 7.44	- 5.5
7	+ 6.98	- 5.8
8	+ 6.67	- 5.8
9	+ 6.50	- 5.7
10	+ 6.81	- 6.7
Concretion no. 3		
11	+ 6.27	- 6.6
12	+ 6.29	- 6.1
13	+ 6.20	- 6.3
14	+ 6.18	- 5.8
15	+ 6.76	- 5.7

Fig 5.8 Carbon and oxygen isotope values for the Coseley siderite concretions.

Early crystalline Mg depleted siderite also occurs within the animal fossils, but is preceded by microbialite formation and brittle failure. The carcasses were buried in the sediment where decay commenced, leaking decay products out into the surrounding sediment. The siderite micobialite formed around the decaying carcass, all but biomineralized tissues then decayed leaving a void in the surrounding microbalite that formed an external mould of the organism.

Microbialites form when microbial communities become lithified through the precipitation of chemical sediments (Ferris *et al.* 1997). Microbialite structures include non-laminated thrombolites that have a distinctly clotted internal fabric composed of coccoid bacteria (Ferris *et al.* 1997). This clotted fabric is reminiscent of the internal structure of the microbial siderite that surrounds the Coseley animal fossils. Bacteria were attracted to surfaces where nutrients were concentrated (Sawicki *et al.* 1995), such as the decaying carcasses, forming biofilms. Bacteria induce mineralization as a by product of interactions between themselves and the surrounding environment. Hence mineralization will depend on what ions are available and the chemical conditions of the surrounding environment (Konhauser 1998). The biofilms around the decaying carcasses provided the chemical conditions for the nucleation sites necessary for mineral formation. The microbial cell walls within the biofilms were negatively charged allowing the bacteria to sorb and bind metal ions from the surrounding media, which in some cases was so great that precipitates were formed (Sawicki *et al.* 1995). The uptake and retention of metal ions by the bacteria within the biofilm also lowered the activation energy barrier that retarded spontaneous crystal growth therefore decreasing the degree of over-saturation needed for mineral precipitation and causing further mineral growth (Ferris *et al.* 1997).

Fine grained iron minerals are associated with nearly all bacterial cells, the availability of iron in the surrounding pore waters served as a source for bacterial reduction. The release of ferrous iron by the bacteria into a solution with excess carbonate would have then led to siderite precipitation (Konhauser 1998) which would have then been attracted to polymers on the bacterial surfaces (Sawicki *et al.* 1995). Bacteria can also enzymatically reduce Fe^{3+} directly to siderite providing another mechanism for siderite precipitation within the biofilm to form a thrombalite.

The micobialite that formed around the decaying organism, like the early crystalline siderite concretions, prevented compaction of the nodule and preserved an external mould of the fossil. The concretion also underwent brittle failure forming cracks in the nodule. The concretion was still capable of plasticity at this point and had a high proportion of unfilled porosity. Again these nodules formed close to the sediment water interface in the zone of methanogenesis where the pore waters were saturated with respect to Fe, C and O (Fisher *et al.* 1998). Once all the labile soft tissues had decayed and the biofilms had stopped growing and precipitating siderite, siderite formation then proceeded by the precipitation of crystallites in void spaces left by decayed tissues forming Mg depleted siderite crystallite layers, this post dated brittle failure as this phase can be seen infilling brittle cracks.

5.4.5. Void filling kaolinite formation

Powdery, white clay mineral films can be observed in the majority of the Coseley fossils occurring as mineral films on the surface of impression fossils and infilling void space in mouldic specimens. The kaolinite occurs as randomly orientated particles that do not preserve any cellular or anatomical detail. It is therefore unlikely that the kaolinite directly replaced soft tissues, and also unlikely that the kaolinite particles formed a mineral coating over the soft tissues as they show no pattern or alignment. The randomly orientated texture of the clay particles is indicative of a void infill, where the kaolinite has infilled voids left in the siderite by the decay of soft tissues, and voids surrounding refractory plant tissues and biomineralized animal tissues.

In both the plant and animal fossils, kaolinite infills the voids in the concretion left by the decay of the organism. The void filling clay mineral found within the

Coseley plant fossils is texturally and chemically distinct from the detrital clay found within the siderite concretions. This clay mineral occurs in a majority of the plant fossils; it occurs as a thin layer usually no more then two millimetres thick on the broken surface of the siderite nodule where the fossil occurs (Fig. 5.9 a) and interspersed with the plant organic remains (Fig. 5.9 b). Texturally, the clay is either very fine-grained and found as small elongate particles that vary in size from 2-20 µm, are commonly found stacked together to form a 'bookend' pattern, or occurs as coarser grained blocky particles that vary in size from 20-30 µm (Fig. 5.9 c). The clay particles are usually more closely packed nearer to the fracture surface of the nodule and become more widely spaced with increasing distance from this fracture surface (Fig. 5.9 d). The clay particles are randomly orientated across the fossils and no consistent pattern in orientation is seen. The clay particles can also be seen as inclusions within larger sulphide crystals. Small elongate clay grains can be seen within the top few millimetres of the siderite adjacent to the fossil.

Fine grained, void filling clay minerals also occur in the animal fossils. Electron microprobe analysis indicates that the composition is that of kaolinite (Fig. 5.10 a). The kaolinite occurs as small elongate particles 2-20 µm in size or as closely packed accumulations of blocky kaolinite. The kaolinite occurs inter-dispersed with the carbonate of the arthropod cuticle, for example in *Euproops danae* (BU 4449) (Fig. 5.10 b), between layers of apatite in the fish scale specimens, for example *Ctenodus* (BU 4447) (Fig. 5.10 c), as a layers of kaolinite on the nodule surface and as inclusions in later sulphide crystals in the fish egg case specimens, for example *Palaeoxyris* (BU 4450) (Fig. 5.10 d).

Kaolinite mineralization began after initial siderite concretion precipitation, following a rapid decline in pH levels bought about by anoxia resulting from bacterial decay of organic matter. These acidic conditions encouraged the formation of a more H^+ enriched and cation depleted mineral phases, such as kaolinite (Gabbott 1998). The kaolinite void fills probably developed authigenically within the voids as decay of organic tissues continued. It is unlikely that detrital colloidal clay particles would settle out of suspension from fluids flowing through the nodule. The kaolinite is also chemically distinct from the detrital clays which are dominated by smectite and illite. If the void filling clays had a detrital origin it would be expected that they would have a similar composition to the detrital clays. Direct supporting evidence for kaolinite authigenesis would be the occurrence of bacteria in the kaolinite. However bacteria are very rarely preserved in decay experiments except where they themselves become mineralized (Sagemann *et al.* 1999).

Clay authigenesis is the formation of clay minerals within the preserving environment by bacterial mediation. Steep chemical gradients between the organic matter and the surrounding water column existed controlling the rate of diffusion of ions and mineral precipitate composition (Sagemann *et al.* 1999). The anoxic environment associated with the organic matter would have had a low pH and hence a high concentration of H^+ ions and been depleted in cations, whereas the surrounding water column would have had a higher pH and therefore a lower concentration of H^+ ions and would have been enriched in cations (Sagemann *et al.* 1999). This gradient enabled cations to rapidly diffuse into the organic matter enabling clay mineralization. The cell walls of the bacteria present in the organic matter were a mosaic of different macromolecules that had an overall electronegative charge (Schultze-Lam *et al.* 1996). The bacterial cell walls contained carboxylate and phosphate groups and the fixation of metal ions arose through the interaction between these groups and free cations in solution (Ferris *et al.* 1987). Once a metal cation had attached itself to either one of the carboxylate or phosphate groups it served as a nucleation site for further metal fixation. These mineral precipitates grew rapidly incorporating surrounding environmental counter ions to form hydrated mineral aggregates, which were initially amorphous but over time lost water and became crystalline (Schultze-Lam *et al.* 1996). Aluminium ions are important in kaolinite formation but so are silicate ions, the bacterial cell surfaces also acted as effective sorption interfaces for silicate ions (Schultze-Lam *et al.* 1996), positively charged amine groups were

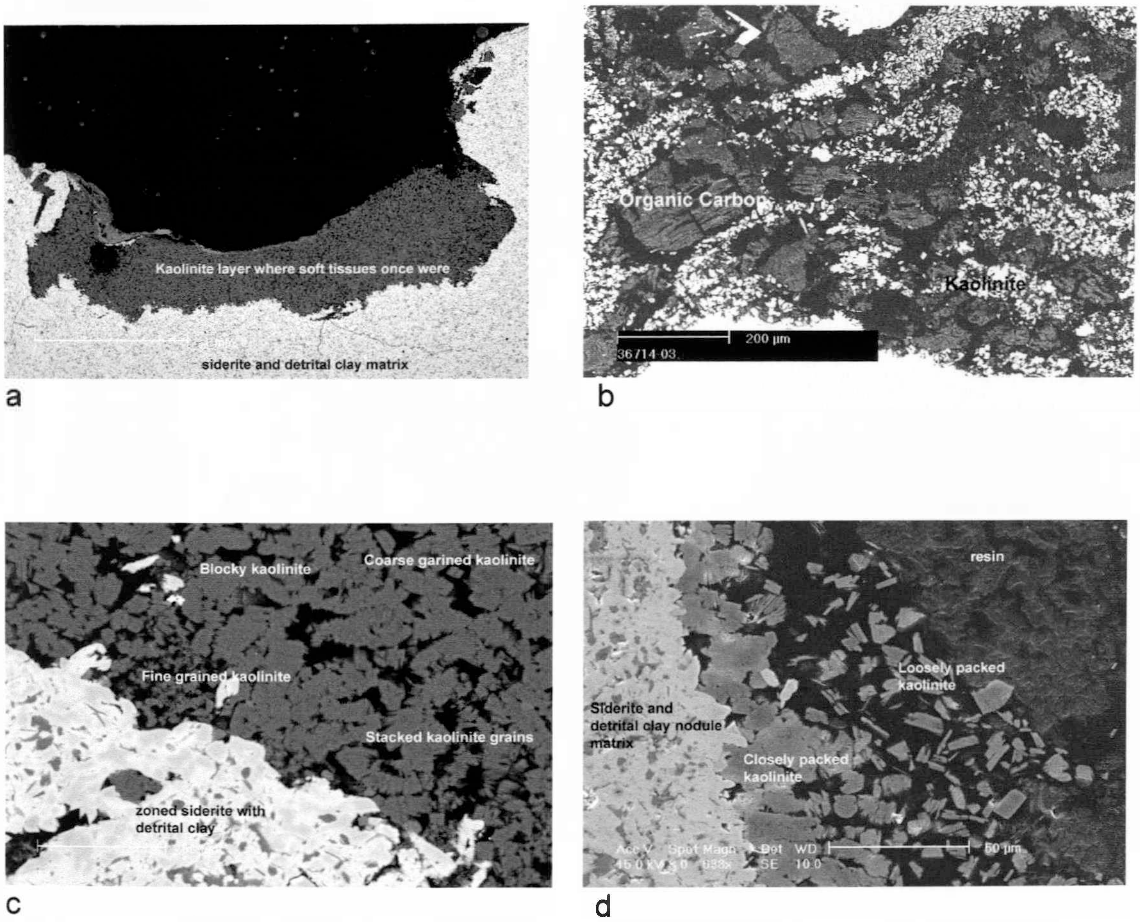


Fig. 5.9 Kaolinite mineral textures observed within the plant fossils of the Coseley Lagerstätte. a) BU 4443 *Lepidodendron*, kaolinite layer over siderite. b) BU 4446 *Lepidostrobus*, kaolinite interspersed with organic carbon. c) BU 4443 *Lepidodendron*, kaolinite showing variation in texture and grain size. d) BU 4443 *Lepidodendron*, variation in packing of the kaolinite grains.

Analysis	1	2	3	4	5	6	7	8	9	10	11	12
SiO_2	31.27	44.13	41.28	37.23	16.16	40.73	44.55	45.09	45.68	43.63	44.73	45.76
Al_2O_3	25.58	35.35	32.95	30.20	12.53	32.97	36.37	36.26	37.10	35.36	36.18	37.08
total	56.85	79.48	74.23	67.43	28.69	73.70	80.92	81.35	72.78	78.99	80.91	82.84

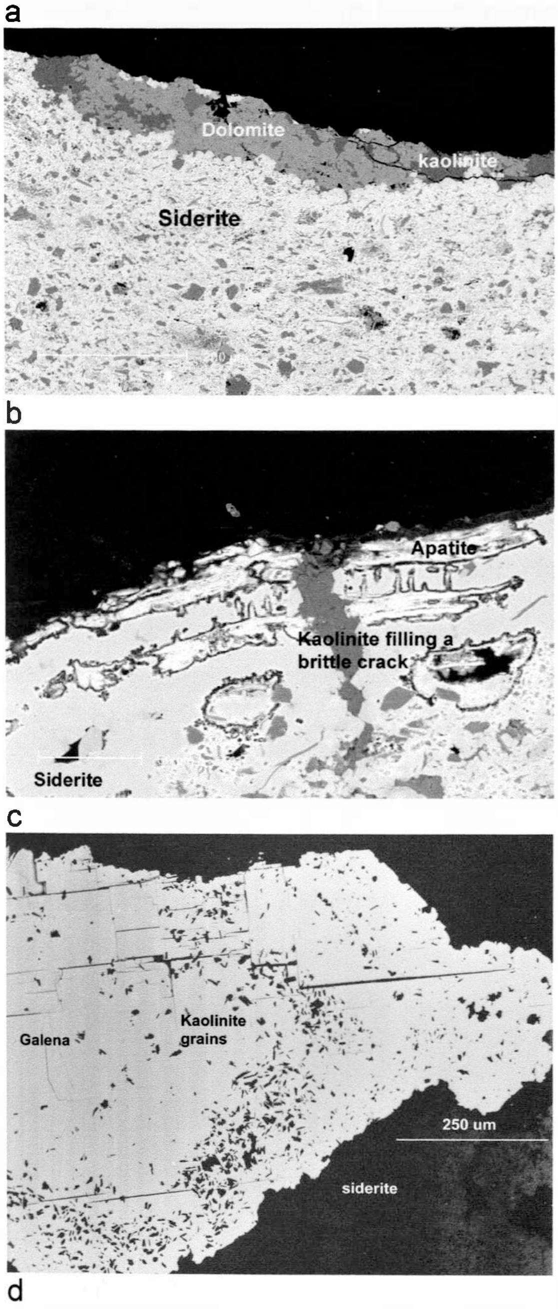


Fig. 5.10 Kaolinite mineral textures observed within the animal fossils of the Coseley Lagerstätte. a) BU 4450 *Palaeoxyris*, analysis of the kaolinite. b) BU 4449 *Euproops*, kaolinite interspersed with dolomite. c) BU 4447 *Ctenodus*, kaolinite filling a brittle crack. d) BU 4450 *Palaeoxyris*, kaolinite as inclusions within a sulphide crystal.

also present in the bacterial cell walls which attracted negatively charged silicate ions out of solution, silica is also deposited by metal ion bridging where multivalent metal ions cross link silicate ions to phosphate ions by electrostatic interaction, like the metal groups the silicates initially formed as hydrated amorphous minerals but become crystalline over time (Schultze-Lam *et al* 1996). Therefore clay mineralization was favoured by increased microbial activity which mediated anaerobically driven authigenic mineralization (Sagemann *et al.* 1999).

