

Fossil Arthropods of Great Britain

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POST-DEVONIAN UPPER
PALEOZOIC HISTORY

Chapter 3

The building of the Laurentian-Gondwanan supercontinent (see Chapter 2) was completed by Variscan times, which assembled and sutured the assembly by 400–350 million years ago (Ma), see Figures 2.2 and 2.3a. Thus, the

Post-Devonian fossil arthropods

led to the Variscan Orogeny, which involved a dramatic crustal shortening event to lay out on the continental crust of the supercontinent. The thickening of the crust to a malayan-scale mountain belt extending from Asia through western Europe and on into the west flank of America, Ireland and Britain, by the north of the most intense deformation

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POST-DEVONIAN UPPER PALAEOZOIC HISTORY

The building of the Laurentian–Avalonian–Baltic continent (see Chapter 2) was extended into Devonian times when Armorica and Iberia joined the assembly (c. 400–370 million years ago (Ma), see Figures 2.2 and 2.3). Then the arrival of the greater mass of Gondwanan continents in Carboniferous times (c. 370–290 Ma) led to the Variscan Orogeny, which was the last dramatic crustal shortening event to impact upon the continental crust of north-west Europe. The thickening of the crust generated a Himalayan-scale mountain belt extending from Russia through western Europe and on into the eastern flank of America. Ireland and Britain lay to the north of the most intense deformation, although there was significant folding and faulting across the south of Ireland and Britain. Nevertheless, the orogeny had a major effect on the tectonic evolution of the whole of the region. The convergence assembled the supercontinent of Pangea, which stretched virtually from pole to pole. During these same Carboniferous times, the British Isles had moved northwards into the equatorial humid belt (Figure 3.1).

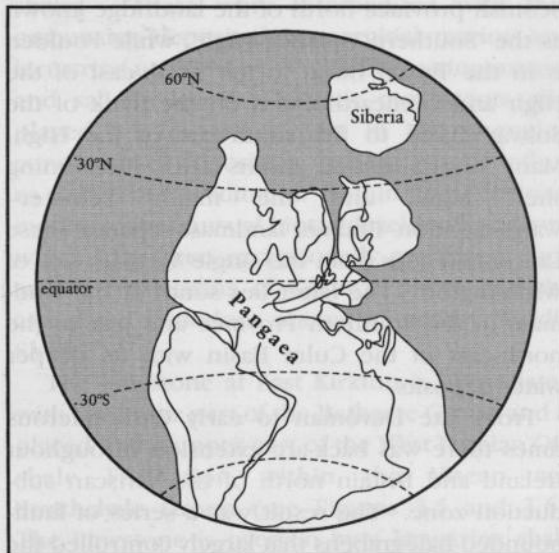


Figure 3.1 Palaeogeographical reconstruction of the continents in Late Carboniferous times, c. 300 Ma. Proto 'UK' is equatorial, and shown at the centre of this depiction. (Holdsworth *et al.*, 2000.)

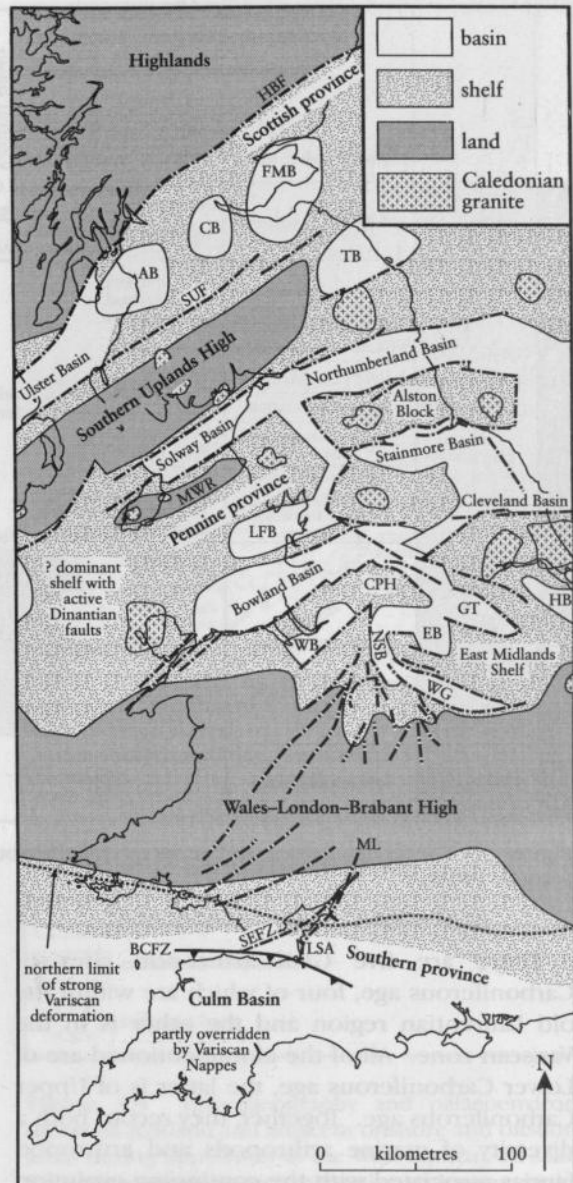


Figure 3.2 Dinantian palaeogeography showing main provinces and fault-bounded extensional basins and platforms that influenced sedimentation through much of the Carboniferous Period. (After Corfield *et al.*, 1996.)

Key:

AB: Ayrshire Basin; BCFZ: Bristol Channel Fault Zone; CB: Central Basin; CPH: Central Pennine High; EB: Edale Basin; FMB: Fife Midlothian Basin; GT: Gainsborough Trough; HBF: Highland Boundary Fault; LFB: Lancaster Fells Basin; LSA: Lower Severn Axis; ML: Malvern Line; NSB: North Staffordshire Basin; SEFZ: Severn Estuary Fault Zone; SUF: Southern Uplands Fault; TB: Tweed Basin; WB: Widnes Basin; WG: Widmerpool Gulf.

Post-Devonian fossil arthropods

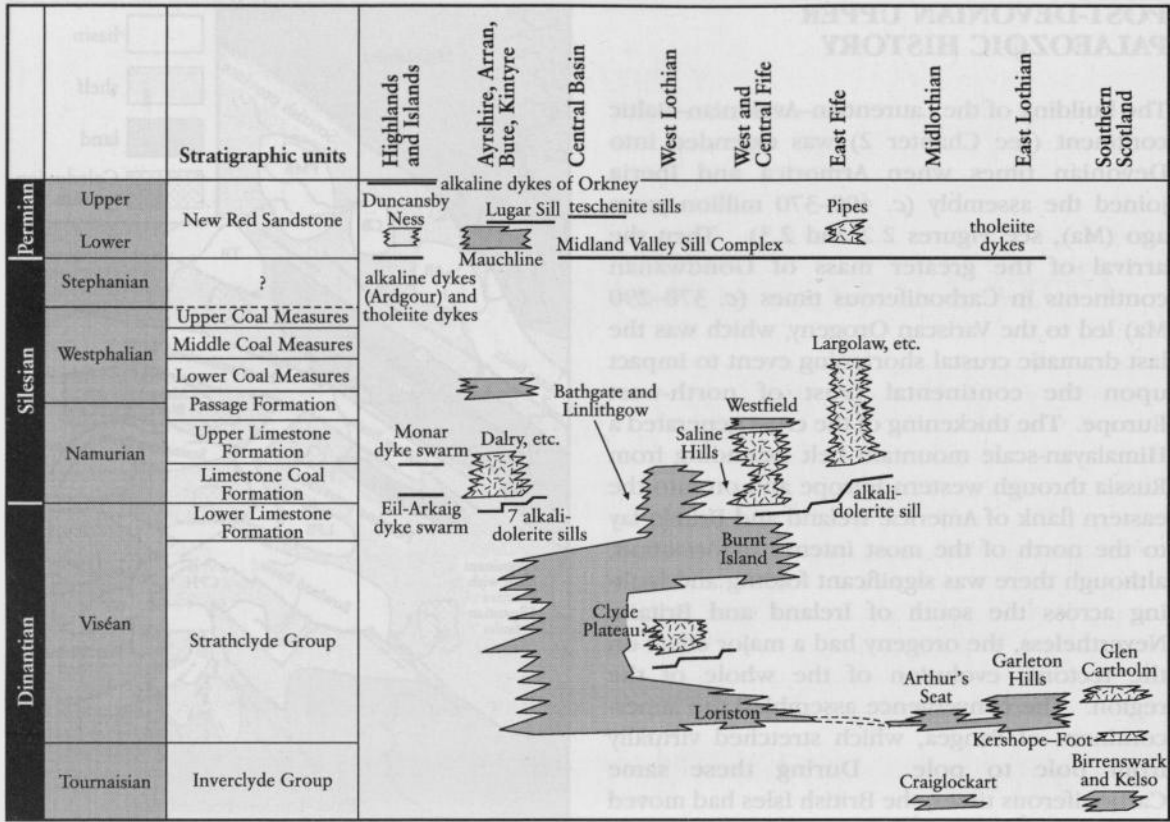


Figure 3.3 The stratigraphical and geographical distribution of Carboniferous volcanic rocks in Scotland. (After Francis, 1991b.)

There are five GCR arthropod sites of Carboniferous age, four of which are within the old Laurentian region and the other is in the Variscan zone. All of the aforementioned are of Lower Carboniferous age, the latter is of Upper Carboniferous age. Together, they record both a diversity of marine arthropods and arthropod faunas associated with the continuing evolution of land plants and their terrestrialization during the period.