5.4.6. Titanium mineral coatings.

A titanium oxide mineral coating is present over the kaolinite in some of the plant material. A fine grained mineral phase occurs over the plant fossils, it can be seen lying across the surface of the kaolinite and siderite (Figs. 5.11 a and b). This mineral phase is very fine grained and preserves the outlines of leaf cushions that are visible on the surface of the fossil stem in hand specimen, for example the specimen *Lepidodendron,* (BU 4443) (Figs. 5.11 c). EDX analysis of this mineral phase reveals that the composition of the mineral is titanium oxide (Fig. 5.11 d). This fine grained Ti mineral phase is also present in the plant specimen (BU 4445) where it occurs as a thin band 10-20 µm across over the surface of the fossil, covering the kaolinite. Where the Ti rich mineral band occurs over the kaolinite, the kaolinite particles become finer grained, less organized, loose their stacked texture and become orientated parallel to the mineral layer (Figs. 5.11 e and f).

The presence of such a titanium oxide mineral coating over the kaolinite in some of the plant fossils of the Coseley Lagerstätte is highly unusual and is the first documented account of such a mineral phase associated with exceptionally preserved fossils. A possible explanation for the occurrence of such an unusual mineral film may be associated with the coal horizons of the original sedimentary setting (see Huggins & Huffman 2004).

Certain lithophile elements notably Ti but also V, Cr and Zr can be found associated with high volatile bituminous coals such as those of the South Staffordshire Coalfield, UK, and the Illinois Basin, USA (Huggins & Huffman 2004). Titanium oxides occur as two forms, rutile and anatase, and can be found in association in coals with quartz, macerals and, as in the Coseley fossils, with clay minerals. For titanium to occur in high rank coals it must have been incorporated into the organic matter at the peat stage of formation, where significant metal fractions including titanium can be attached to organic particles in the peat by ion exchange (Huggins & Huffman 2004).

As coalification occurs, and low rank coals are converted to higher rank ones, decarboxylation occurs. The loss of carboxyl groups and oxygen functionality results in the mineralization of many elements (Huggins & Huffman 2004). As coal rank increases the moisture content decreases and becomes supersaturated with respect to dissolved metal species. These metal species are then transferred from the tenuous carboxyl sites to stable mineral forms (Huggins & Huffman 2004). Titanium makes strong bonds with the carboxyl groups which persist to high levels of coalification, where it is then liberated for incorporation into mineral such as clays to form oxides (Huggins & Huffman 2004).

It is probable that during the coalification of the coal horizons, such as the 'Thick Coal', in the South Staffordshire Coal Field, that the pore waters became supersaturated with respect to titanium. Due to the affinity of titanium for clay minerals, the titanium was attracted to the accumulations of kaolinite within the fossils where it formed titanium oxide mineral coatings. The presence of the titanium mineral coating within the plant relates to the degree of kaolinite mineralization the fossils had undergone. Only the plants that had significant accumulations of kaolinite attracted the titanium.

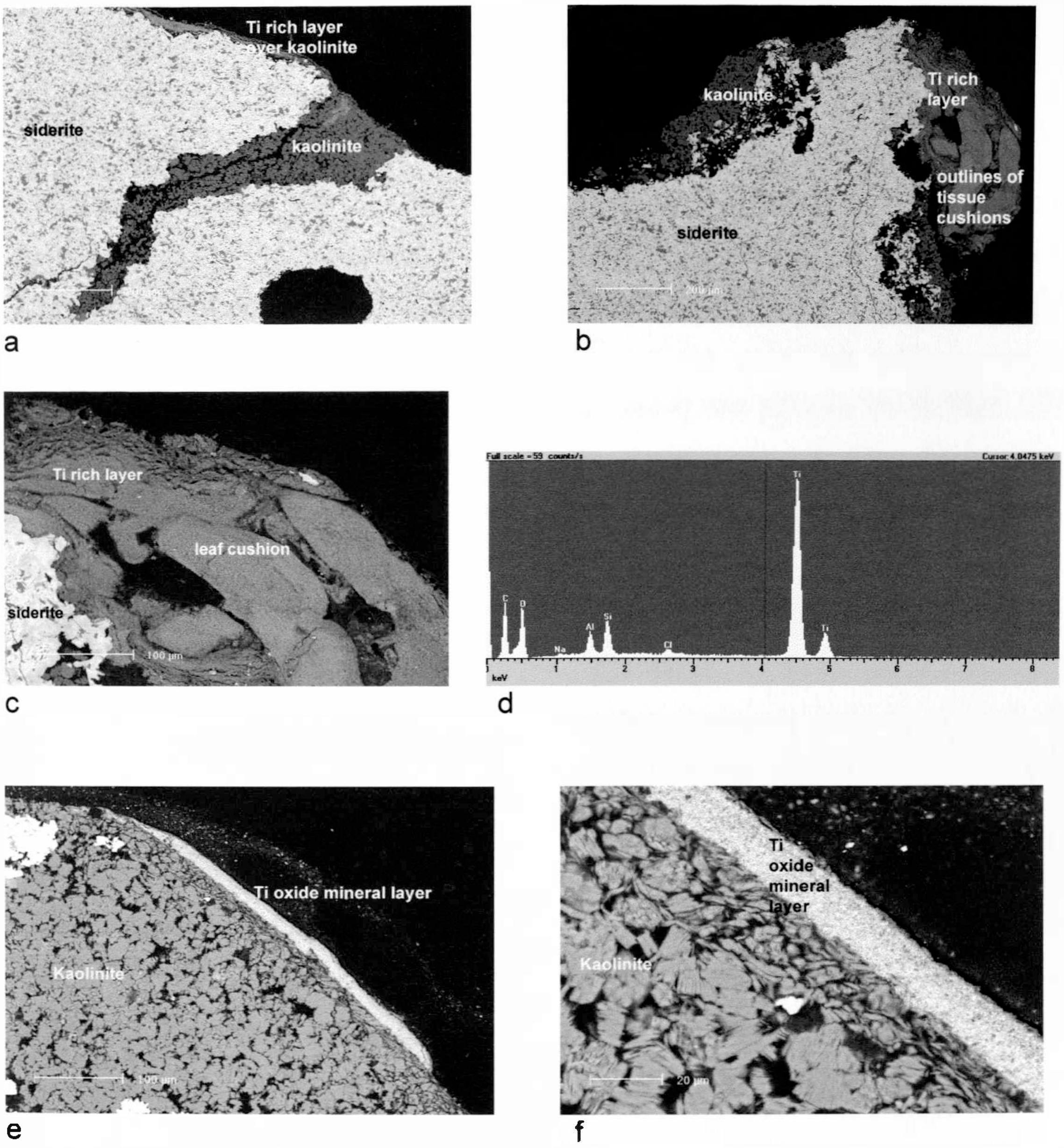


Fig. 5.11 Titanium oxide mineral textures observed within the plant fossils of the Coseley Lagerstätte. a) BU 4443 *Lepidodendron*, Ti layer over kaolinite. b) BU 4443 *Lepidodendron*, Ti layer over kaolinite preserving the structure of leaf cushions. c) BU 4443*Lepidodendron*, higher magnification image of (b). d) BU 4443 *Lepidodendron*, analysis of the titanium mineral. e) BU 4445 *Lepidostrobus*, titanium mineral layer over kaolinite. f) BU 4445 *Lepidostrobus*, higher magnification image of (e).

5.4.7. Late siderite formation

After kaolinite formation had ceased the pH levels around the organic remains began to rise and a second phase of siderite precipitation began.

Late siderite in plant fossils. In the nodules surrounding the plant fossils siderite precipitation recommenced enlarging earlier formed siderite crystallites with outer Mg-rich zones and the growth of Mg-rich rhombic crystallites in void spaces in the nodule and between kaolinite particles, gradually infilling in residual pore space. For example in specimen (BU 4445) the siderite crystallites exhibit Mg-rich outer zones (Fig. 5.12 a) and rhombs of siderite can be seen precipitating between loosely packed kaolinite particles (Figs. 5.12 b and c).

Late siderite in animal fossils. The late stage siderite formation in the animal fossils initiated precipitation of siderite crystallites in void spaces within the microbial siderite. Rhombic siderite crystallites therefore indicate a void filling mode of formation (Fig. 5.13 a). Rhombic siderite crystals can also occur adjacent to the fossil, for example, in the xiphosuran specimen *Euproops danae* (BU 4449) rhombic siderite crystallites occur adjacent to the fossil, probably where the siderite has grown into voids adjacent to the kaolinite infill (Fig. 5.13 b). It is also probable that during this later stage of siderite formation the dolomite precipitated in the void spaces between the kaolinite grains in the xiphosuran *Euproops* (Figs. 5.13 b and c). Mg-rich siderite also precipitated in pore spaces of what was originally the cuticle of the crustacean *Pygocephalus* (Fig. 5.13 d).

Both plant and animal fossils exhibit late stage Mg-enriched siderite crystallites. Once pH levels had begun to recover carbonate precipitation was re-initiated. At this stage, due to earlier carbonate precipitation, organic matter and iron oxides were depleted in the surrounding sediment causing rates of iron and carbon dioxide reduction to fall. Consequently Mg diffused in from the overlying water column increasing Mg/Fe ratios in the pore waters. Therefore, later formed

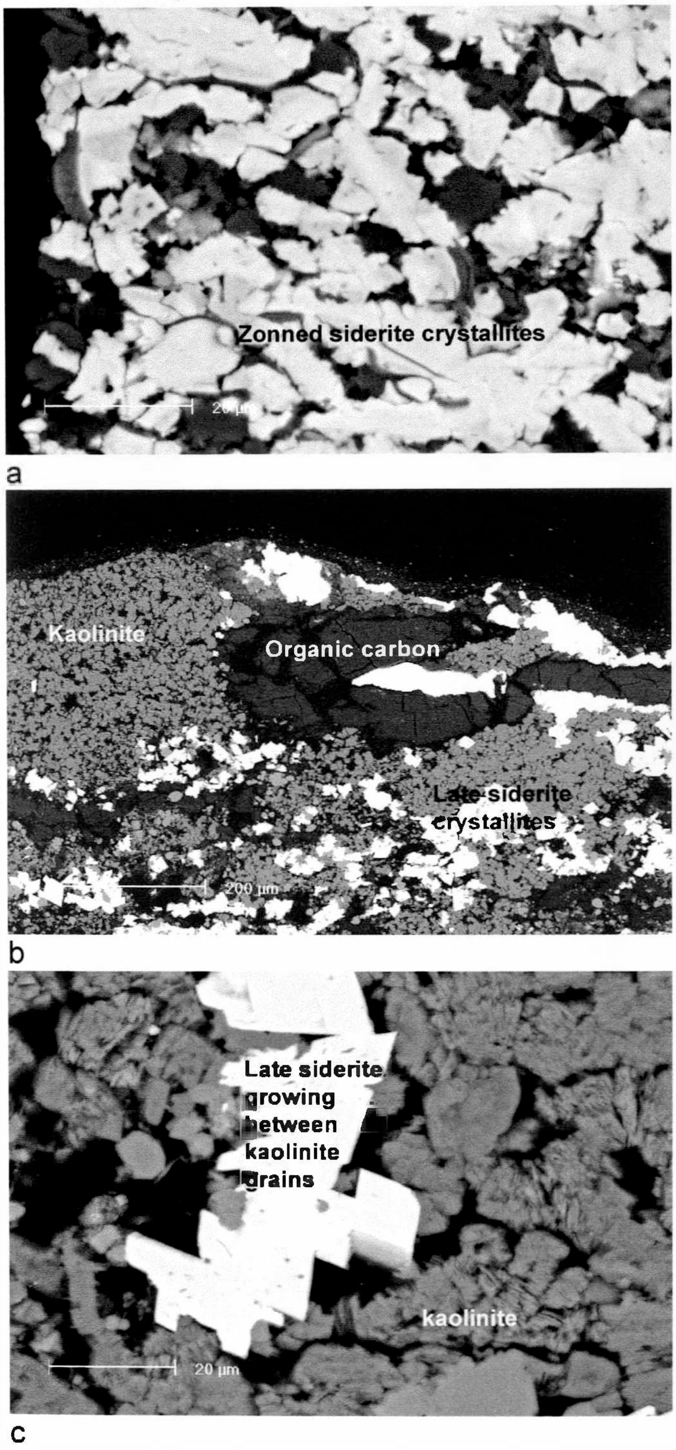


Fig. 5.12 Late siderite mineral textures observed within the plant fossils of the Coseley Lagerstätte. BU 4445*Lepidostrobus* a) siderite crystallites with darker Mg rich outer zones. b) and c) siderite crystallites growing between and displacing kaolinite grains.

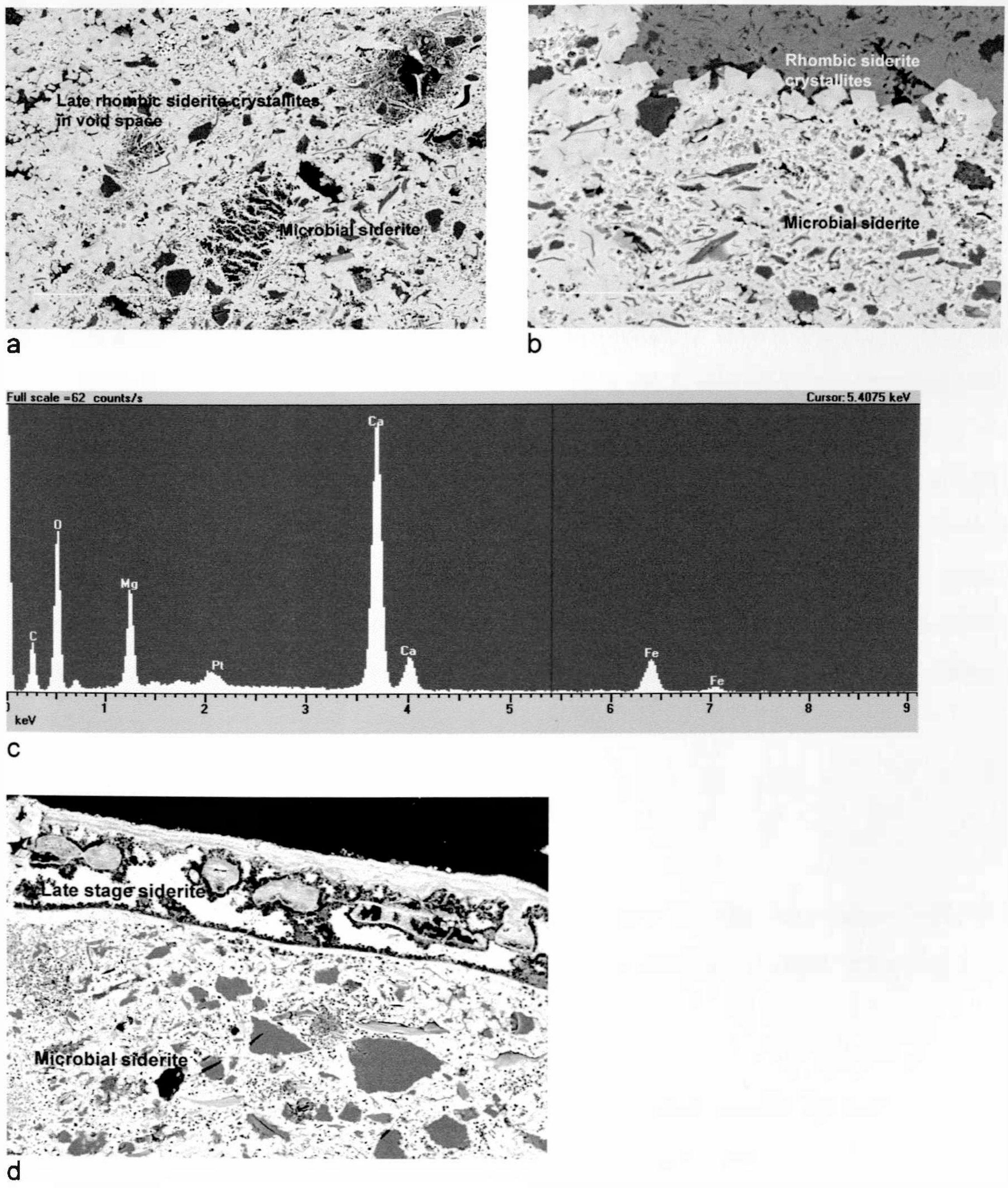


Fig. 5.13 Late stage siderite mineral textures observed within the animal fossils of the Coseley Lagerstätte. a) BU 4449 *Euproops*, rhombic siderite crystallites that have grown into a void in the surrounding microbial siderite. b) BU 4449 *Euproops*, rhombic siderite crystallites that have grown into a void adjacent to the fossil. c) BU 4449 *Euproops*, analysis of the late stage siderite. d) BU 4448 *Pygocephalus*, late stage siderite that has precipitated in a void below the fossil cuticle.

siderite became enriched in Mg with respect to iron (Fisher *et al.* 1998). This can be seen as Mg-enriched outer zones on the siderite crystallites in the plant fossils, where precipitation occurred as the nodule continued to grow pervasively, utilizing Mg in replace of Fe. Mg-enriched siderite rhombs have also precipitated within pore space within the fossil displacing the loosely packed kaolinite grains.

This same pattern can be seen in the animal fossils where Mg-rich siderite rhombs have precipitated within pore spaces within the microbialite and in pore spaces adjacent to and within the fossil. It is probable that dolomite precipitation may have also occurred at this time due to the high levels of Mg in the system.

The precipitation of this later Mg-rich siderite phase and the re-initiation of pervasive nodule growth and residual pore infilling occurred further down in the sediment profile, due to an increase in Mg/Fe ratios associated with a gradual decrease in iron reduction with depth (Fisher *et al.* 1998). As the residual pore space in the concretions became in-filled the nodules became more brittle in nature and were no longer capable of plasticity.

5.4.8. Late void filling mineralization.

Any residual pore space in the concretions and fossils has been infilled by several phases of late stage mineralization including quartz, sulphides and carbonates.

Quartz overgrowths. Quartz occurs within the plant fossils as well developed euhedral crystals that have an average size of 20 μm. The crystals can be seen incorporating and displacing earlier siderite and kaolinite mineral phases (Fig. 5.14 a) and as inclusions within sulphides (Fig. 5.14 b). Therefore the quartz precipitated after siderite and kaolinite formation but before sulphide precipitation.

Sulphides. The sulphide minerals in the Coseley plant fossils mainly occur as void fills in the lycopsid cone and stem specimens. The range of void filling sulphide minerals includes sphalerite, galena and pyrite. These minerals occur as large crystals up to 2 mm in length that are euhedral to subhedral in shape. The shape of the mineral may be governed by the shape of the void it is filling and are common in plant stems and cones. The minerals occur in the middle of the concretion surrounding the fossil (Fig. 4.14 c) or within voids and cracks within the concretion (Fig. 5.14 d). Where the sulphide minerals occur in the fossil they are commonly well formed and euhedral in shape with a cubic habit, and where the sulphides occur in cracks within the siderite they are anhedral in shape and take on the shape of the void. In both cases, however, the sulphides contain kaolinite inclusions and show sharp boundaries with the surrounding siderite. The sulphides can be seen to be surrounding kaolinite grains and filling up space between the grains and may show displacive growth relative to the kaolinite in places, for example specimen (BU 4443) (Figs. 4.14 b and d). Galena is also a common void filling mineral and is commonly zoned, for example specimen (BU 4445) (Figs. 5.14 e and f).

Void filling sulphide minerals also occur in the animal fossils but are less extensive indicating less residual pore space left for mineralization. Void filling sulphide minerals have been identified within the fish egg capsule *Palaeoxyris,* where a well developed euhedral cubic crystal of galena occurs on the surface of the fossil. The galena was again identified using EDX analysis and shows kaolinite inclusions (Fig. 5.14 g). Large pyrite void fills are also present in the fish scale *Ctenodus.*

Carbonate void fills. Calcite is occasionally seen as a void filling mineral phase, it is most abundant in the specimen *Lepidodendron* (BU 4444) where it infills the three dimensionally preserved stem (Fig 5.14 H). The exact timing of void filling carbonate mineralization is unknown but it post dates secondary siderite precipitation.

Residual pore space within the siderite concretions has been filled by a variety of minerals including quartz, carbonates and sulphides, the degree of mineralization varies between the fossils due to the amount of void space left for mineralization after the second and final phase of siderite precipitation. The timing of the precipitation of these void fills is somewhat later then the timing of fossil preservation and nodule growth. Quartz mineralization occurred first, followed by galena and sphalerite formation followed by pyrite precipitation. Calcite void fills also occur and may have formed at any stage following quartz precipitation.

This late void filling mineralization may be associated with mineralization of the South Pennine Orefield, which lies at the southern edge of the Pennine Hills in Central England (Mostaghel & Ford 1985). The South Pennine Orefield can be classified as a Mississippi-Valley type ore deposit where the ore body has a sedimentary and diagenetic origin (Mostaghel 1985), and comprises a galena-sphalerite-baryte-fluorite mineral assemblage that occurs in void filling veins and stratiform ore bodies (Ixer & Townley 1979). The ore body is dominated by calcite, fluorite and baryte with the metallic sulphides comprising less than ten percent. Mineralization was initiated shortly after the start of the Variscan orogeny and continued intermittently until the Late Triassic (Mostaghel & Ford 1985).

The ore deposits of the South Pennine Orefield were generated by refluxing connate brines during diagenesis of the surrounding sedimentary strata (Mostaghel 1985). These hydrothermal fluids were produced by compaction of the underlying Carboniferous sediments and dehydration of clays and shales accompanied by fluids expelled from deeply buried mature strata under the North Sea. As the fluids migrated through the rocks they became enriched in Pb, Zn, F and B (Mostaghel & Ford 1985). Sulphur was supplied to the fluids by bacterial reduction of sulphate and from hydrocarbons which migrated through the rocks in front of the advancing hydrothermal fluids. These fluids moved through the rocks at high temperatures ranging between 50 and 150°C (Mostaghel 1985).

Three phases of mineralization can be identified within the orefield. The first is coeval with Late Carboniferous sedimentation, when Namurian and Westphalian sediments were deposited including the Staffordshire Coal Measures. Early diagenesis and petroleum generation followed, forming framboidal pyrite by bacterial sulphate reduction. This early formed sulphide phase acted as a source for later metal sulphide deposition (Mostaghel & Ford 1985) and is observed extensively in the Coseley fossils. The main phase of ore mineralization then occurred during the Permian and Triassic. Earlier sediments were partially eroded and Permo-Triassic red beds deposited along with the migration of hydrocarbons and hydrothermal fluids. As the fluids migrated through the rocks they removed metals which then precipitated out in zones of lower pressure (Mostaghel & Ford 1985) such as within siderite bearing sediments, forming void infills.

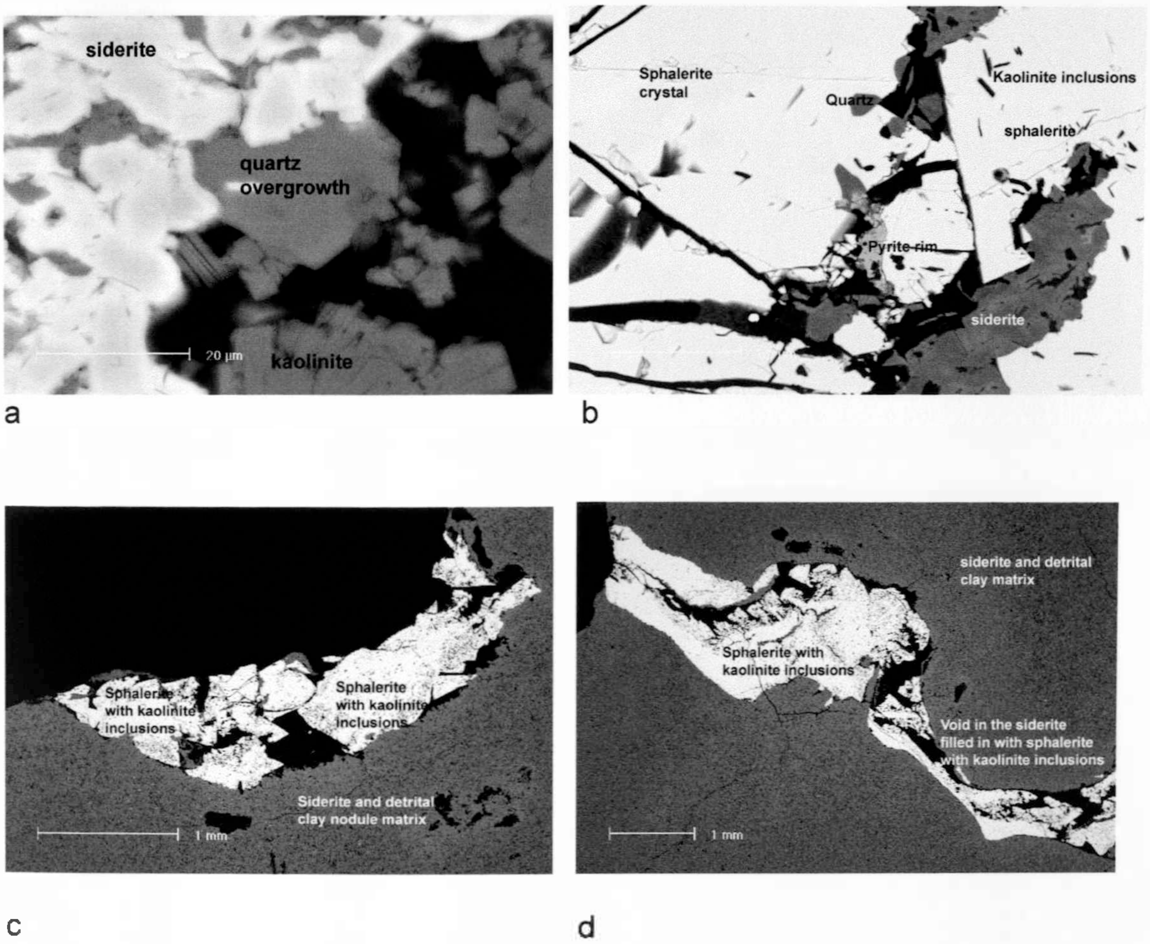


Fig. 5.14(a) Late void filling mineral textures observed in the fossils of the Coseley Lagerstätte. a) BU 4443 *Lepidodendron*, quartz overgrowths. b) Void filling sphalerite with a pyrite rim. c) Sphalerite with kaolinite inclusions. d) Sphalerite with kaolinite inclusions filling a void in the siderite.

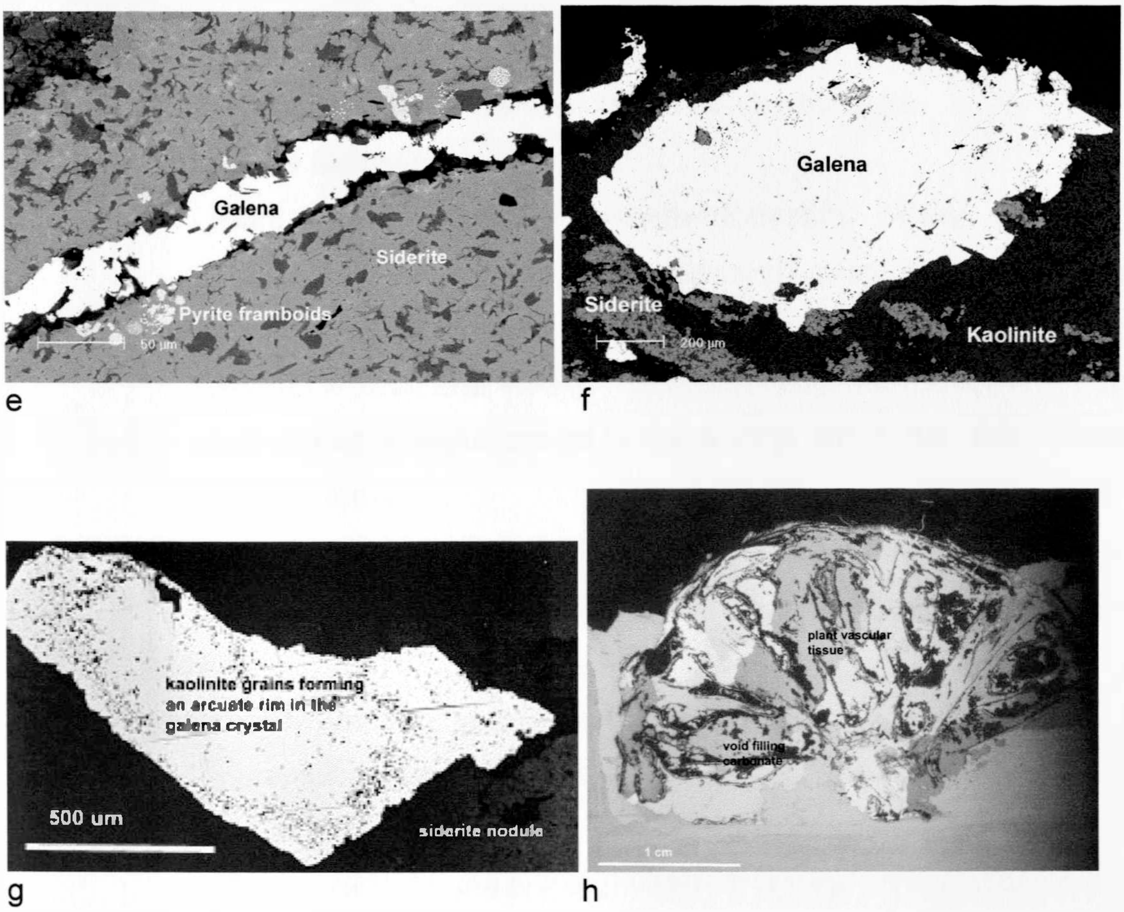


Fig. 5.14(b) (e) BU 4445 *Lepidostrobus*, galena filling a void in the siderite. f) Galena filling space within the kaolinite. g) BU 4450 *Palaeoxyris*, galena filling a void within the egg case with kaolinite inclusions. h) BU 4444*Lepidodendron*, calcite filling a plant stem.