The Laurentian (Scottish) sites range in age from Foulden of earliest Carboniferous age (Tournasian *c.* 348 million years old) to Granton Shore of late Visian age (*c.* 332 million years old). The Variscan (south-west English) site of Writhlington is by contrast of late Upper Carboniferous, late Westphalian age (*c.* 307 million years old).

The considerable sedimentological differences between the sites reflect the separate palaeogeographical provinces that were established by important tectonic features emanating from the Variscan Orogeny (Figure 3.2). East Kirkton and Granton Shore lie within the

Scottish province north of the landridge known as the 'Southern Uplands High', while Foulden is in the Tweed Basin to the north-east of the High and Glencartholm is on the flank of the Solway Basin to the south-east of the High. Many fault-bounded basins with intervening shelf highs and the major Leinster-Wales-London-Brabant landmass separate these Laurentian sites from the single Variscan site of Writhlington. The latter lies south of the landmass in the Southern Province and just to the north-east of the Culm Basin with its deeper water deposits.

From late Devonian to early Carboniferous times there was back-arc extension throughout Ireland and Britain north of the Variscan subduction zone. The result was a series of fault-bounded half-grabens that largely controlled the palaeogeography of the Lower Carboniferous with its rates and depths of subsidence and types of sediments. The underlying structural control on the basins and highs was largely inherited from older Caledonian features.

The Scottish Province

During Carboniferous times there were a number of basins of deposition in Scotland, mostly within the structural and topographical depression of the Midland Valley (Figure 3.2). The Viséan age sites of East Kirkton and Granton Shore are located within the north-easternmost of these depocentres – the Fife Midlothian Basin. These Midland Valley depocentres were separated from depositional basins to the south by the Southern Uplands High and its north-eastern extension, the Mid-North Sea High. However, there was one embayment, the Tweed Basin, which extends south of the Midland Valley and it is here that the Foulden site is located. The remaining Scottish site, Glencartholm, lies on the south-western flank of the Southern Uplands High at the edge of the Solway Basin, which extends north-eastwards into the Northumberland Basin.

A significant factor in these environments of deposition was volcanism that continued throughout the Carboniferous Period (Figure 3.3 and see Figure 3.10). The activity produced a topography dominated by volcanoes that separated the basinal depocentres (Figure 3.4). Within each basin, water circulation was restricted, leading to stratified water columns and the preservation of organic matter in the form of oil shales. These were interbedded with thin carbonates deposited in marginal marine and lacustrine environments with fluctuating oxygen and salinity levels. Eustatic movements also played an important part in the changing conditions of deposition with occasional influxes of riverborn sediment. Within these environments, some unusual biotas developed, some of which have been exceptionally preserved, such as the crustaceans of Granton Shore and the associated conodont animal at nearby Wardie Shore.

The limestone at East Kirkton is intercalated with the lower part of the Bathgate Group and is placed in the upper part of the West Lothian Oil-shale Formation within the Viséan age Strathclyde Group (see Figures 3.5 and 3.6). The limestone is overlain by a lacustrine shale and a tuff. The whole sequence was deposited in an isolated lake fed by silica-rich hot springs. River deltas and volcanoclastic detritus prograded into the lake at times. To begin with the lake was surrounded by extensive seedfern-dominated woodland that frequently suffered wildfire



Figure 3.4 Palaeogeography and palaeoenvironments of Scotland and adjacent onshore and offshore areas during deposition of the West Lothian Oil-shale formation, showing probably active structures, highs, and directions of coarse-grained siliciclastic input. Grey shading indicates land areas. CP: Clyde Plateau; CB: Cumbria Block; SH: Saline Hills; LC: Leven Coalfield. (After Corfield *et al.*, 1996.)

outbreaks. Subsequently drier conditions altered the woodland vegetation, the lake deepened and was subject to algal blooms and oxygen depletion. Finally, increasing rainfall encouraged a lycopsid-dominated vegetation. Throughout this time the lake became the depository of abundant animal and plant remains, both aquatic in origin and derived from the surrounding woodland. Altogether the biota is of international importance especially for its

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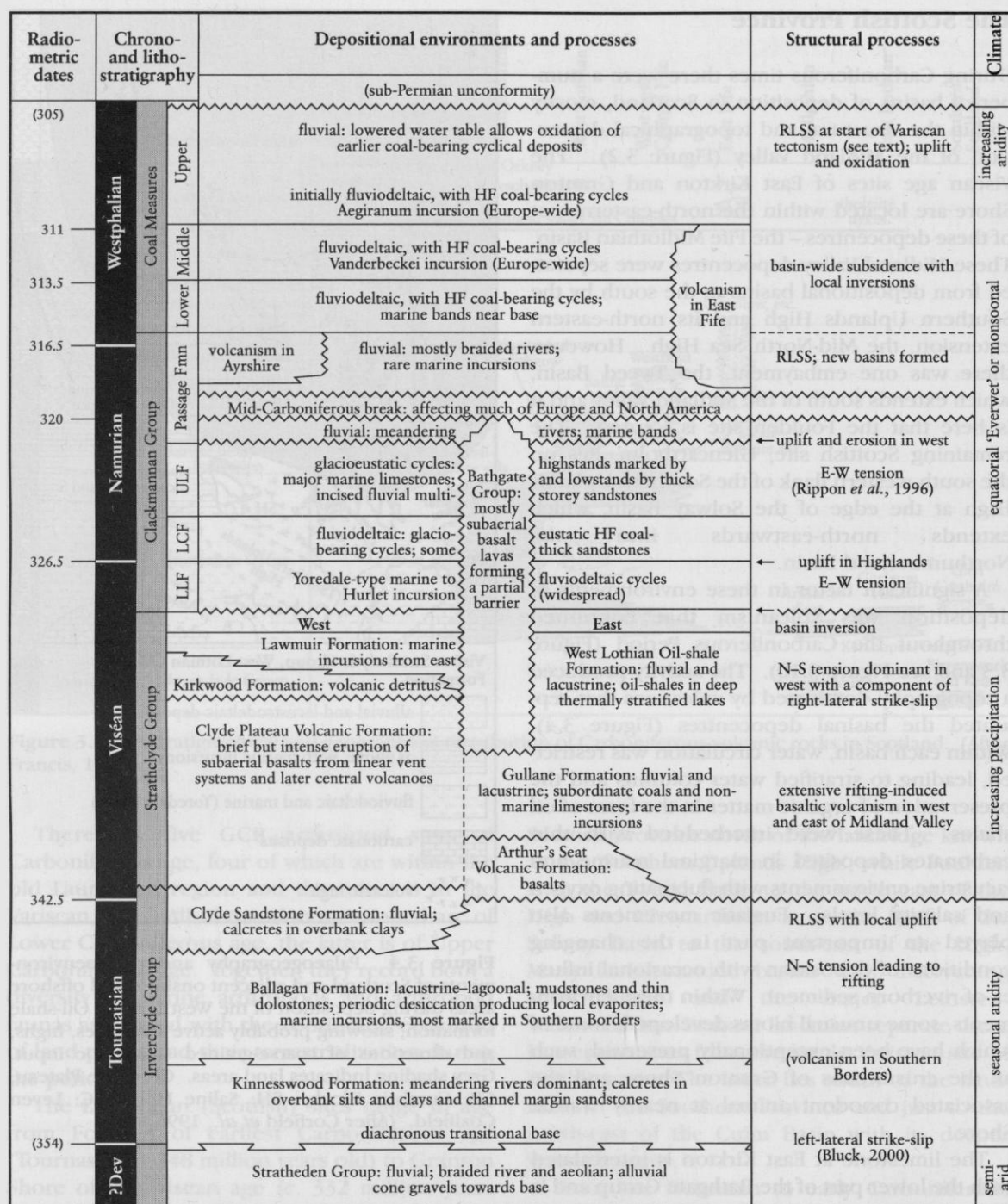


Figure 3.5 Summary of Carboniferous geological history for the Midland Valley and adjacent areas, showing outlines of changes in depositional environments, structural control and climate. Radiometric dates are from Menning *et al.* (2001). RLSS = right-lateral strike-slip. LLF = Lower Limestone Formation; LCF = Limestone Coal Formation; ULF = Upper Limestone Formation; HF = high frequency.

Post-Devonian Upper Palaeozoic history

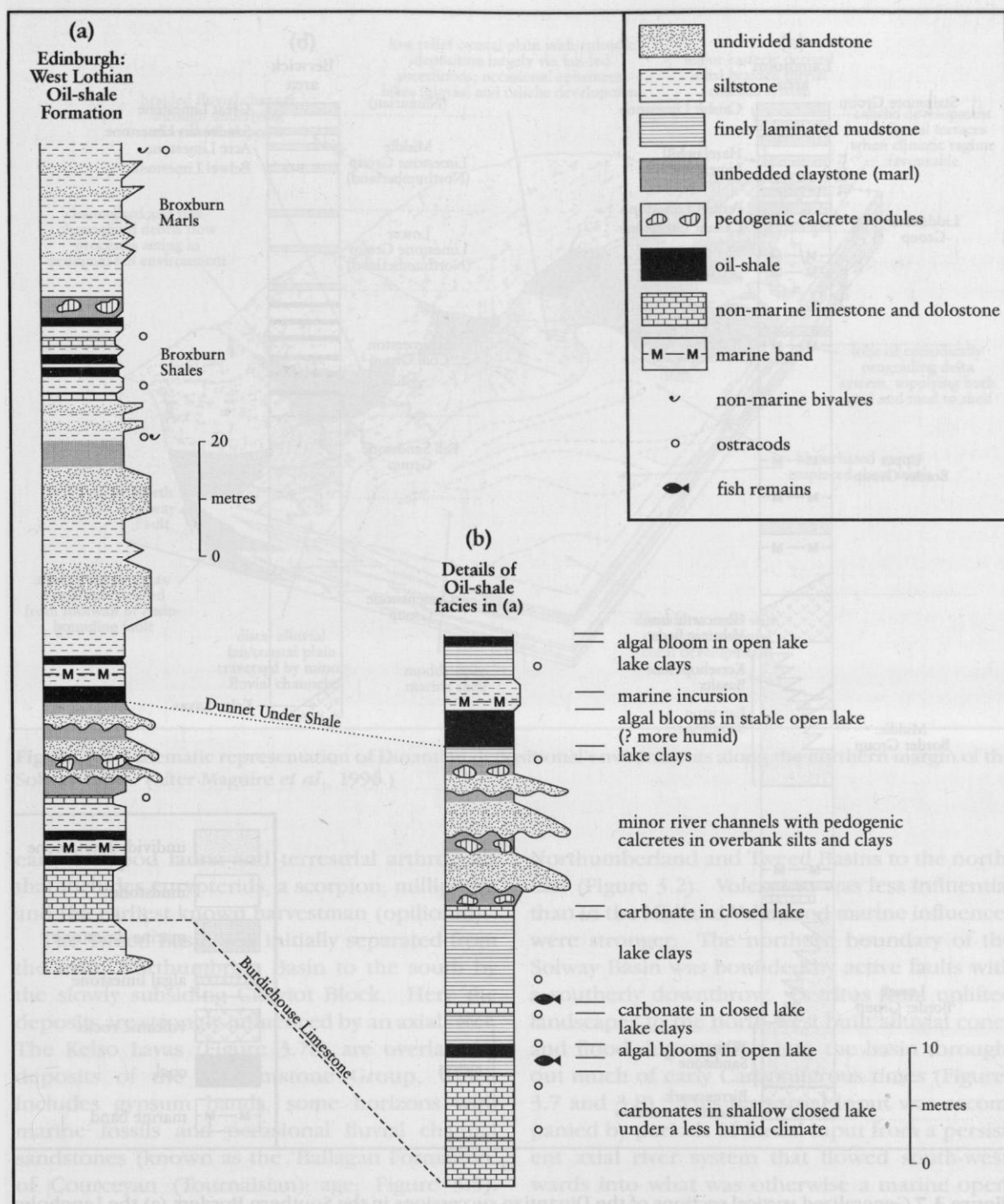


Figure 3.6 Generalized vertical sections of (a) the upper part of the West Lothian Oil-shale Formation in the Edinburgh area and (b), a detailed representative section.

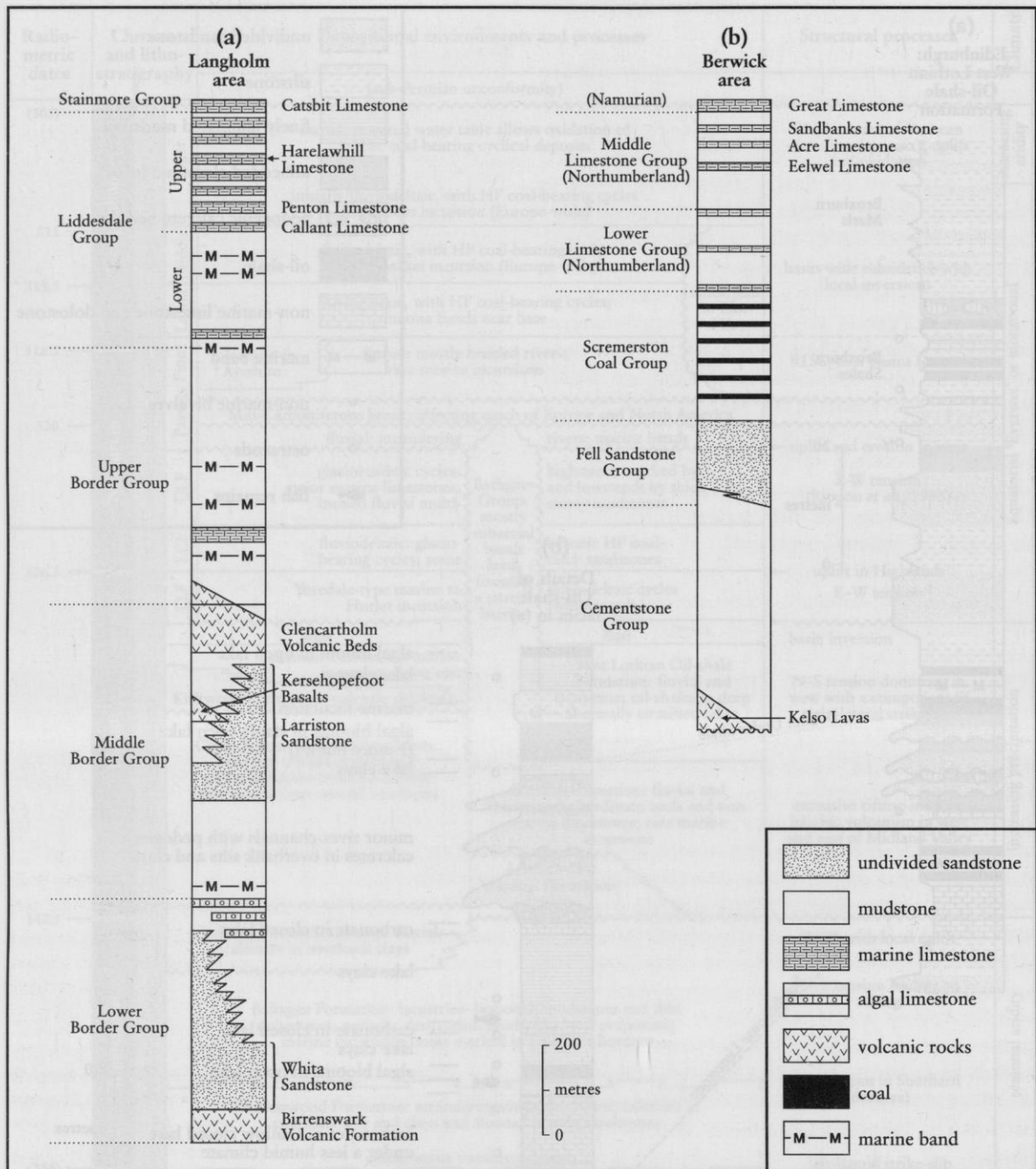


Figure 3.7 Generalized vertical sections of the Dinantian successions in the Southern Borders (a) the Langholm area in the west and (b) the Berwick area in the east.

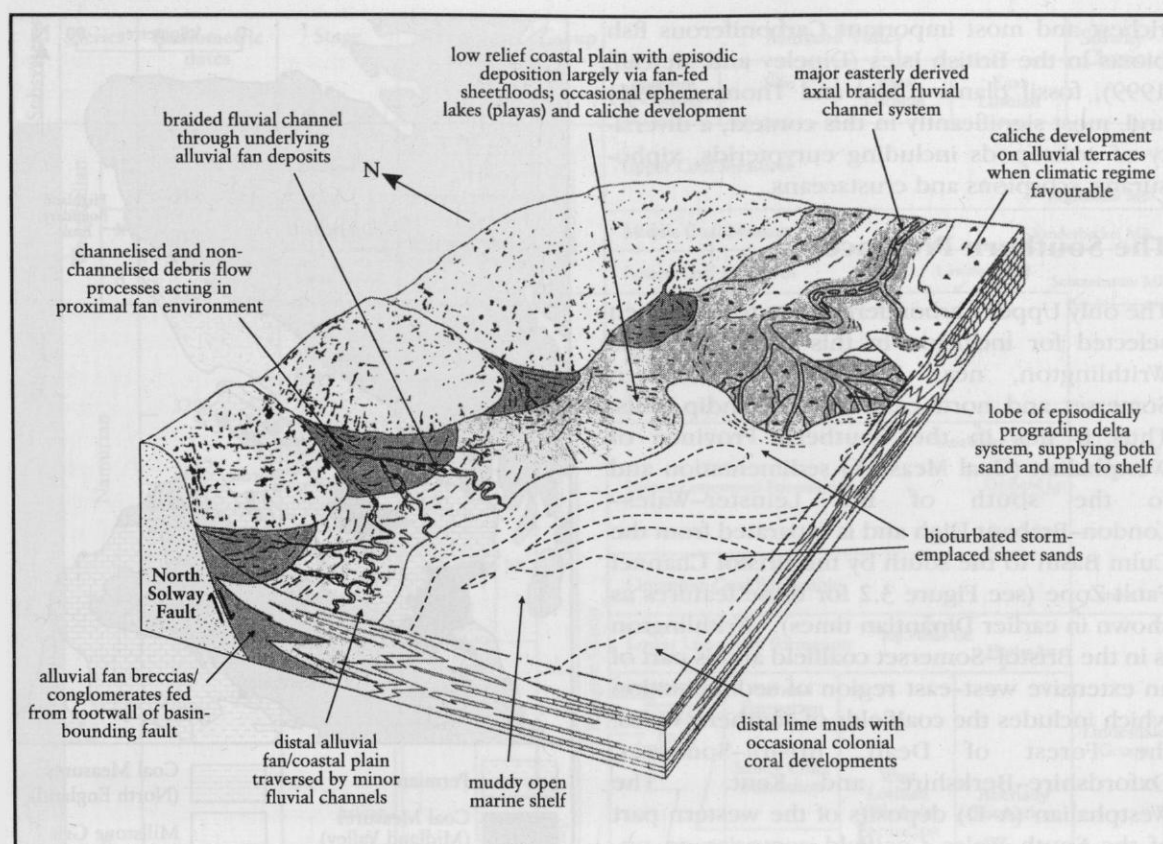


Figure 3.8 Schematic representation of Dinantian depositional environments along the northern margin of the Solway Basin. (After Maguire *et al.*, 1996.)

early tetrapod fauna and terrestrial arthropods that includes eurypterids, a scorpion, millipedes and the earliest known harvestman (opilionid).