5.5. Summary of the preservation of the Fossils of the Coseley Lagerstätte

0. Burial of the organism and initiation of decay
1. Earliest pyrite formation, framboids followed by euhedra
2. Early siderite formation:

   Plant = Microcrystalline siderite formation infilling pore spaces around detrital minerals and refractory plant tissues forming an external mould in the developing nodule.

   Animal = Microbial siderite formation around the decaying carcass forming an external mould in the developing nodule, biomineralized tissues remain.

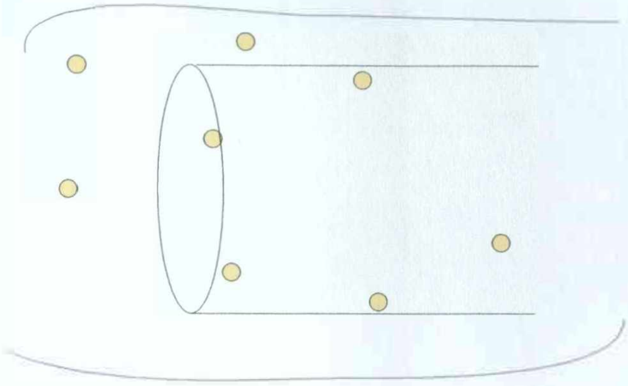
   2.1 Brittle failure and fracture formation in the concretion

   2.2 Crystalline Mg depleted non-microbial siderite formation in the animal fossils.
3. Authigenic formation of void filling kaolinite.
4. Plants = precipitation of titanium oxide mineral coatings.
5. Later siderite formation:

   Plant = Siderite precipitation recommences enlarging early siderite crystallites and occluding pore spaces.

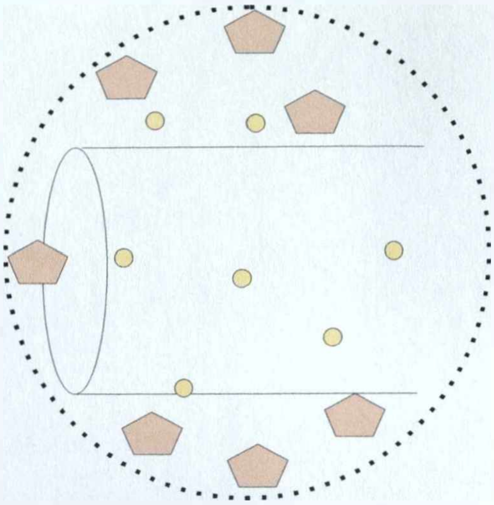
   Animal = Initiation of precipitation of crystalline siderite in void spaces, including high Mg siderite and dolomite.
6. Quartz overgrowth formation.
7. Late void filling galena and sphalerite and calcite mineralization
8. Late void filling pyrite precipitation

   (Figs. 5.15 and 5.16)

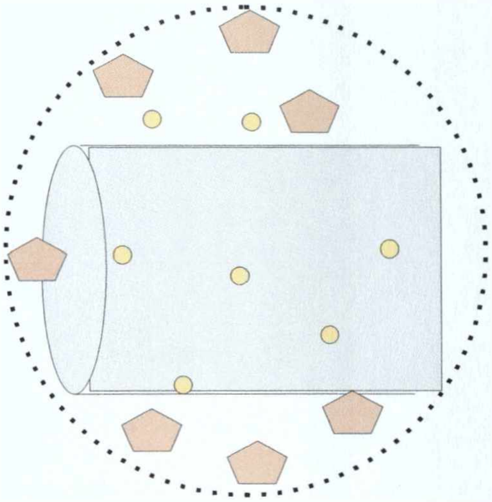


0. Burial and initiation of decay.

1. Early pyrite framboid fromation.

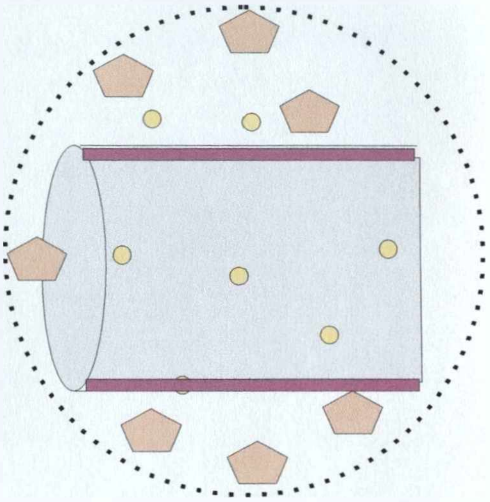


2. Early microcrystalline siderite formation around decaying plant tissues, forming an external mould in the growing nodule.

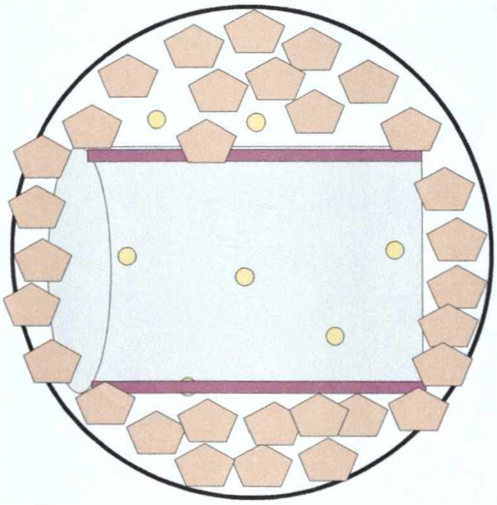


2i. Brittle failure and cracks formation.

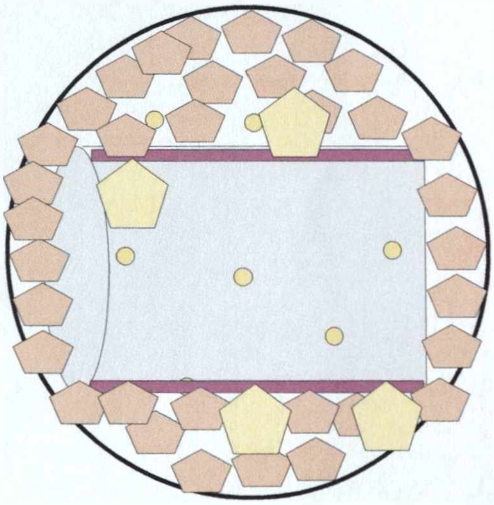
3. Formation of authigenic void filling kaolinite.



4. Precipitation of titanium oxide minera coatings over the kaolinite.

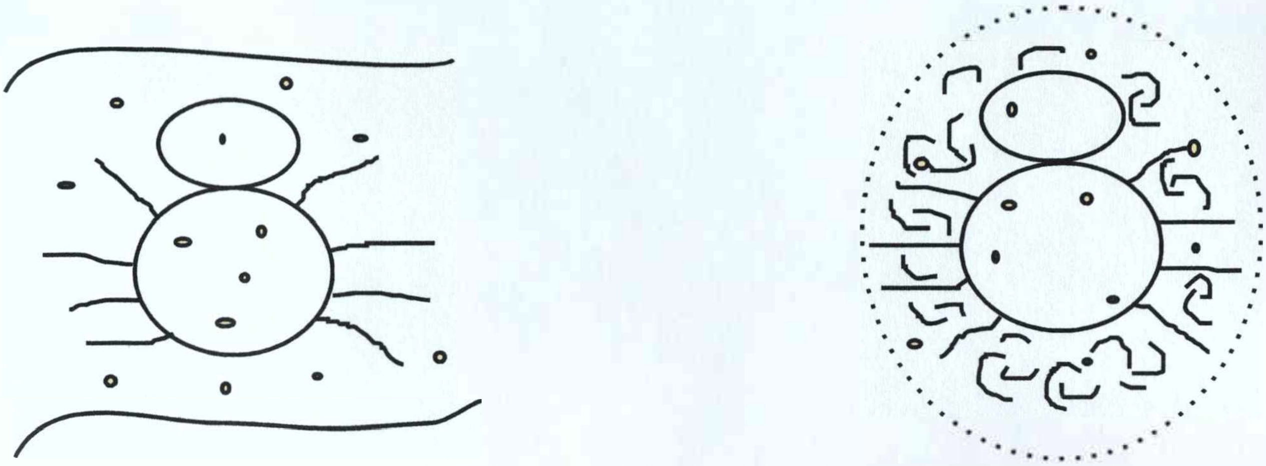


5. Siderite precipitation recommences enlarging earlier crystallites and occluding pore spaces.



6,7,8. Late stage precipitation of void mineral phases.

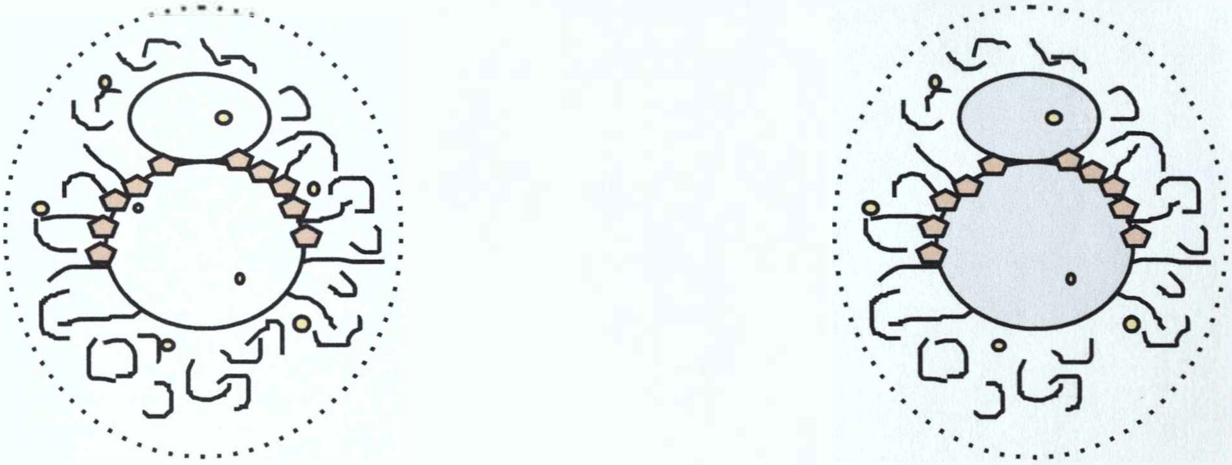
Fig. 5.15 Stages of preservation for plant fossils of the Coseley Lagerstätte.



0. Burial and initiation of decay.

1. Early pyrite framboid formation.

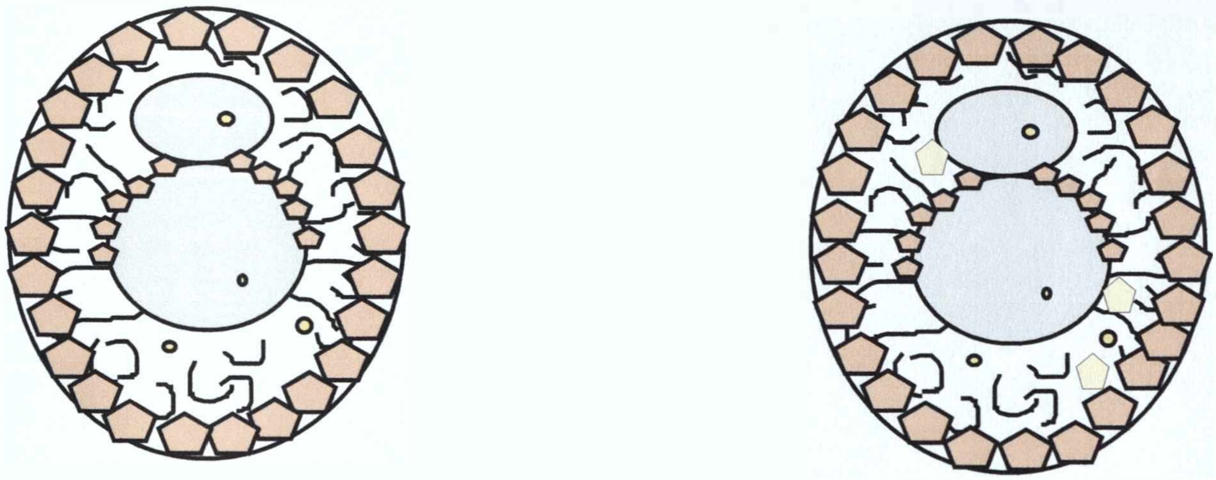
2. Microbial siderite develops around decayin
carcass. Tissues decay forming an external
mould in the siderite.



2i. Brittle failure and crack formation.

2ii. Precipitation of non-microbial siderite in
void space left by decaying carcass.

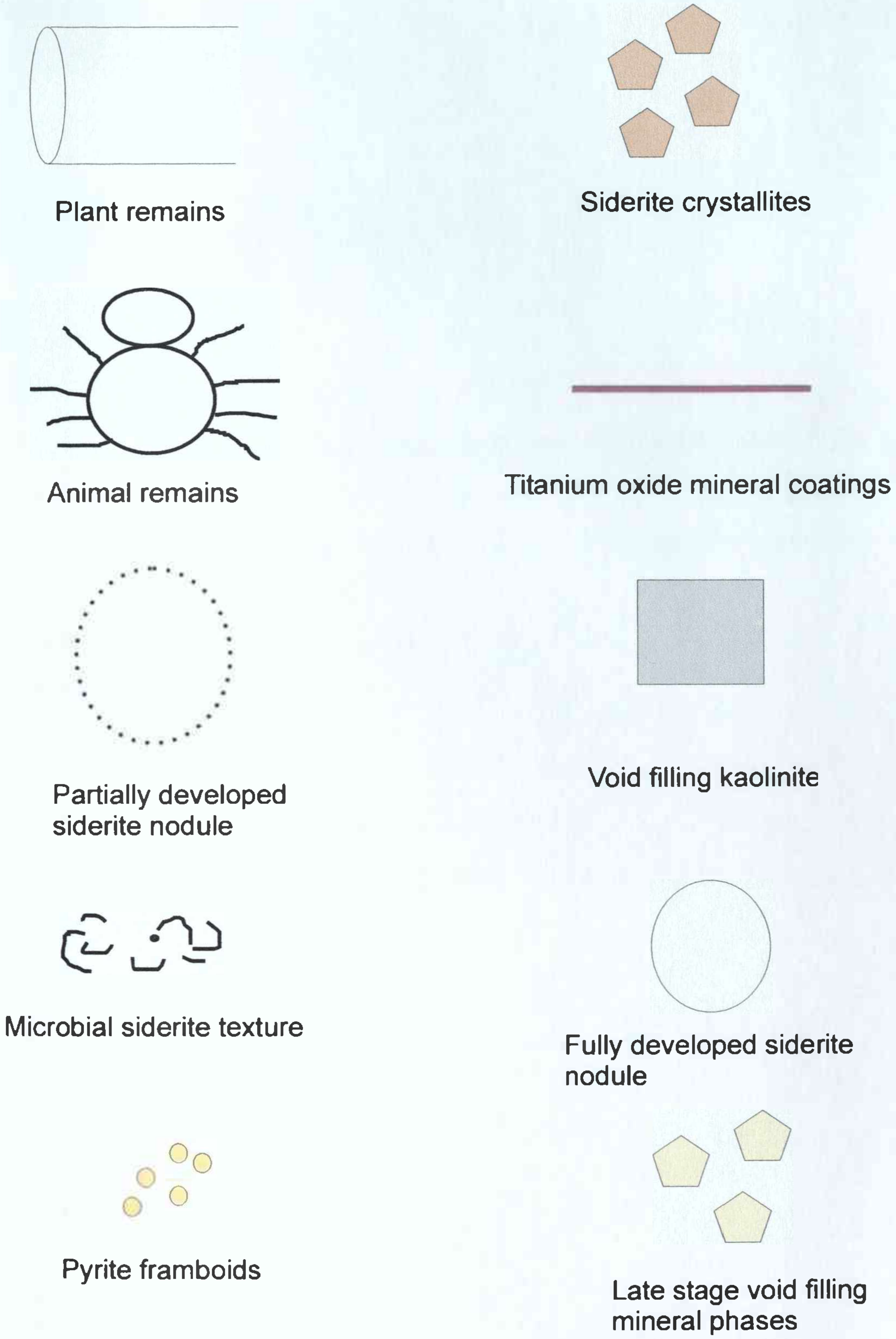
3. Precipitation of authigenic void filling
kaolinite.



5. Precipitation of crystalline siderite
in void spaces.

6,7,8. Precipitation of late stage void
filling mineral phases

Fig. 5.16 Stages of preservation for animal fossils of the Coseley Lagerstätte.



Kay to figs. 5.15 and 5.16

5.6. Comparison of the preservational style of the fossils of the Coseley Lagerstätte with other Upper Carboniferous siderite hosted Lagerstätten.

5.6.1. Preservational style of other Upper Carboniferous siderite hosted Lagerstätten.

Preservational style of the Crock Hey Lagerstätte

The overall preservation style of the fossils of the Crock Hey Lagerstätte is similar to that of the Coseley Lagerstätte. The fossils occur within siderite concretions that vary in size from 20 mm to 200 mm and are spherical to oval in shape. However the nodules containing the Crock Hey fossils are lighter in colour then the Coseley nodules. The fossils generally occur as external moulds and impressions. The fossils occur predominantly as black organic films on the surface of the nodule with some void filling sulphide and carbonate minerals.

Three main groups of fossils occur in the Crock Hey Lagerstätte: plants, arthropods and fish, however only plant specimens were available for taphonomical analysis. The preservational style of the plant fossils is summarized in Table 5.6.

Plant group	Plant organ	Original composition	Present composition	Additional minerals	Type of preservation
Sphenopsids	Stems	Cuticle of cutin and cutan	Organic carbon/ kaolinite	No	External moulds and Impression fossils
	Cones	Cuticle of cutin and cutan	Organic carbon/ kaolinite	Calcite, pyrite	External moulds and Impression fossils
Lycopsids	Cones	Cuticle of cutin and cutan	Organic carbon/ kaolinite	Occasional pyrite, calcite	External moulds and Impression fossils
	stems	Cuticle of cutin and cutan	Organic Carbon/ kaolinite	No	Impression fossil
Ferns	Leaves	Cuticle of cutin and cutan	Organic carbon/ kaolinite	No	Impression fossils
Pteridosperms	Leaves	Cuticle of cutin and cutan	Organic carbon/ kaolinite	No	Impression fossil

Table 5.6 Summary of the preservation style of the Crock Hey plant fossils.

Preservational style of the plant fossils. The Crock Hey plant fossils most commonly occur as black organic films with some clay mineralization on the surface of the nodule, this style of preservation exists across all of the plant groups. The lycopsid and sphenopsid cone and stem specimens of the Crock Hey Lagerstätte generally occur as external moulds with occasional impression fossils, three dimensional preservation is absent. (Figs. 5.17 a and b). Leaf specimens of ferns and pteridosperms occur as impression fossils with black organic rich films on the surface (Fig. 5.17 c). All of the plant fossils preserve

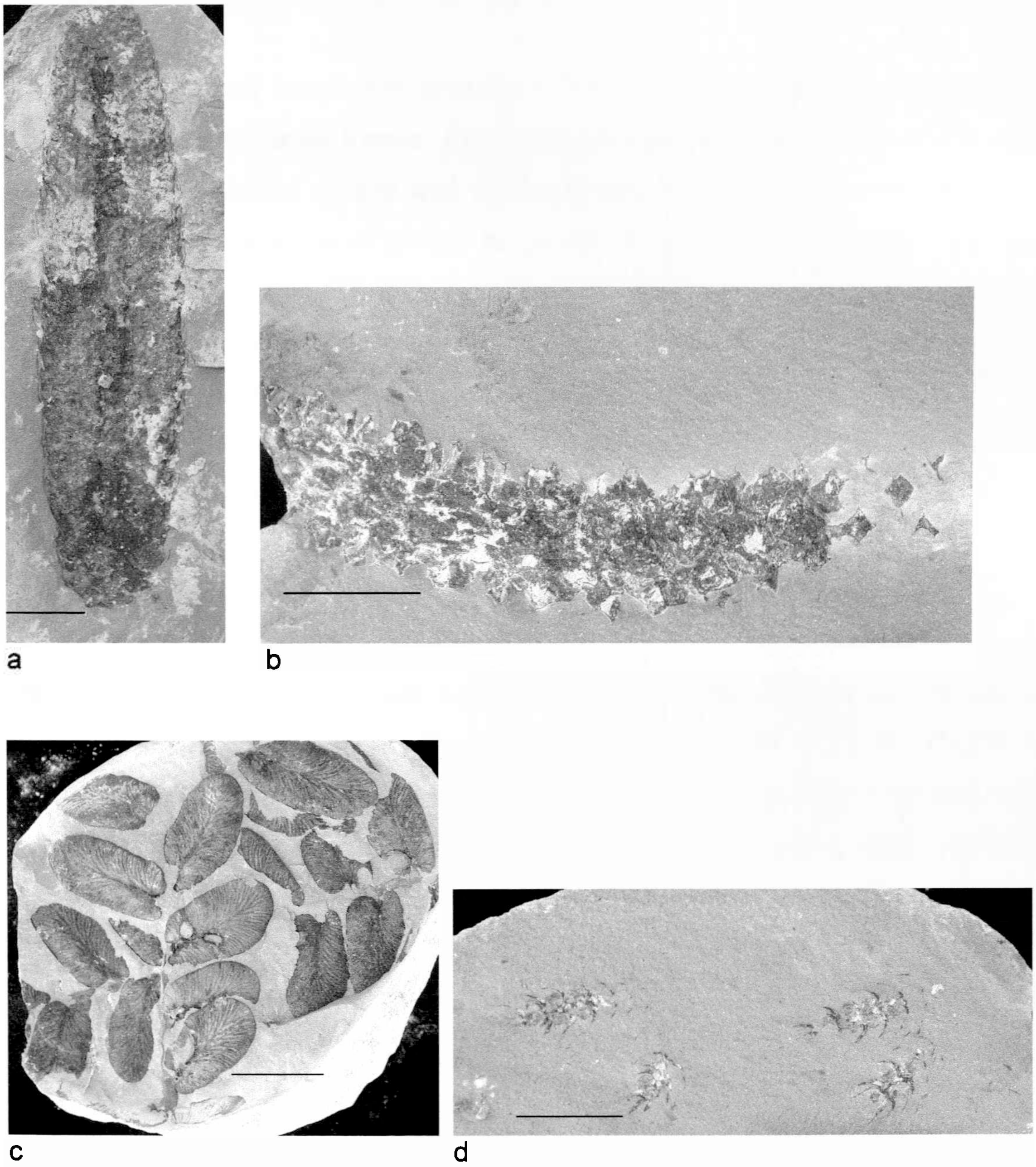


Fig. 5.17 Hand specimen photographs of plants from the Crock Hey Lagerstätte. a) BIRUG 36906 *Sigillariostrobus*, a lycopsid cone preserved as a coalified film. b) BIRUG 36885 *Palaeostachya*, a sphenopsid cone preserved as an external mould. c) BIRUG 36880 *Neuropteris*, pteridosperm leaves preserved as impression fossils. d) BIRUG 36916 calamite cone (indeterminate), with a calcite void infill. (scale bar = 1cm).

surface detail but not internal morphological detail. The black organic material occurs as a loose coalified film over the surface of the nodule.

The degree of soft tissue preservation is lower than the degree of preservation observed in the Coseley fossils. Fine hairs on reproductive, cellular and vascular structures are absent as are leaf cushions and leaf scars on plant stems. Any additional mineralization is limited to pyritic films over the organic carbon and occasional calcitic void fills (Fig. 5.17 d). The reduction in high fidelity soft tissue preservation when compared to Coseley and the abundance of coalified organic matter, indicates that the Crock Hey Lagerstätte probably represents later stage preservation than the Coseley fossils and probably represents coalification of more refractory plant tissues after the more labile ones had decayed.

Preservational style of the Mazon Creek Lagerstätte

The fossils of the Mazon Creek Lagerstätte occur inside orange to red coloured siderite concretions, the concretions have an average size of 30 to 120 mm and do not exceed 300 mm; therefore, there are no large organisms preserved. The nodules show a similar shape and size to the fossil found within them, and when split open reveal well preserved three dimensional organisms. The fossils show little compaction they are however slightly flattened towards the edge of the nodule (Baird *et al.* 1986). The preservation of three dimensional soft bodied organisms, the minimal amount of decay (e.g. bivalves are seen at the end of their escape trails), and the minimal amount of compaction indicates that organisms were rapidly buried and quickly surrounded by siderite concretions (Baird *et al.* 1986) the presence of juvenile millipedes exhibiting aggregation behaviour (Wilson in press) also indicates rapid burial. The Mazon Creek Lagerstätte therefore represents very early precompactional preservation that led to high fidelity soft tissue preservation. The preservational style of the Mazon Creek fossils is summarized in Table 5.7.

Fossil	Style of preservation	Mineralization	Other comments
Plants	3D moulds, moulds, impression fossils	Moulds in filled with coaly residue and kaolinite. Void precipitates include calcite, sphalerite and galena. Occasional permineralization in pyrite.	Fruiting organs and seed interiors are preserved uncrushed showing internal cellular detail.
Jelly fish e.g. *Essexella asherae*	Flattened composite impression	Microcrystalline pyrite, kaolinite and sphalerite on fossil surface	
Tullimonstrum gregarium	Flattened composite impression	Microcrystalline pyrite, kaolinite and sphalerite on fossil surface	
Polycheate worms	Flattened composite impression	Kaolinite and sphalerite on fossil surface	
Larval fish	Flattened composite impression	Kaolinite and sphalerite on fossil surface	
Bivalves	mould	Sediment or calcite in filled or kaolinite and sphalerite on fossil surface	
Gastropods	mould	Sediment or calcite in filled or kaolinite and sphalerite on fossil surface	
chitins	mould	Sediment or calcite in filled or kaolinite and sphalerite on fossil surface	
Crustaceans	mould	Degraded organic cuticle	
arachnids	mould	Degraded organic cuticle	
Insects	3D preservation	Degraded organic cuticle	Uncompressed 3D preservation of soft labile tissues
Coprolites	3D preservation	Pyrite, kaolinite	Uncompressed 3D preservation of soft labile tissues

Table 5.7 Summary of the preservation style of the Mazon Creek fossils (adapted from Baird *et al.* 1986).

Preservational style of the plant fossils. The plant fossils of the Mazon Creek Lagerstätte are preserved in a very similar manner to those of the Coseley Lagerstätte with cone and stem specimens of lycopsids preserved as three dimensional moulds and leaf specimens of ferns and pteridosperms and sphenopsids preserved as impression fossils. The three dimensionally preserved plant specimens commonly display a coaly residue often with a kaolinitic film; the voids are filled with calcite, sphalerite and galena. Occasionally plants may occur permineralized in pyrite (Baird *et al.* 1986). Leaf impressions, in contrast, occur as carbonaceous and kaolinitic films within the nodule (Fig. 5.18 a and b). These impression fossils preserve external morphological detail but lack any internal cellular structure. The three dimensional moulds do, however, preserve external and internal morphological detail and in some cases fruiting organs and seed are preserved uncrushed, preserving megaspores and microspores with flexible waxy membranes (Baird *et al.* 1986).

Preservational style of animal fossils. The quality of the preservation of animal fossil varies along an east to west gradient from Mazon Creek to Vermilion River in LaSalle County. This reflects an increasing taphonomic overprint of burrowing and aerobic decay associated with slower sedimentation rates near the delta margin (Baird *et al.* 1986). Where the fossils occur well preserved, soft bodied organisms such as medusae jellyfish, *Tullimonstrum gregarium*, polychaete worms and some larval fish occur as flattened impression fossils with a kaolinitic surface film that may also exhibit sphalerite or microcrystalline pyrite (Figs. 5.18 c and d). Other labile specimens such as insects and coprolites are preserved in three dimensions as degraded organic cuticle and kaolinite and pyrite respectively (Fig. 5.18 e). Bivalves, gastropods and chitons are preserved as moulds which are either infilled with sediment or calcite, or occur as kaolinite films along with sphalerite (Fig. 5.18 f). Arthropods such as crustaceans and arachnids also occur as moulds with the tissues preserve as degraded organic cuticle (Fig. 5.18 g).