The Tweed Basin was initially separated from the main Northumbrian Basin to the south by the slowly subsiding Cheviot Block. Here the deposits are strongly influenced by an axial river. The Kelso Lavas (Figure 3.7b) are overlain by deposits of the Cementstone Group, which includes gypsum bands, some horizons with marine fossils and occasional fluvial channel sandstones (known as the 'Ballagan Formation' of Courceyan (Tournaisian) age; Figure 3.5). The deposits have been interpreted as those of a semi-arid coastal plain intersected with intermittent rivers (Figure 3.8). There were also shallow freshwater lakes that supported restricted fish faunas but were also subject to flooding, which may have introduced other faunal elements such as the arthropods. The latter include the earliest-known limuloid and an unusual eurypterid.

The Solway basin in the west was part of a composite trough that included the

Northumberland and Tweed Basins to the north-east (Figure 3.2). Volcanism was less influential than in the Midland Valley and marine influences were stronger. The northern boundary of the Solway Basin was bounded by active faults with a southerly downthrow. Detritus from uplifted landscapes to the north-west built alluvial cones and flood deposits out into the basin throughout much of early Carboniferous times (Figures 3.7 and 3.8). This terrestrial input was accompanied by periods of fluvial input from a persistent axial river system that flowed south-westwards into what was otherwise a marine open-shelf environment of deposition. There was an eruption of volcanicity that began locally (Langholm area) in early Tournaisian times and subsequently became more extensive forming the Glencartholm Volcanic Beds (late Holverian-early Asbian age, Figure 3.3) within the Middle and Upper Border Group. The latter includes marine mudstones and limestones with thin sandstones (many of which are volcanoclastic). The succession has yielded one of the

richest and most important Carboniferous fish biotas in the British Isles (Dineley and Metcalf, 1999), fossil plants (Clea and Thomas, 1995) and, most significantly in this context, a diversity of arthropods including eurypterids, xiphosurans, scorpions and crustaceans.

The Southern Province

The only Upper Carboniferous site to have been selected for inclusion in this GCR volume is Writhlington, near Radstock in northern Somerset and north-east of the Mendip Hills. Thus it lies in the Southern Province of Westphalian (Coal Measure) sedimentation and to the south of the Leinster–Wales–London–Brabant High and is separated from the Culm Basin to the south by the Bristol Channel Fault Zone (see Figure 3.2 for these features as shown in earlier Dinantian times). Writhlington is in the Bristol–Somerset coalfield and is part of an extensive west–east region of sedimentation which includes the coalfields of southern Wales, the Forest of Dean, Bristol–Somerset, Oxfordshire–Berkshire and Kent. The Westphalian (A–D) deposits of the western part of the South Wales Coalfield comprise an unbroken sequence some 1800 m thick in places but thin eastwards. Re-activation of older east–west basement structures during Variscan compression produced contemporaneous faulting, folding and positive areas over which the Westphalian succession thins.

However, to the east and southeast of the Usk Axis the succession thickens again. A broad structural basin, known as the ‘Radstock Syncline’, accumulated a considerable thickness of around 7800 m of Upper Carboniferous sediments. In the upper part of the succession (upper Bolsovian–upper Westphalian D) includes coal seams and associated strata. They were deposited in densely vegetated fluvial plains. The Writhlington site consists of rejected shale debris that was adjacent to the worked coal seams. Careful collecting has provided abundant arthropod fossils including cockroaches (blattodeans) plus various other insects and a xiphosurid.

Climate

The Carboniferous period was one of progressive climate change enhanced by changes in atmospheric circulation as a result of Variscan

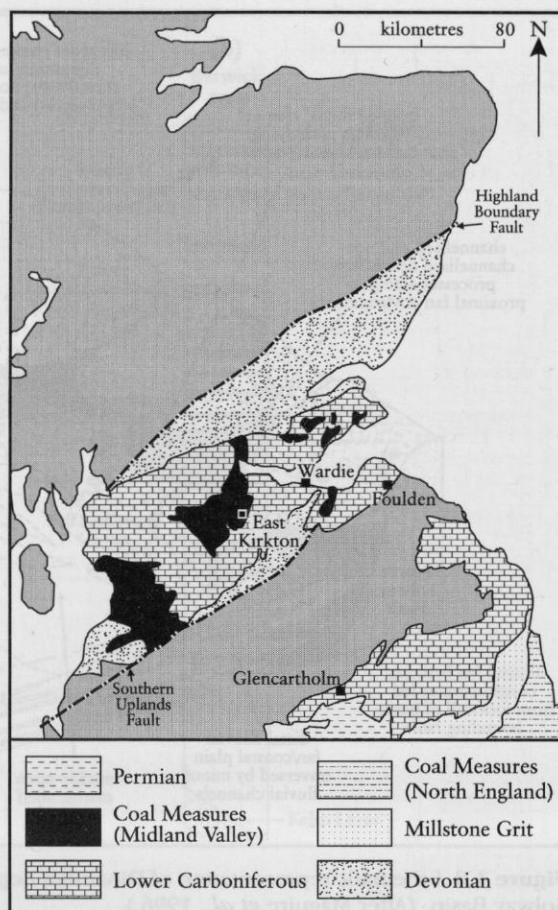


Figure 3.9 Geological sketch map of southern Scotland and northern England with the positions of the Scottish Carboniferous GCR arthropod sites shown. Wardie is near to the Granton Shore GCR site.

mountain building and northwards plate movement, which took the British Isles and adjacent regions across the equator. Strongly seasonal, possible monsoonal, climates prevailed through early Carboniferous times and there is evidence for semi-arid conditions by late Viséan times. Subsequently, during later Carboniferous times (Namurian and Westphalian) there were fluctuating seasonal to all-year humid climates with interspersed drier phases linked to glacial events. Changing freshwater input from major rivers and fluctuating sea levels, again linked to glaciation, resulted in complex depositional cycles with repeated formation of luxuriant vegetation and peats in lowlying areas. With subsequent burial they were transformed into the well-known coal deposits that eventually fuelled Britain’s Industrial Revolution. By the end of

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Subsystems	Series		Radiometric dates	Stage	Microspore zone	Group	Midland Valley				Solway-Cheviot		
							Ayrshire & Central	Fife	West Lothian	East Lothian			
Silesian	Westphalian	C	308	Bolsovian	XI	Coal Measures	Upper Coal Measures				Aegiranum MB Vanderbeckei MB Lowstone MB Subcrenatum MB		
			311		X								
		B	313.5	Duckmantian	IX		Middle Coal Measures						
		A	316.5	Langsettian	VIII VII SS		Lower Coal Measures						
	Namurian			Yeadonian-Chokierian	FR	Clackmannan Group	Passage Formation				Stainmore Group Catsbit Lst		
					KV								
		320			SO								
		324	Arnsbergian	TK	Upper Limestone Formation								
					Castlecary Lst Orchard Lst Index Lst								
			Pendleian		NC		Limestone Coal Formation						
Dinantian	Viséan		326.5	Brigantian		Strathclyde Group	Lower Limestone Formation				Liddesdale Group Upper Border Group Glencartholm Volcanic Beds Middle Border Group		
					VF		Top Hosie Lst Hurlet Lst						
			331				Bathgate Group	Lawmuir Fmn Kirkwood Fmn	Pathead Formation	West Lothian Oil-shale Formation		Aberlady Formation	
				Asbian	NM				Sandy Craig Formation				
								Pittenweem Formation					
	Tournaisian		(342.5)	Holkerian-Arundian		Inverclyde Group	Clyde Plateau Volcanic Formation	Anstruther Formation	Gullane Formation		Lower Border Group		
								Fife Ness Formation	Arthur's Seat Volcanic Formation Garleton Hills Volcanic Formation				
				Chadian				Clyde Sandstone Formation					
			(354)	Courceyan	CM			Ballagan Formation					
						Kinnesswood Formation							

Figure 3.10 Lithostratigraphical and chronostratigraphical divisions of the Carboniferous Period in the Midland Valley and Southern Borders. Key marine bands (MB) and limestones (Lst) used in correlation are noted. No clear evidence for Chokierian or Alportian stages has been found in Scotland, possibly reflecting a mid-Carboniferous depositional break.

Carboniferous times (late Westphalian to Stephanian times) there was increasing aridity caused by the rain-shadow in the lee of the Variscan mountains and prevailing tradewinds blowing from the east. Of late Westphalian age, the Writhlington deposits were laid down at the beginning of the latter phase of climate change.

FOULDEN, BORDERS (NS 921 552)

Introduction

Foulden is one of a network of Lower Carboniferous localities (including Glencartholm, Granton Shore and East Kirkton, see Figure 3.9) that have yielded an important biota including arthropods that are both typical of the Lower Carboniferous of Scotland and Northern England and unique to its strata. Fossils were first collected in abundance from strata of the Cementstone Group sequence (see Figure 3.7b) at Foulden (around 348 million years old) in 1910–12 by T.M. Ovens, a local collector who died in 1912 at the age of nineteen. His collection of almost 150 specimens was described by Kidston (1923–5), White (1927) and Edwards (in White 1927). Little further collecting occurred until the 1960s when A.G. Long collected fossil cupules containing seeds. Excavations made at that time with the assistance of C.D. Waterston and R.J. Reekie of the Royal Scottish Museum yielded many plants, including a compressed pteridosperm, approximately 2 m in length.

In 1953 the site was recommended by the Geological Survey as a Site of Special Scientific Interest (SSSI) on account of the rich fauna and flora. Following a re-survey of the site in 1960, it was officially notified in 1961 as a geological SSSI by the Nature Conservancy Council. S.P. Wood visited the area several times prior to the excavations of 1980–1, principally to collect vertebrates. Excavations in 1980–1, funded jointly by S.P. Wood, the Nature Conservancy Council, the Hunterian Museum and the Royal Scottish Museum, yielded many new specimens, as well as stratigraphical and sedimentological information determined from careful bed-by-bed collecting. The biota from Foulden, and its taphonomy and palaeoecology were described in a thematic series of papers published in 1985 in the *Transactions of the Royal Society of Edinburgh*:

Earth Sciences (see References - **which ones?**).

In addition to the fossil arthropod importance of this site, the area is also independently selected for the GCR for the Carboniferous–Permian Fish/Amphibia selection category (Dineley and Metcalf, 1999).

Description

The Foulden succession crops out in the bank of the Foulden Burn (the ‘Crooked Burn’ of Anon, 1927) near Foulden Newton Farm, 8.4 km north-west of Berwick-upon Tweed. The sequence dips 28° towards 170° and forms part of an unnamed formation within the Cementstone Group of the Calciferous Sandstone Measures (Francis 1983), the lithostratigraphy of which requires local study and definition. Miospores obtained by Clayton (1985) during the 1980–1 excavations indicate a late Tournaisian (TN3; = Courceyan Stage of the Dinantian) age (see Figure 3.10).

The arthropods at Foulden represent the earliest Carboniferous fauna with well-preserved terrestrial and non-marine representatives. The fossils come from the so-called ‘Fish Bed’, which consists of 0.39 m in the base of Bed 16 (Wood and Rolfe, 1985; Figure 3.11), which is set in a unit of 1.1 m of finely laminated siltstone, becoming more shaly upwards. The Fish Bed is subdivided into an upper 0.31 m portion, separated from a basal bioturbated part where fossil fishes are less-well preserved. The Fish Bed sequence lies within the lower part of the Lower Carboniferous Cementstone Group of Berwickshire and is probably of Tournaisian (Courceyan) age. The Fish Bed is approximately 100 m above the base of the Cementstones, which, with the exception of Foulden, are sparsely fossiliferous and its fauna is mainly of ostracods, bivalves and fish fragments, plus some plant material.

The field and laboratory methodology used in the 1980–1 study at Foulden was based on that used on a Carboniferous fish bed in Illinois by Zangerl and Richardson (1963). A large slab was lifted and removed to the laboratory, having been marked up with a grid and north arrows. The Fish Bed is rubbly, which made re-assembly difficult. A polished vertical section was cut as a basis for the detailed log, and as the beds were stripped off one by one, their contents were plotted with reference to two marker horizons. The fossils were coded for three-dimensional

Foulden

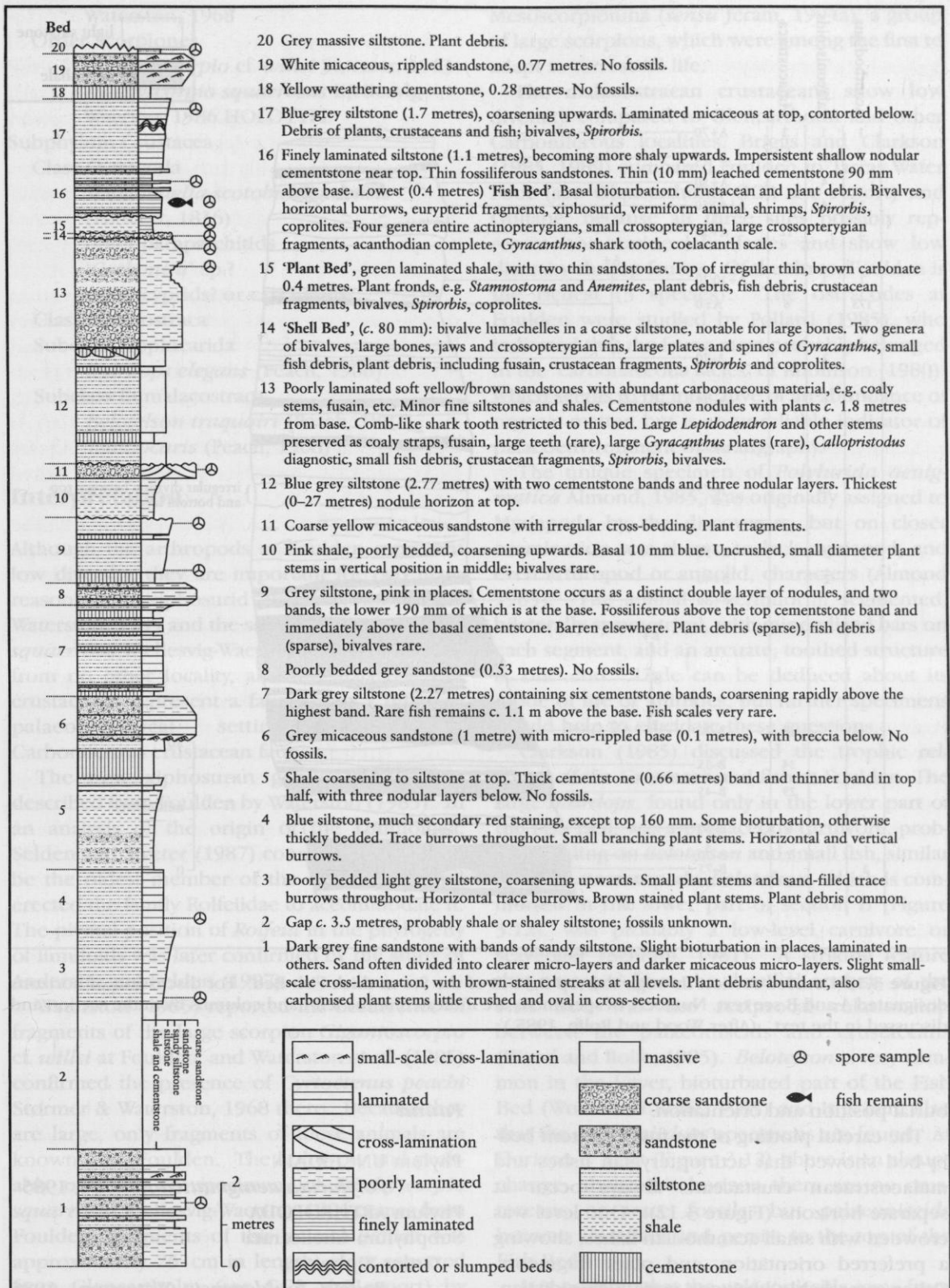


Figure 3.11 Foulden stratigraphical column. (After Wood and Rolfe, 1985.)