Overall, the Mazon Creek Lagerstätte shows a near identical preservational style to that of the Coseley Lagerstätte. The main difference is the presence of a wider range of soft-bodied organisms and the degree of pyritization, which reflects the

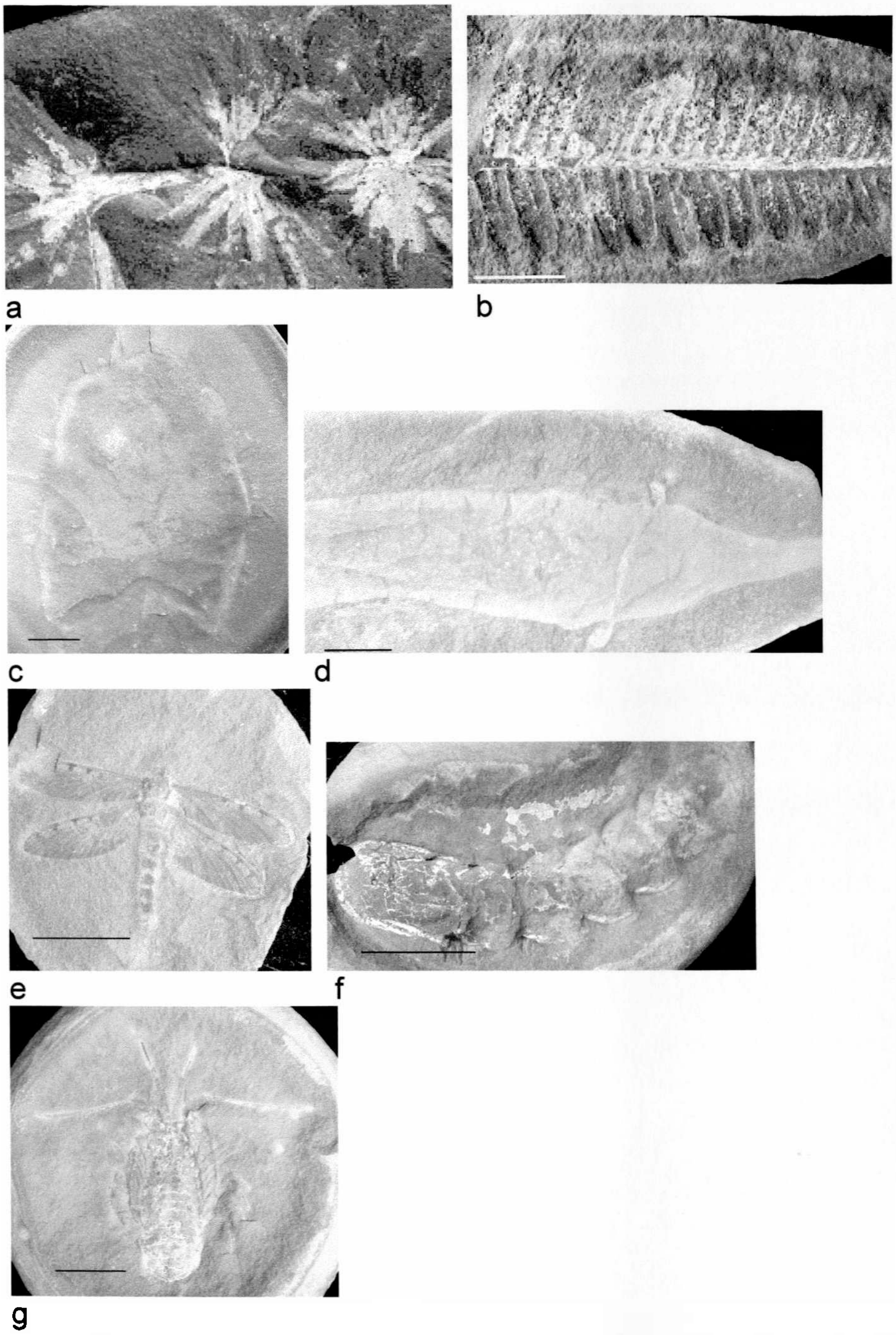


Fig. 5.18 Hand specimen photographs of the fossils of the Mazon Creek Lagerstätte. a) B4237 *Annularia* and b) B4935 *Pecopteris*, leaf impression fossils with carbonate in-fills. c) *Essexella asherae* Foster, 1979. PE 47546, impression fossil with a pyritic film. d) *Tullimonstrum gregarium* Richardson, 1966 PE 40121, impression fossil. e) *Eubleptus danielsi* Handlirsch, 1906 PE 40223, impression fossil preserving the delicate wing structures. f) *Glaphurochiton concinnus* (Richardson). PE 31886, preserved as a mould with a kaolinite film. g) Pygocephalomorpha crustacean PE 36891 preserved as a mould with a kaolinite film. Scale bars = 1cm.

differences in the original biota – that is the presence of a brackish to marine biota in Mazon Creek which is absent from the Coseley Lagerstätte.

5.6.2. Comparison of the preservational style of the Coseley Lagerstätte with that of the Crock Hey and Mazon Creek Lagerstätten.

FOSSIL TYPE	COSELEY	CROCK HEY	MAZON CREEK
Impression fossil	Yes	Yes	Yes
External mould	Yes	Yes	Yes
3d preservation	Yes	No	Yes

Table 5.8. Comparison of the preservational style between the Coseley, Crock Hey and Mazon Creek Lagerstätten.

The fossils of the Crock Hey and Mazon Creek Lagerstätten are preserved near identically to those of the Coseley Lagerstätte, except that three dimensional preservation is absent in the fossils of the Crock Hey Lagerstätte (Table 5.8).

5.6.3 Comparison of the mineral textures observed in the fossils of the Coseley, Crock Hey and Mazon Creek Lagerstätten.

MINERAL PHASE	COSELEY	CROCK HEY	MAZON CREEK
Organic carbon	Yes	Yes	No
Framboidal and polyhedral pyrite	Yes	Yes	Yes
Microbial siderite	Yes	Yes	Yes
Rhombic siderite	Yes	Yes	Yes
Void filling kaolinite	Yes	Yes	Yes
Titanium enrichment	Yes	No	No
Quartz overgrowths	Yes	Yes	Yes
Void filling sulphides	Yes	Some pyrite	Yes
Void filling carbonates	Yes	Yes	Yes
Detrital minerals	Yes	Yes	Yes

Table 5.9. Comparison of the different mineral phases present within the fossils of the Coseley, Crock Hey and Mazon Creek Lagerstätten.

Organic Carbon. Organic carbon is found preserved in the fossils of the Crock Hey Lagerstätte but not in those of the Mazon Creek Lagerstätte. The organic carbon in the fossils of the Crock Hey Lagerstätte can be seen when examined under SEM as fractured blocks and grains similar to the organic carbon present in the fossils of the Coseley Lagerstätte. However, the organic carbon in the Crock Hey fossils does not preserve any vascular tissue as is found preserved in the Coseley fossils.

Pyrite mineral textures. Pyrite is common in both the Crock Hey and Mazon Creek fossils, it is more abundant in the Mazon Creek fossils than the other two assemblages, and occurs as a fine-grained disseminated phase. The pyrite occurs as small (2 µm) polyhedral crystallites disseminated through the siderite (Fig. 5.20 a). Pyrite framboids are rare to almost absent in the Crock Hey and Mazon Creek fossils where as in the Coseley fossils framboids are abundant.

Siderite mineral textures. The siderite of both the Crock Hey and Mazon Creek fossils, like Coseley, shows two distinct phases. The first is an early formed, fine-grained, Mg-depleted phase that exhibits a distinctive clotted microbial texture (Figs. 5.19 a and b and 5.20 b). The microbial phase also occurs in the Coseley fossils but is more common in the animal component whereas it occurs in the Mazon Creek and Crock Hey plants. The second siderite phase present in both the Crock Hey and Mazon Creek fossils, also occurs in the Coseley fossils, and comprises a later stage, coarse-grained, Mg-enriched phase, where well developed rhombic siderite crystallites can be seen growing in void spaces (Figs. 5.19 c, d and e and 5.20 c).

Kaolinite mineral textures. Void filling kaolinite is present in all three of the fossils assemblages as small elongate particles and larger blocky masses (Figs. 5.19 c and f and 5.20 c, d and e).

Titanium enrichment. The unusual titanium oxide enrichment of kaolinite was only observed in the Coseley plant fossils and not in the Crock Hey or Mazon Creek assemblages.

Later void filling minerals. Void filling sulphide minerals are more limited in the Mazon Creek and Crock Hey assemblages when compared to the fossils from Coseley. The Crock Hey Lagerstätte shows very little void filling mineralization with only several specimens exhibiting pyrite void fills. Whereas the Coseley fossils show a more extensive a wider range of void filling minerals including sphalerite and galena. Carbonate void infills occur in all three assemblages and is limited to just calcite precipitation (Fig. 5.20 f). All three assemblages also exhibit quartz overgrowths and a similar detrital mineral component.

5.6.3. Summary of the Coseley, Crock Hey and Mazon Creek Lagerstätten.

Overall the fossils of the Coseley, Crock Hey and Mazon Creek Lagerstätten show a very similar mode of preservation where decaying tissues were surrounded by an early Mg-depleted microbial-textured siderite or siderite crystallites along with fine grained disseminated and framboidal pyrite. The tissues then decayed leaving a void that was in-filled with authigenically derived kaolinite followed by Later Mg-rich rhombic siderite crystallites. Any residual pore space was then in-filled by a range of void filling sulphide and carbonate minerals.

Organic carbon was observed in both the Coseley and Crock Hey plants, but vascular tissue was only preserved in the Coseley plants indicating slightly earlier preservation. Organic carbon was not observed in the Mazon Creek plants, but this may be due to the fact that only leaf specimens were available for destructive analysis and no cone or stem specimens that would have contained more 'woody' material were analyzed. Kaolinite was observed in the fossils from all three Lagerstätten where it had the same texture, indicating similar mode of formation.

The siderite from all three Lagerstätten was also similar comprising two phases, the earlier Mg-depleted microbial phase and the later Mg-rich rhombic phase. This also indicates a similar method of precipitation between all three Lagerstätten, where by bacterially mediated siderite precipitate first, consuming the majority of the iron in this system, and later stage siderite grew into voids and incorporated Mg into its structure. The only differences between the Lagerstätten was that the microbial siderite was not observed in the Coseley plants but was observed in the Mazon Creek and Crock Hey plants.

The Mazon Creek fossils contained a higher proportion of fine-grained disseminated pyrite when compared to Coseley indicating that there was more sulphate available in the system. Mazon Creek was a deltaic system and sulphate could have been derived from sea water. However the Coseley fossils contained a higher proportion and more diverse range of void filling sulphide minerals indicating higher degrees of hydrothermal fluid mineralization in the South Staffordshire Coal Field or more residual pore space left in the Coseley fossils then in the fossils of the other two localities.

All three assemblages had similar detrital minerals within the siderite and comprised illite and smectite clays, feldspars and micas with quartz overgrowths indicating similar sedimentary sources.

These observations indicate that the fossils of the Coseley, Crock Hey and Mazon Creek Lagerstätten underwent similar preservational processes indicating common links between the physical and chemical processes operating within the three assemblages. This may have important implications for the mode of formation of other siderite hosted Lagerstätten which may, when examined, have formed in the same way. To produce a universal model for preservation in siderite–hosted Lagerstätten, the controls on the taphonomical processes as well as the processes themselves must be examined, so that the key parameters for fossils preservation and siderite concretion formation can constrained.

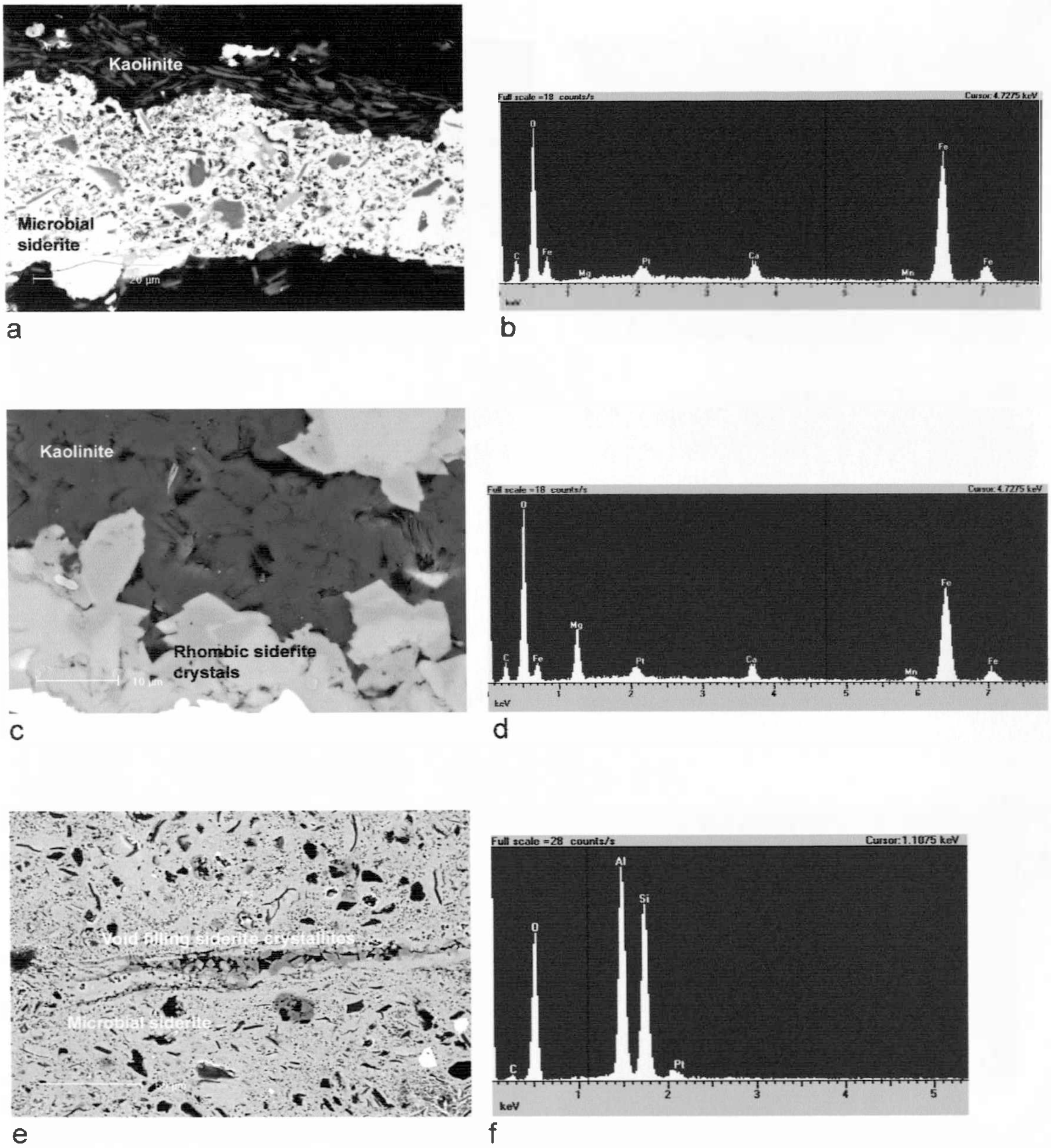


Fig. 5.19 Mineral textures observed in the fossils of the Crock Hey Lagerstätte. a) Plant cone (indeterminate), Microbial siderite with kaolinite overlying. b) Plant cone (indtr), analysis of the early low Mg siderite. c) Plant cone (indeterminate), Late stage Mg enriched rhombic siderite crystallites. d) Plant cone (indeterminate), analysis of late stage Mg enriched siderite. e) Plant cone (indeterminate), rhombic siderite crystallites growing in a void in the early siderite. f) Plant cone (indeterminate), analysis of the kaolinite.