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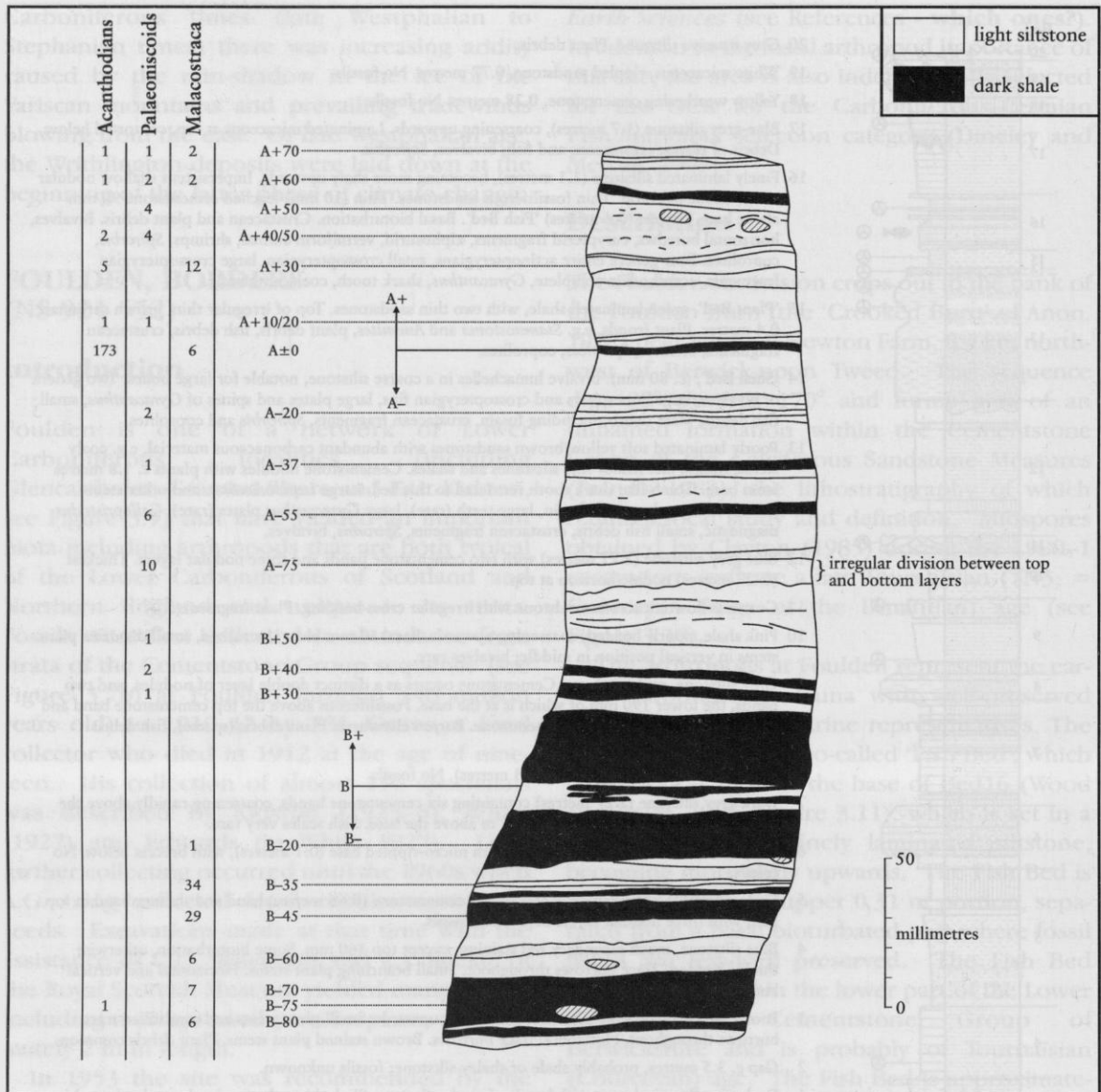


Figure 3.12 Detailed section through the top 0.31 m of the 9.4 m thick Fish Bed. For discussion of horizons designated A and B see text. Numbers of specimens are indicated in the left-hand columns from the section and discussed in the text. (After Wood and Rolfe, 1985.)

burial position and orientation.

The careful plotting of the fossil content bed-by-bed showed that actinopterygian fishes and malacostracan crustaceans always occur at separate horizons (Figure 3.12). One level was crowded with small acanthodian fishes, showing a preferred orientation, and plant fragments. Other remarkable horizons were a rhipidistian-rich layer, a coprolite horizon and a bivalve-malacostracan horizon.

Fauna

Phylum UNCERTAIN

Polylurida aenigmatica Almond, 1985

Phylum ARTHROPODA

Subphylum Chelicerata

Order Xiphosura

Rolfeia fouldenensis Waterston, 1985

HOLOTYPE

Order Cyrtoctenida

Cyrtoctenus peachi Størmer &

- Waterston, 1968
 Order Scorpiones
Gigantoscordio cf. *willsi* Størmer, 1963
Trachyscordio squarrosus Kjellesvig-Waering, 1986 HOLOTYPE
 Subphylum Crustacea
 Class Ostracoda
Sbemonaelia scotoburdigalensis (Hibbert, 1836)
 other paraparchitids
 'Carbonita' sp.?
 other cyprids? or cavellinids?
 Class Malacostraca
 Subclass Hoplocarida
Bairdops elegans (Peach, 1908)
 Subclass Eumalacostraca
Belotelson traquairi (Peach, 1882)
Tealliocaris (Peach, 1908)

Interpretation

Although the arthropods at Foulden represent low diversity, they are important for two main reasons: the xiphosurid *Rolfeia fouldenensis* Waterston, 1985 and the scorpion *Trachyscordio squarrosus* Kjellesvig-Waering, 1986 are known from no other locality, and the malacostracan crustaceans represent a fauna from a different palaeoecological setting than other Carboniferous crustacean faunas.

The new xiphosuran genus *Rolfeia* was described from Foulden by Waterston (1985). In an analysis of the origin of the Limuloidea, Selden and Siveter (1987) considered *Rolfeia* to be the oldest member of the superfamily, and erected the family Rolfeiidae to accommodate it. The pivotal position of *Rolfeia* in the phylogeny of limuloids was later confirmed by the study of Anderson and Selden (1997).

Waterston (1985) reported the occurrence of fragments of the large scorpion *Gigantoscordio* cf. *willsi* at Foulden, and Waterston *et al.* (1985) confirmed the presence of *Cyrtoctenus peachi* Størmer & Waterston, 1968 there. Because they are large, only fragments of these animals are known from Foulden. The holotype, and probably only known specimen, of *Trachyscordio squarrosus* Kjellesvig-Waering, 1986 comes from Foulden; fragments of this animal (which was approximately 25 cm in length) were reported from Glencartholm (see GCR site report) by Kjellesvig-Waering (1986), but Jeram (1994a) was unable to confirm the assignment of these fragments. *Trachyscordio* belongs in the

Mesoscordionina (*sensu* Jeram, 1994a), a group of large scorpions, which were among the first to adapt to terrestrial life.

The malacostracan crustaceans show low diversity compared to Glencartholm and other Carboniferous localities. Briggs and Clarkson (1985, 1989) compared Foulden to Tarras Water Foot (see Glencartholm GCR site report) and Gullane, because all three sites possibly represent non-marine lake facies and show low diversity shrimp faunas. Of the three, Foulden is the richest (3 species). The ostracodes at Foulden were studied by Pollard (1985), who indicated that the fauna most probably belonged in the 'carbonaceous facies' of Robinson (1980), which seems to be indicative of an abundance of organic matter, but is an unreliable indicator of palaeoenvironment or stratigraphy.

The unique specimen of *Polylurida aenigmatica* Almond, 1985, was originally assigned to Myriapoda by the discoverers, but on closer examination was shown to lack myriapod, and even arthropod or annelid, characters (Almond 1985). The animal is vermiform, segmented, bilaterally symmetrical, with mineralized bars on each segment, and an arcuate, toothed structure at one end. Little can be deduced about its mode of life or affinities, but further specimens would help to elucidate these questions.

Clarkson (1985) discussed the trophic relations of the Crustacea and fish at Foulden. The large *Bairdops*, found only in the lower part of the Fish Bed, was a predaceous carnivore, probably feeding on *Belotelson* and small fish, similar to living stomatopods. *Belotelson*, which is commonest in the lower part of section B (Figure 3.12), was probably a low-level carnivore or scavenger (Schram, 1981). A striking feature that emerged from the detailed analysis of the Fish Bed was the reciprocal relationship between the palaeoniscids and crustaceans (Wood and Rolfe, 1985). *Belotelson* is very common in the lower, bioturbated part of the Fish Bed (Wood and Rolfe, 1985) and it is here also that the only *Bairdops* specimens are found. At Horizon B + 30 (Figure 3.12), there is an abrupt change; above this horizon there are no crustaceans or trace fossils, but palaeoniscids become abundant and persist to the top of the Fish Bed.

It is possible that the palaeoniscids came from a nearby lake during a time of high water level. The acanthodian-rich layer at Horizon A (Figure 3.12), possibly indicates an episode of mass

mortality, but at the same horizon bioturbation became apparent once more and *Belotelson* returns, though fewer in number than before. Palaeoniscids occur together with crossopterygians in the upper part of the sequence, especially at Horizon A + 40–50 (Figure 3.12) where biotic diversity reaches a maximum. Presumably conditions were optimal here. The reciprocity between fish and crustaceans might be due to the crustaceans being the prey of the palaeoniscids, which appear at Horizon B + 30. The crustaceans were eliminated by the palaeoniscids and a stable predator–prey balance was not set up until later (Horizon A, Figure 3.12). This suggestion does not explain the return of bioturbating organisms as well as crustaceans at Horizon A + 30.

Another hypothesis put forward by Clarkson (1985) is that the faunal changes were caused by changes in salinity. Water level started high, allowing very large rhizodonts to live in the lake. The substrate was firm enough at that time to support a rich fauna of euryhaline bivalves. Repeated muddy turbidite flows then caused the substrate to become softer, but not so soft as to prohibit infauna. A balanced, though somewhat restricted, possibly brackish-water, assemblage then lived in the lake; fish were few, though the crustacean *Belotelson* was very common, preyed upon by *Bairdops*. Following a rise in water level, palaeoniscids invaded the lake, adapted to a different, presumably lower, salinity, which the crustaceans and infaunal elements could not tolerate. The mass-mortality episode, which killed many acanthodians, may have been caused by a fall in water level. At this time the lake returned to near its first level as did salinity, as indicated by the return of trace fossils as well as *Belotelson*. Both the fishes and the crustaceans may well have had some tolerance of changing salinity, but it seems evident that the rich biota from Horizon A (Figure 3.12) onwards (other than during the brief episode that killed the acanthodians) must have been optimal in terms of salinity condition and food availability for all the animals present. These conditions persisted until the lake finally silted up.

The scorpion fauna at Foulden is low diversity (two species) compared to Glencartholm, which has a diversity of eight species of scorpion. Single scorpion specimens also occur in the Scottish Lower Carboniferous at two other localities. A poorly preserved specimen of *Phoxiscorpio peachi* Kjellesvig-Waering, 1986 is

known from the Viséan of Dalmeny railway cutting, Edinburgh, and two fragments of *Scoloposcorpio cramondensis* Kjellesvig-Waering, 1986 occurred in the Viséan of Cramond, near Edinburgh. A similar low diversity is seen in the eurypterids and other chelicerates from Foulden, though their fragments are quite widespread at other localities. Possibly, the forms that occur at Foulden were adapted to living in the unusual habitats and salinity conditions (see above) that occurred there.

Malacostracan crustaceans are widespread in the Scottish and Borders Lower Carboniferous strata, as discussed by Schram (1979), Briggs and Clarkson (1989) and Cater *et al.* (1989). At Willie's Hole, 5 km west of Foulden, *Pseudotealliocaris etheridgei* (Peach, 1908) is found, and at Pathhead Mill near Duns (Schram 1979, locality 8), Peach (1908) recorded '*Anthracocephalus dunsiana*' (probably *Belotelson traquairi* (Peach 1908)). The differences between these faunas might suggest isolated temporary or semi-permanent lakes with endemic faunas. A number of other contemporaneous occurrences of fish and arthropods occur in the region, such as at Coomsdon Burn and Chattlehope Burn, Redesdale, south of the Cheviot Hills, Northumberland. The younger Glencartholm biota (Viséan Upper Border Group) was discussed by Schram (1983) (see GCR site report). Although it contains *Belotelson traquairi* and *Bairdops elegans*, there are many other species of crustaceans at Glencartholm, and the rich fish fauna has only the genus *Phanerosteon* in common with Foulden. There are numerous marine elements in the fauna, but since the Glencartholm section has not been sampled bed-by-bed, as has Foulden, it is not known from which horizons within the sequence they came. There may have been marine and non-marine alternations with specific faunas in particular layers. In general, the Glencartholm biota contrasts with that of Foulden, which is more restricted and lived in presumably a less saline habitat lacking fauna less tolerant of lowered salinities.

The Foulden biota consists largely of nektonic and nektobenthonic forms, with an infauna only in the early and late stages, and an epifauna only of vagile crustaceans, sessile bivalves and rare xiphosurids. Salinity and, to a lesser extent, the nature of the substrate were the primary determinants of the palaeoecology of the Foulden Fish Bed (Clarkson, 1985).

Conclusions

Though yielding a less diverse arthropod fauna than Glencartholm, the locality at Foulden has been recently sampled in a detailed, bed-by-bed analysis that synthesized data from sedimentology, palaeoecology and all groups of plant and animal palaeontology. To some extent, therefore, the importance of the locality lies in the tremendous amount of information collected about the entire fauna, of which arthropods form a vital part. In particular, the reciprocity of fishes and crustaceans (i.e. where crustaceans occur in the section, fishes are rare and *vice versa*) has provoked a number of explanatory hypotheses.

Of particular interest among the arthropods from Foulden are the unique species that have been described from there, known from nowhere else in the world. These include the earliest limuloid xiphosuran *Rolfeia*, the large, early terrestrial scorpion *Trachyscorpio*, and the enigmatic metazoan *Polyhurlida*, referred to here because of its original interpretation as a myriapod.

The accessibility of Foulden, and the huge database of sedimentological and stratigraphical information about the site, make it a key Scottish Lower Carboniferous locality.

GLENCARTHOLM, DUMFRIES AND GALLOWAY (NY 376 796–NY 375 807)

Introduction

Glencartholm is situated in lower Carboniferous rocks (some 340 million years old) in the bed of River Esk (Figure 3.13), about 4 km north-west of Canonbie and 5.5 km SSE of Langholm, Dumfries and Galloway (see Figures 3.7a and 3.9). In addition to the remarkably diverse fossil fauna of arthropods (more than 30 species) and fishes that have made it famous, the fauna from Glencartholm comprises marine brachiopods and bivalves, and a diverse terrestrial flora is also known (Cleal and Thomas, 1995). It is a key site in studies of Carboniferous biotas and arthropod evolutionary history and is part of a network of Scottish lower Carboniferous sites that includes Foulden, Granton and East Kirkton (see Figure 3.9).

Fossils were first discovered at Glencartholm

in 1879 by the collector A. Macconochie during work for the Geological Survey, as reported by Geikie (1881). The arthropods were first described by Peach (1882b,c, 1890), the fishes by Traquair (1881, 1884a,b, 1888a,b, 1890), and the plants by Kidston (1883, 1903). Further collecting took place in 1933–1936 by Moy-Thomas (Schram, 1983), when the use of explosives removed all the fossiliferous strata that were thought to be accessible at that time (Lumsden *et al.*, 1967). The geology of the area has been described by Peach and Horne (1903), Nairn (1956), Lumsden *et al.* (1967), Leeder (1974), and Cater *et al.* (1989). No discussion of Carboniferous crustaceans or chelicerates is complete without a mention of the Glencartholm fauna, so this site was a prime candidate for inclusion in the list of GCR sites. The site itself, though suffering somewhat from inundation being close to the river water level, is nevertheless undamaged (except by some irresponsible collecting) and amenable to further research. Indeed, it would be an obvious site to be selected for a research project proposal. In addition to the fossil arthropod importance of this site, the area is also independently selected for the GCR for the Carboniferous–Permian Fish/Amphibia, Palaeozoic Palaeobotany, Carboniferous–Permian Igneous and Westphalian selection categories (Dineley and Metcalf, 1999, Cleal and Thomas, 1995, 1996 Stephenson *et al.*, 2003).

Description

The arthropod-bearing horizon, low in the Viséan succession, occurs as a thin unit within the Glencartholm Volcanic Beds (Figure 3.10), a sequence of tuffs, shales and sandstones at the base of the Upper Border Group of the Calciferous Sandstone (Lumsden *et al.*, 1967). In the section for the Langholm area, George *et al.* (1976, p. 42) showed these volcanic rocks to be largely Holkerian, possibly partly Asbian, in age, based on Foraminifera. The rocks are poorly exposed, but a complete section was provided by the Archerbeck Borehole (Lumsden and Wilson, 1961). This borehole, however, did not encounter the fossil beds of Glencartholm. British Geological Survey palaeontologists D.K. Graham and P.J. Brand located a shrimp bed at Glencartholm in 1971, which yielded essentially the same diversity of shrimps as the bed collected in the previous century and may represent

Post-Devonian fossil arthropods

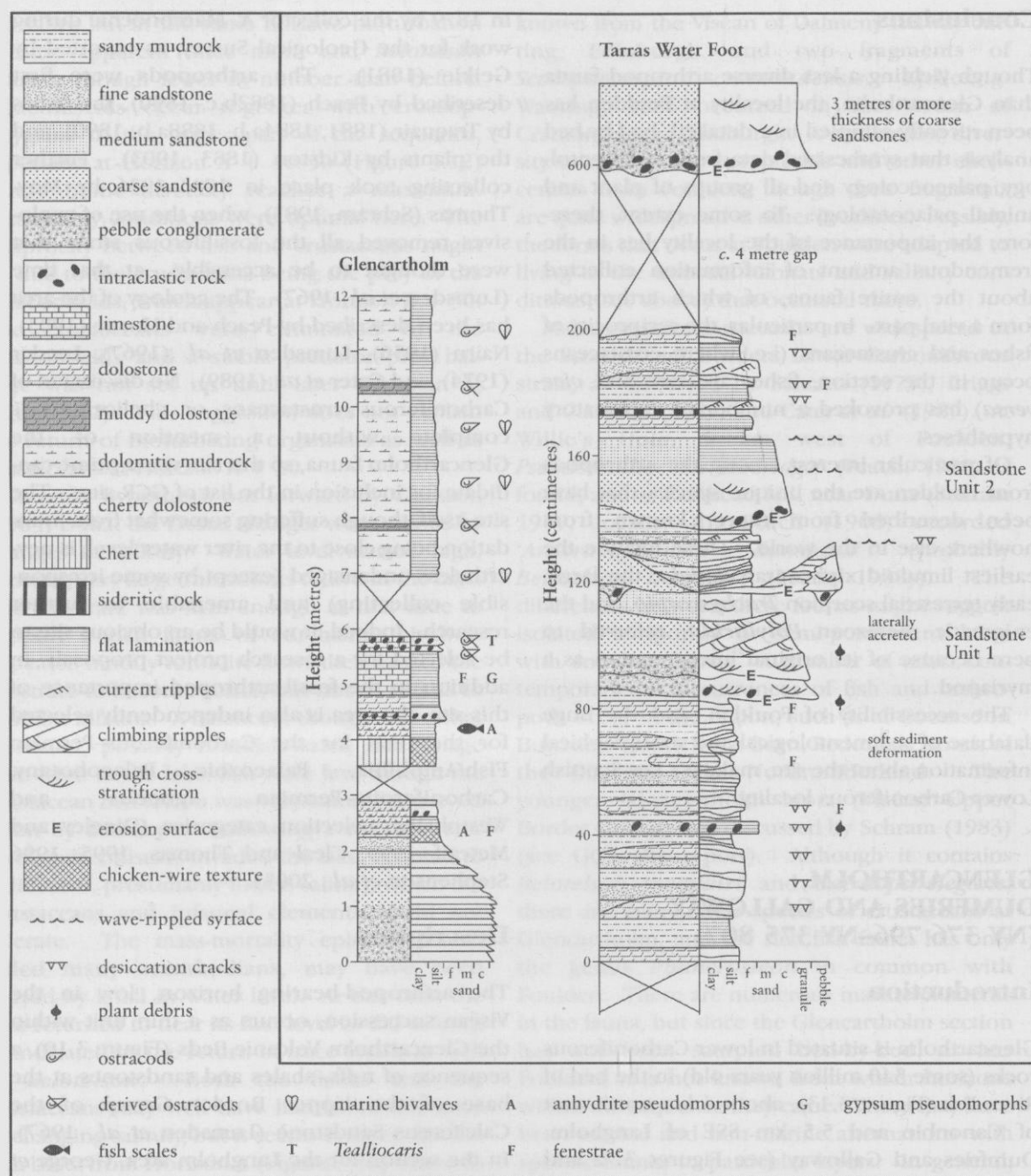


Figure 3.13 Stratigraphical sections at Glencartholm and the nearby Tarras Water Foot. For discussion of localities, see text. (After Cater *et al.*, 1989.)