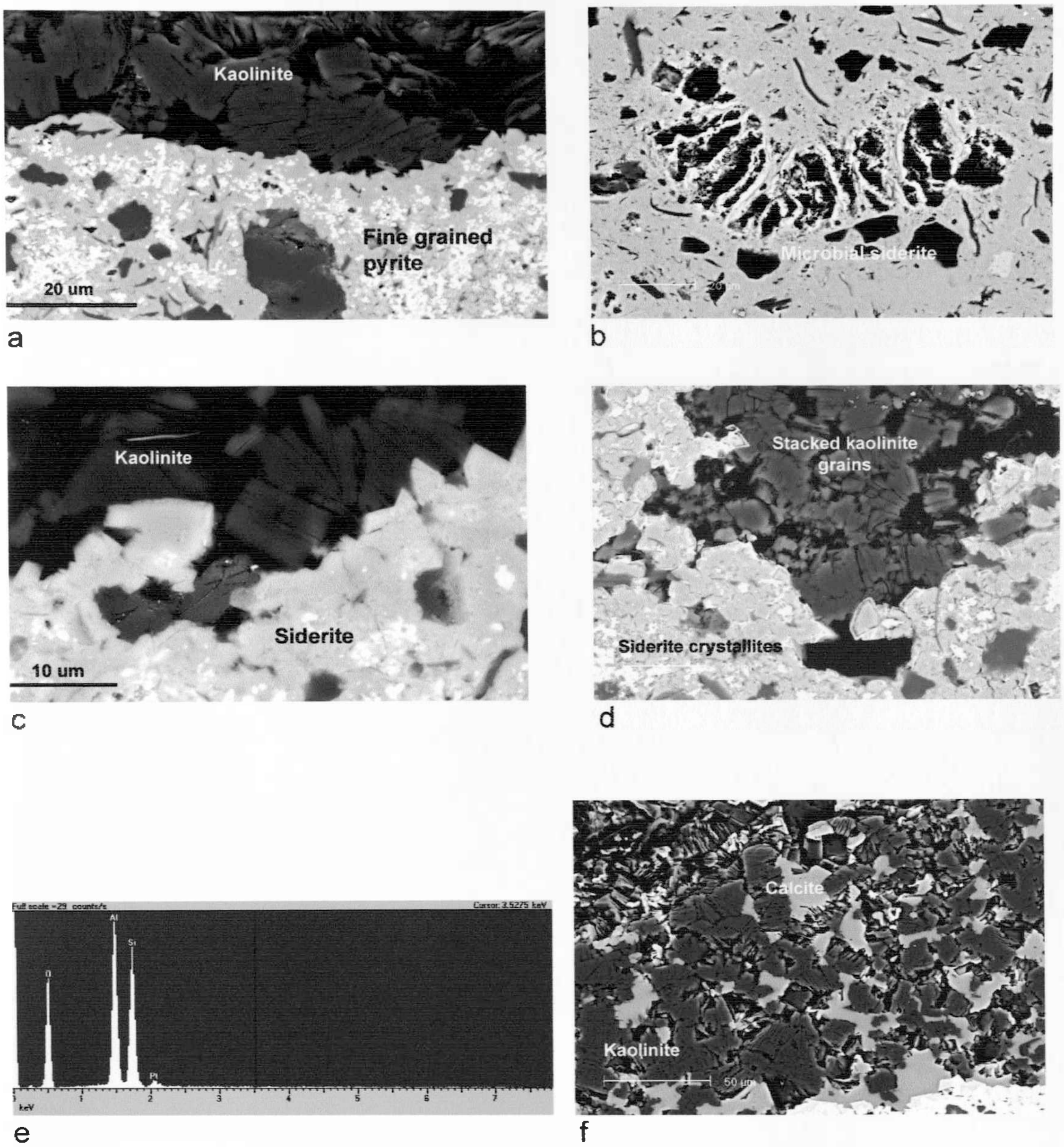


Fig. 5.20 Mineral textures observed in the fossils of the Mazon Creek Lagerstätte. a) BIRUG B4237 *Pecopteris,* fine grained pyrite within the siderite nodule. b) BIRUG B4935 *Annularia*, microbial siderite textures. c) BIRUG B4237 *Pecopteris,* rhombic siderite crystallites. d) BIRUG B4237 *Pecopteris,* stacked kaolinite grains. e) BIRUG B4935 *Annularia*, analysis of the kaolinite. f) BIRUG B4935 *Annularia*, void filling calcite around kaolinite grains.

6. Taphonomical and preservational controls on the siderite–hosted Coseley Lagerstätte.

6. 1 Death, decay and burial

The fossils of the Coseley Lagerstätte are dominated by articulated, flattened impressions of volatile soft tissues and more three dimensionally preserved refractory ones. This can be explained by the mode of death and burial of the organisms. The majority of the Coseley fossils died autogenically and were then either transported to, or settled down through, the swamp lakes to the preserving environment at the bottom. During this time period between death and burial a taphonomic window for the onset of decay occurred. This period of decay varied between the aquatic and terrestrial biota's. The aquatic organisms sank to the lake bed relatively rapidly after death and the majority of small specimens remained articulated whereas plants that were transported in from terrestrial locations had longer to decay and are generally disarticulated.

The coal swamp environments of the Carboniferous were also conducive to preservation of the Coseley fossils. The bottom waters were anoxic therefore reducing the level of aerobic bacterial decay undergone by soft tissues upon burial. The sedimentation rates were relatively high so organic remains were quickly buried therefore helping to exclude oxygen, and thirdly the lake bottoms received a high level of organic input which also helped to remove oxygen from the porewaters.

6.2 Oxygen supply, availability of ions and pH levels.

The main factors that controlled the preservation of the Coseley fossils and determined what mineral phases were precipitated were oxygen and pH levels and the composition and availability of ions in the surrounding pore waters. As mentioned above aerobic respiration was limited in the lake bottoms due to the huge amounts of decaying organic matter which consumed any available oxygen more quickely than it could diffuse in from the surrounding environment. In the resulting anaerobic environment bacterial decay commenced using other electron acceptors. Bacterial sulphate reduction commenced first using sulphate from the oxidation of either iron sulphide or organic sulphur. This phase of pyrite formation occurred in the uppermost sedimentary layers and was limited by the low levels of sulphate in the pore waters. This sulphate source along with the anoxic conditions led to the precipitation of framboidal and euhedral pyrite within plant vascular tissues and in the sediment surrounding the decaying organisms. Hydrogen sulphide reacted with iron minerals and transformed iron monosulphides to pyrite:

$$18CH_2O + 9SO_4^{2-} + 6FeOOH > 18HCO_3^- + 3FeS + 3FeS_2 + 12H_2O$$

(Canfield & Raiswell 1991)

6.3 Controls on siderite formation

In a freshwater setting sulphate concentrations would have been limited and rapidly consumed, once sulphate reduction had ceased bacterial decay proceeded further down in the sediment profile by methanogenesis. The main controlling factor on siderite formation is the level of dissolved sulphide in the sediment porewaters (Postma 1982). If sufficient hydrogen sulphide Is produced by bacterial sulphate reduction then precipitation of pyrite and other iron sulphides will never allow ferrous iron concentrations to reach levels whereby siderite becomes stable (Postma 1982). Once levels of dissolved sulphide had fallen, after frambiodal pyrite formation, to rates that inhibited bacterial sulphate reduction, siderite precipitation commenced. Siderite formation requires sources of ferrous iron and bicarbonate and can be produced by a variety of pathways:

- By the reduction of ferric oxyhydroxides by organic matter (Postma 1982):

$4FeOOH + CH_2O + 3H_2CO_3^- > FeCO_3 + 6\ H_2O$

- By direct Fe (III) reduction:

$Fe^{2+} + HCO_3^- > FeCO_3 + H^+$ (Raiswell & Coleman 1993)

$Fe^{2+} + OH^- + HCO_3^- > FeCO_3 + H_2O$ (Al-Agha *et al.*1995)

If iron reduction occurs in a system with abundant dissolved biocarbonate produced form deeper reactions, for example methanogenesis of buried organic matter, then siderite precipitation will occur. Iron reduction will produce a positive chemical feedback causing extensive concretionary growth, as in the Westphalian Hepworth concretions from Yorkshire, UK (Coleman & Raiswell 1993).

The formation of siderite will obviously be limited by the supply of bicarbonate and ferrous iron. Iron will only be available for incorporation into carbonates once it has been reduced and available in solution (Raiswell & Coleman 1993). Iron reduction however also introduces bicarbonate into the system so siderite production will be accompanied by high level of iron reduction (Pye *et al.* 1990). pH will also influence siderite production as low pH levels brought about by high H^+ levels, lead to carbonate dissolution whereas neutral pH levels or low H^+ levels will promote carbonate production. The reduction of Fe (III) to ferrous iron in solution consumes H^+ during the generation of bicarbonate therefore promoting siderite precipitation (Raiswell & Coleman 1993).

In summary siderite precipitation and concretion growth will occur under the following conditions (Fig. 6.1):

- Anoxic porewaters
- Low levels of dissolved sulphide
- High rates of iron reduction

- High rates of biocarbonate production
- Low H^+ levels

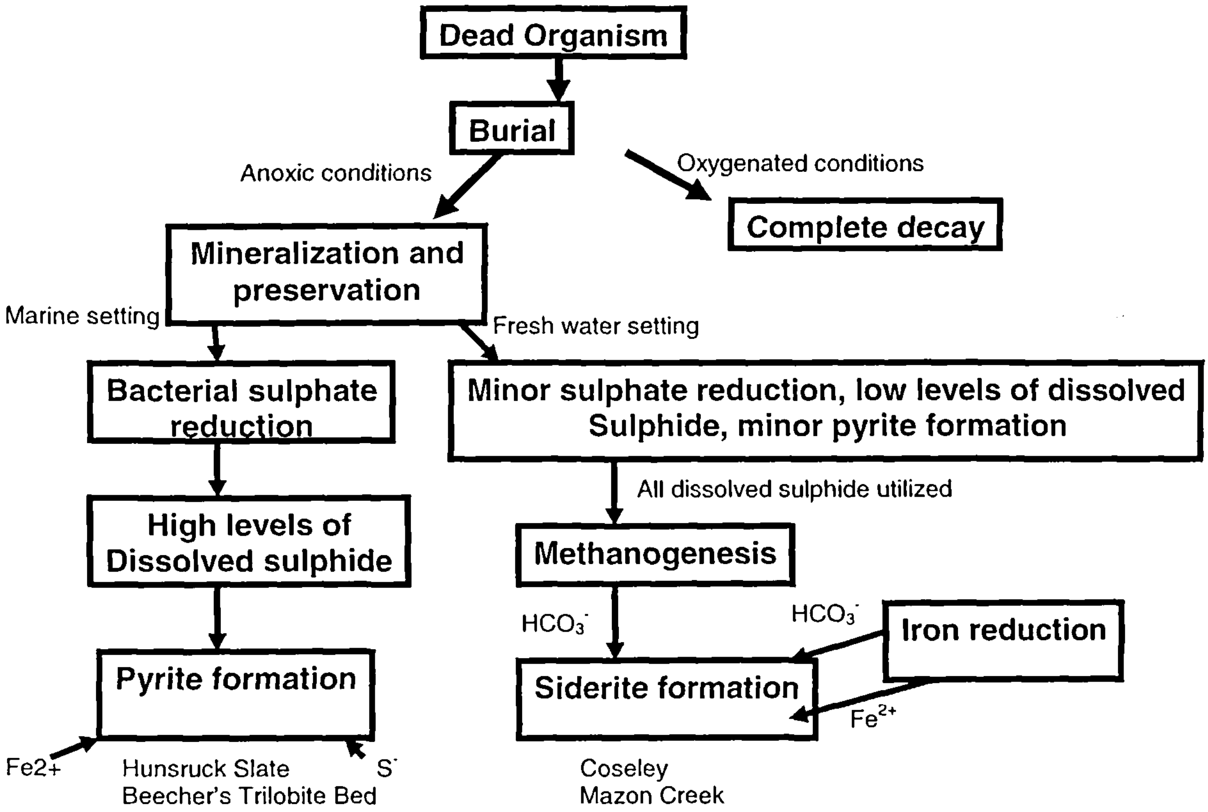


Fig 6.1 Flow diagram showing the formation of siderite

Siderite precipitation in the Coseley lake sediments occurred around decaying plant and animal remains encasing them in concretions. It is probable that the decaying carcasses acted as nuclei for concretion growth as they were sites of bacterial colonization (Pye *et al.* 1990) and siderite precipitation is bacterially mediated. The siderite precipitated as fine-grained euhedral microcrysts around plant remains and as a microbialite around animal ones. The difference in siderite texture is probably linked to the degree of bacterial colonization of the organic matter. Siderite precipitated as euhedra with low levels of bacterial activity and as a microbialte with higher levels of bacterial activity. The bacterial levels depended on the nature of the decaying organic matter, animal carcasses had more labile soft tissues to decay and promoted higher levels of bacterial activity and microbilate formation whereas plant remains were composed of mainly refractory lignins and cutins and led to lower levels of bacterial activity and crystalline siderite formation.

Regardless of the texture of the concretionary siderite, preservation occurred in the same manner. The nodules formed around the decaying organisms encasing them in siderite, the majority of the tissues then decayed leaving an external mould in the surrounding siderite. The moulds preserve external morphological detail, occasionally in three dimensions.

The precipitation of the siderite altered the chemical conditions within the pore waters particularly affecting the concentration of H^+ ions. The precipitation of the siderite had consumed bicarbonate ions and generated H^+ ones:

$Fe^{2+} + HCO_3^- > FeCO_3 + H^+$ (Raiswell & Coleman 1993)

The rapid precipitation of siderite led to a build up of H^+ ions in the pore waters and the generation of more acidic conditions, these acidic pore waters were not conducive to carbonate precipitation (Raiswell & Coleman 1993) which halted allowing the formation of more H^+ and cation depleted mineral phases (Gabbott 1998). This alteration of pore water chemistry was probably localized and restricted to the pore waters around the carcass. Chemical gradients were established and cations such as Si^{4+} and Al^{3+} diffused in to the carcass from the surrounding environment (Sagemann *et al.* 1999), bacteria within the fossils then utilized these ions to form void-filling authigenic kaolinite.

The siderite concretions at this point still had a large residual porosity, the H^+ ions and other decay products could eventually diffuse away from the decaying carcass leading to a recovery in pH levels. This rise in pH was associated with the re-commencement of siderite precipitation leading to the growth of original siderite crystallites and the growth of new void filling precipitates, which filled residual concretion porosity. The precipitation of earlier siderite along with lower levels of iron reduction associated with increasing depth of burial, allowed Mg to diffuse in from the overlying water column causing an increase in Mg/Fe ratios in the surrounding pore waters (Fisher *et al.* 1998). An increase in Mg within the pore waters caused a corresponding increase in Mg substitution in the developing siderite (Curtis *et al.* 1986) as Mg was utilized in replace of iron. This second phase of siderite precipitation is therefore characterized by a Mg-rich phase that occurs either as Mg rich outer zones on previous crystallites or as Mg-rich void filling crystallites.

The second and final phase of siderite precipitation filled in the majority of the residual pore space forming a brittle nodule that preserved the Coseley fossils as external moulds. Later Permo–Triassic hydrothermal fluid activity led to the precipitation of void filling sulphides that vary between specimens depending on the degree of pore space that was available to be filled.

Ion source. The type of mineral species that develops as a result of bacterial mediation will always depend on what ions are available locally for the bacteria to utilize. The pore waters of the Coseley lacustrine sediments were depleted in dissolved sulphate, hence limiting bacterial sulphate reduction and pyrite formation. The lack of sulphate in the sediments prevented complete pyrtization of the fossils and allowed precipitation of siderite. The sulphate for pyritization was probably sourced from oxidation of organic sulphur in the decaying organic matter that covered the lake floors. Other important ions for siderite precipitation were ferrous iron and bicarbonate. Iron would have been readily available in the surrounding pore waters and bicarbonate produced by methanogenesis of deeper buried organic matter. Mg for late siderite formation could either have been available from the overlying water column or released during clay mineral reactions in the surrounding pore waters (Fisher *et al.* 1998). The breakdown of clay minerals such as smectite and illite could also account for the source of the Al and Si ions that diffused into the carcasses for bacterially mediated kaolinite formation.

6. 4 conclusions

The preservation of the fossils of the Coseley Lagerstätte was due to complex interactions between a series of environmental, chemical and bacterial processes. Firstly the rapid burial of the organisms after death in an anoxic environment with rapid sedimentation rates and high organic inputs ensured initial preservation of the organisms. This was then followed by a series of linked chemical and biologically mediated reactions that resulted in the precipitation of several mineral phases that secured the continued preservation of the fossils.

Concretionary fossil assemblages such as Coseley and Mazon Creek represent rapidly buried, un-compacted, exceptionally preserved, stratiform conservation stagnation deposits. Importantly the assemblage is composed of an allochthonous collection of articulated and fragmentary fossils that died autogenically and were then transported to the preserving environment. This indicates that obrution and other mass mortality events are not always necessary for exceptional preservation. The key to the development of a fossil Lagerstätte is a short time period between death and burial. The longer this taphonomic window the more disarticulated and decayed the carcasses become and the more information is lost. The fossils of the Coseley Lagerstätte, particularly the aquatic organisms, which in general remain articulated, were rapidly buried after death, due to high sedimentation rates, leading to an assemblage of exceptionally preserved fossils that more faithfully reflect the original life assemblage. The length of time between death and burial of the plant and animal fossils differs, a short decay period occurred between the death of the small aquatic organisms, which are generally articulated where as terrestrial plants which are generally disarticulated.

The environment of preservation of the Coseley fossils was also conducive to preservation as the fine-grained sediments and high inputs of organic detritus excluded oxygen and halted aerobic bacterial decay. The limited availability of sulphate in the surrounding pore waters restricted pyrite development to early framboidal growth, this along with the generation of ferrous iron and bicarbonate from iron reduction led to the precipitation of siderite. The degree of bacterial colonization of the decaying carcasses controlled the texture of the developing siderite, with animal carcasses promoting high levels of bacterial colonization and the formation of microbial films, and the plants with less labile tissues promoting less bacterial colonization and crystalline siderite development. Extensive siderite precipitation altered pH levels of the pore waters by consuming bicarbonate and releasing hydrogen ions, the resulting acidic conditions encouraged the formation of bacterially mediated kaolinite. A subsequent rise in pH then encouraged a second phase of siderite formation, a decrease in iron reduction with increased depth of burial allowed Mg to diffuse in and be substituted for iron in the developing siderite, leaving the fossils preserved as external moulds in the encasing siderite with kaolinitic void fills.

7. Conclusions

7.1 Palaeoenvironment of the Upper Carboniferous Coseley Lagerstätte

The Coseley fossils were recovered from lacustrine siltstones at Clay Croft open cast coal mine near Coseley, this comprises one of five different lithofacies of the Coal Measure Group sediments. Together these sediments form a lacustrine delta complex that had formed within a freshwater swamp forest within what is now the South Staffordshire coalfield.

The Coseley Lagerstätte comprises over 2000 specimens dominated by an allochthonous plant assemblage of isolated fragments of stems, leaves, cones, seeds and pollen sacs of lycopsids, sphenopsids, ferns and pteridosperms. The lycopsids are dominated by *Lepidodendron*, the sphenopsids by *Calamites*, the ferns by *Pecopteris* and *Sphenopteris* and the pteridosperms by *Neuropteris.* The plants can be divided up into three vegetational habitats as proposed by Cleal and Thomas (1994): the flood basin dominated by the lycopsids, areas surrounding open water dominated by the sphenopsids and the river levees dominated by the pteridosperms.

The Coseley fauna comprises molluscs, a diverse assemblage of arthropods, and vertebrates: it is dominated by freshwater bivalves, xiphosurans, crustaceans and fish with terrestrial organisms such as arachnids, hexapods and myriapods comprising a very small fraction of the biota. The Lagerstätte can be divided into a transported and an autochthonous component with the aquatic organisms and the calamite horsetails comprising the autochthonous component and the terrestrial organisms, the pteridosperms, ferns and lycopsids comprising the transported component. Animals dominate the autochthonous component due to higher preservation potential as the organisms were living within the preserving environment compared with the terrestrial animals, where as plants dominate the transported component. Pteridosperms are the dominant plant fossil in the assemblage due to taphonomic bias, they grew on the river levees above rivers so when the leaves fell off they directly transported to the preserving environment, where as lycopsids would have been the dominant plant at the time as they occupied a much more extensive area then the pteridosperms.

The trophic structure of a typical Carboniferous swamp forest community can be constructed from the information provided by the Coseley fossils. An aquatic web can be constructed where epifaunal suspension feeders such as bivalves and small scavengers such crustaceans support larger predators like the xiphosurans and smaller fish, with large fish such as the xenacanthids occupying the highest trophic niche. The trophic structure for the terrestrial organisms can also be constructed where small detrivores such as millipedes supported small arachnids and other insects with larger arachnids such as the trigonotarbids lying at the top of the food chain.

7.2 Palaeoenvironment, palaeoecology and biostratinomy of other Upper Carboniferous siderite–hosted Lagerstätten

An open cast coal mine at Crock Hey near Merseyside exposes, Westphalian A, Lower Coal Measure sediments that contain *in situ* fossiliferous siderite concretions. The sedimentary lithofacies exposed here are the same as those exposed at Saltwells nature reserve in Dudley, therefore Crock Hey also represents a lacustrine delta complex like Coseley. Slight sedimentological differences do occur as very coarse and fine grained sediments are absent at Crock Hey indicating that it represents a more intermediate position on the flood basin with respect to Coseley.

Around 1500 fossils have been collected from Crock Hey and include plants, arthropods, bivalves and fish specimens. The plants form an allochthonous assemblage of fragmentary leaf, stem, cone and seeds of lycopsids, sphenopsids, ferns and pteridosperms similar to the plant assemblage of the Coseley Lagerstätte. These plants can also be divided into the three vegetational habitats as proposed by Cleal and Thomas (1994). A distinct difference compared to Coseley occurs with the Lycopsids which are dominated by *Sigillaria* and not *Lepidodendron* indicating a higher clastic input or more peripheral position of the Crock Hey flood basin. The surrounding compression flora has also been analysed as the nodules were found *in situ*, this reveals a very similar plant assemblage as that found in the nodules but with less cone and seed specimens indicating earlier preservation in the nodules preserving more labile tissues compared with the compression flora. Large *in situ* fossilized tree trunks also occur here preserved in sandstone horizons. These form a transect through the flood basin with calamites dominate at one end representing the forest edge around areas of open water and lycopsids dominant at the other end representing the forest middle. The presence of these fossil trees supports the Cleal and Thomas model (1994) where different plant species grow in different habitats.

The animal fossil assemblage is almost identical to that of Coseley and the same trophic webs can be applied to these organisms. The animal fossils were collected *in situ* therefore the exact stratigraphic position was known. The main fossil bearing horizon was dominated by terrestrial organisms at the base and aquatic ones at the top indicating deepening water conditions, so aiding with the palaeoenvironmental interpretation. The biostratinomical analysis was also very similar to the analysis of the Coseley fossils, collecting bias could be more easily distinguished with the Crock Hey assemblage and had led to a disproportionate amount of cone specimens being collected.

The Mazon Creek Lagerstätte is the American equivalent to Coseley and comprises a terrestrial and freshwater component and a brackish to marine component all preserved in siderite concretions. The Palaeoenvrionment of Mazon Creek was different to that of Coseley and comprised a river influenced coastal system. The terrestrial and freshwater Braidwood biota is very similar to the Coseley biota whereas the brackish to marine Essex biota does not have any species in common with Coseley. The Braidwood biota comprises an allochthonous plant assemblage of isolated organs of lycopsids, sphenopsids, ferns and pteridosperms, very similar at group and generic level to the Coseley plants. These plants would have grown in a forest swamp and then transported after death to the coastal system.

The Braidwood animal component is dominated by bivalves and arthropods very similar at generic level to the Coseley animal fossils, a striking difference occurs with the vertebrate fossils where a more diverse fish assemblage occurs along with tetrapod and reptile remains, which do not occur in the Coseley biota. The aquatic and terrestrial food webs from Coseley can be applied to the Braidwood fossils with some minor amendments, the tetrapods and reptiles would have formed the top predators. The Essex biota in contrast comprises a more abundant and diverse assemblage the either the Coseley or Braidwood biota's and is dominated by soft-bodied sessile and planktonic organisms which include some species unique to the Mazon Creek such as the problematic form *Tullimonstrum gregarium.*

7.3 Exceptional fossil preservation and mineral paragenesis in siderite hosted Lagerstätten.

The fossils of the Coseley Lagerstätte occur as hard parts and mineralized soft tissues with varying degrees of lability sealed within siderite concretions. The fossils occur as tissue outlines and more refractory tissues that are uncompressed. They do not show any very labile tissue indicating that mineralization was delayed until very soft tissues had decayed. The Coseley organisms died and were the transported to the preserving environment indicating that obrution is not always necessary for exceptional fossil preservation.

Plant preservational style:

Lycopsids: Three dimensional moulds, external moulds with varying degrees of relief, exhibit a wide range of void filling minerals.

Sphenopsids: External moulds, impression fossils.

Ferns: Impression fossils

Pteridosperms: Impression fossils

Animal preservational style:

Molluscs: external moulds preserving only external morphological detail.

Arthropods: external moulds preserving only external morphological detail.

Fish: Teeth as three dimensional fossils still as apatite.

Scales as external moulds preserving external detail and some original apatite.

The Preservation of the Coseley fossils occurred in at least seven different stages:

1. Burial and initiation of decay
2. Early pyrite formation.

Framboidal pyrite development through bacterially mediated sulphate reduction.

3. Early siderite formation.

Siderite precipitation in the zone of methanogenesis around a decaying carcass, forming an external mould in the developing concretion, either as crystalline siderite or a microbalite.

4. Bacterially mediated authigenic, void filling kaolinite formation.
5. Titanium oxide mineral coatings.

An unusual aspect of the plant fossils is the development of a titanium oxide mineral coating over the kaolinite formed during decaboxylation of the surrounding coals.

6. Late siderite formation.

Secondary precipitation of magnesium enriched siderite either as enlargement of existing crystallites or the growth of new ones infilling residual porosity.

7. Late void filling mineralization.

Infilling of any pore space by quartz overgrowths, sulphides that include sphalerite, pyrite and galena and carbonates. Mainly associated with the formation of the Permo-Triassic South Pennine Orefield.

The fossils of the Crock Hey and Mazon Creek Lagerstätte also show a very similar style and mode of preservation where decaying tissues were surrounded by a magnesium depleted microbial or crystalline siderite phase along with framboidal pyrite development. The tissues then decayed leaving an external mould in the nodule that became in filled with kaolinite, secondary siderite and sulphides. The similarity in preservational style between these three different fossil assemblages indicates that similar preservational processes operated between them indicating that this model for preservation can be applied to other siderite hosted Lagetrstätten.

Concretionary fossil assemblages such as Coseley and Mazon Creek represent rapidly buried, un-compacted, exceptionally preserved, stratiform conservation stagnation deposits. Importantly the assemblage is composed of an allochthonous collection of articulated and fragmentary fossils that died autogenically and were then transported to the preserving environment. This indicates that obrution and other mass mortality events are not always necessary for exceptional preservation. The key to the development of a fossil Lagerstätte is a short decay period between death and burial. The fossils of the Coseley Lagerstätte, particularly the aquatic organisms, which in general remain articulated, were rapidly buried after death, due to high sedimentation rates, leading to an assemblage of exceptionally preserved fossils that more faithfully reflect the original life assemblage.

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The key factors that control the formation of siderite hosted Lagerstätte:

- Short time period between death and preservation.
- Anoxic environment bought about by fine grained sediments and high levels of organic detritus.
- Low levels of dissolved sulphate, bacterial sulphate reduction and pyrite formation.
- High levels of available iron and biocarbonate from iron reduction and methanodgenesis.
- Neutral to alkaline pH, (low H^+).

This model for siderite concretion formation and fossil preservation of the Coseley Lagerstätte can be applied to other such assemblages such as Mazon Creek and may provide a universal model for the preservation of fossils in concretionary siderite.

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