the original band. The local extent of the Glencartholm fossil beds is unclear because of faulting at the site, and it had been assumed that the fossiliferous bed was worked out because explosives had been used for collecting (Lumsden *et al.*, 1967). However, Schram (1983) discovered similar fossiliferous shales and thin limestones 'some 20 paces north of the

classic locality' containing an almost complete actinopterygian fish, *Acrolepis ortholepis*, the matrix and preservation of which were identified with that of the Shrimp Bed. However, the new section is separated from the original site by faulting and, though similar in many respects, the sedimentology and fauna differ sufficiently from Macconochie's section so that it is not clear

how the two are related. Thus, this important Lower Carboniferous arthropod-, fish- and plant-bearing site still awaits detailed study.

Peach and Horne's (1903) section at the collecting site showed two fossiliferous horizons: the Shrimp Bed, containing crustaceans, fishes and molluscs, and the Scorpion Bed, containing an extensive flora, as well as sparse crustaceans and arachnids. It is not possible, however, to distinguish these two elements in Macconochie's collections, or in the catalogue thereof, at the British Geological Survey in Edinburgh.

A nearby locality at Tarras Water Foot has been confused with Glencartholm. For example, Dineley and Metcalf (1999) stated that the fish from Tarras Water Foot are identical to those from Glencartholm, and mentioned that a separate locality could not be found during the survey by Lumsden *et al.* (1967). However, Størmer and Waterston (1968) reviewed the problem, and traced some of the confusion to Macconochie, who described his locality as 'River Esk, Glencartholm, Langholm at Foot of Tarras Water, 3 m. [4.8 km] S. of Langholm'. Later collectors, such as Jex and Stock, and Moy-Thomas, seem not to have distinguished separate outcrops along the Esk, which would explain why the fish faunas are similar. Similar confusion may well have occurred with the arthropods. Following Watson *et al.* (1948), Størmer and Waterston (1968) mentioned a locality in the Tarras Water just below the (now disused) railway bridge, about 2.5 miles (4 km) SSE of Langholm. Cater *et al.* (1989), following Leeder (1974), described a small outcrop in the river Esk, 1 km upstream from the main Glencartholm site (but the grid reference given refers to a place on the Tarras Water; however, the grid reference in this paper for Glencartholm is also erroneous). These authors also referred to another outcrop higher in the same (Whita) formation in the Tarras Water. The Whita Formation is older (Courcayan) than at Glencartholm (Holkerian), possibly yields a different arthropod fauna, and represent a different depositional environment than at Glencartholm (Cater *et al.* 1989). For these reasons it is proposed that the Glencartholm site be extended to include the river Esk section upstream to the Tarras Water and the lower reach of Tarras Water as far as the railway bridge, as a composite site.

Geological setting

The Glencartholm sequence is part of the Glencartholm Volcanic Beds within the Middle Border Group of southern Scotland, which roughly equates with the Fell Sandstone Group to the east and the lower part of the Oil Shale Group of the Scottish Midland Valley. The exposed section on the eastern bank of the River Esk is some 10 m long and 3 m high. The rocks dip to the south at about 15°, and the section is cut by three post-burial faults with known displacements (Cater *et al.*, 1989).

Cater *et al.* (1989) described the depositional environment in detail, on which this review is based. The sequence is transgressive, fining upwards from coarse, non-marine sandstones to fully marine shales (Figure 3.13). The basal 2 m consists of thinly plane-bedded, pebbly sandstones; the pebbles are mostly well-rounded vein quartz. The coarse sandstone is composed of metamorphic quartz, pyritic volcanoclastic material and perthitic feldspars. These fine up into finer-grained sandstones rich in volcanic ash and pyrite, some of the latter being of diagenetic origin. The sandy sediments pass up into generally thinly laminated and organic-rich, nodular cherty shales and cherty dolomicrites below an erosion surface. The only fossils recorded from this sequence are a few scales of the large euryhaline fish *Rhizodus*, found just below the erosion surface, and rare plant spores. The chert laminae show enterolithic and 'chicken-wire' textures. Microscopic lath-shaped pseudomorphs after anhydrite occur just below the erosion surface, and desiccation cracks are also present in the sequence. Abundant pyrite occurs at the edges of the chert layers.

The erosion surface (4.4 m above the base of the measured section) is overlain by a 10 cm intraclastic layer that fines upwards into laminated dolomicrites, containing quartz sand grains scattered along organic-rich laminae, and cherty laminae showing displacive textures. The dolomicrites are overlain by over 1 m of dark micritic limestone, devoid of burrows or fossils. It is composed of non-ferroan calcite mud with large lensoid fenestrae and pseudomorphs after gypsum, and cut by ferroan and non-ferroan calcite veins. It is overlain by two erosion-surface-based, normal-graded, 10 cm thick units, each containing abundant and diverse derived ostracods including the brackish water *Beyrichiopsis plicata*, and non-ferroan micrite intraclasts set

in organic-rich micrite. Several specimens of the shrimp *Tealliocaris* were found in the fine-grained top of one of these layers.

Above this is a gap of 1 m without exposure (about 6–7 m above the base of the measured section). A sequence of 5 m of black dolomitic silt-shales and silty dolostones, lacking burrows but containing an exceptionally well-preserved fauna of arthropods, fishes, ostracods and bivalves, follows. Some of the bivalves are of quasi-marine type, including articulated specimens of *Leiopteria bendersoni* and *Edmondia* sp. cf. *uniformis*. Fully marine fauna are rare, but include orthocones and echinoderms, representing 1% and 0.04% of the fauna, respectively (Schram, 1983). The sediments show indistinct organic-rich laminae, gradually passing into muddier layers; more dolomitic layers appear to have been slightly coarser-grained initially, and contain laminae rich in derived ostracods.

The interpretation of the basal sequence is one of volcanoclastic input from the Glencartholm Volcanic rocks mixed with vein quartz derived from the Southern Uplands and acid igneous material probably derived from the intrusive rocks of Galloway and Kirkcudbrightshire. The thin, normal-graded plane beds probably record deposition from sheet-floods, possibly at the toe of an alluvial fan. The distance from source of some of the clasts, and the presence of overlying subaqueous deposits (see below), suggests that this was a fan-delta fed by a large river. The fining-upwards transition to the cherty sediments records the abandonment of the fan-delta. The overlying sediments contain evidence of evaporites; the abundant pyrite probably resulted from bacterial reduction of sulphate evaporites. The pseudomorphs after anhydrite also indicate sulphate supply, either from the sea or from the oxidation of the pyrite-rich volcanoclastic rocks. The organic-rich laminae may have originated from algal blooms in shallow, ephemeral water bodies that were hostile to life, probably due to poor oxygenation. The remains of the fish *Rhizodus*, which may have exceeded 3 m in length, imply access to a large water body.

The sequence as a whole records deposition on a desiccating coastal mud-flat, marginal to a lake or the sea. The beds immediately above the erosion surface probably record the effects of a storm, which eroded the mud-flat and spread intraclastic debris across it; mud-flat deposition then resumed. The pseudomorphs after gypsum

in the micritic limestone beds indicate that shallow evaporating conditions prevailed during its deposition. The non-ferroan calcite veins may record hydrothermal activity related to the Glencartholm Volcanic rocks. The overlying graded units are interpreted as storm deposits derived from peripheral muddy areas in which ostracods lived, and deposited in poorly oxygenated conditions that favoured the preservation of organic matter. The top part of the sequence represents a changeover to fully marine conditions, although the critical part of the transition is not exposed. The sediments were protected from wave activity; the more dolomitic layers may be low-energy (distal) storm deposits, preferentially dolomitized due to a slightly greater permeability than that of the enclosing mudrocks. It was in these poorly oxygenated, low-energy marginal marine to fully marine conditions that the diverse arthropod fauna of Glencartholm flourished.

The Whita Formation at Tarras Water Foot is part of the Lower Border Group of southern Scotland (Leeder, 1974). Only 2 m of well-exposed sediments crop out on the left bank of the Esk below a thick sandstone unit (Figure 3.13), but the lithologies and facies are essentially the same higher in the Whita Formation where it crops out in the Tarras Water. The Whita Formation is a stratigraphical/structural unit bounded by syn-sedimentary faults (Leeder, 1974).

The Tarras Water Foot sequence is interpreted as a coastal plain succession; lacustrine, crevasse-splay, stream-flood and fluvial distributary channel facies are represented. At the base of the sequence (Figure 3.13) are unoxidized, grey, mud-shales lacking burrows representing shallow, poorly oxygenated water without infauna. Desiccation cracks record periods of emergence, without plant colonization. Leeder (1974) observed pseudomorphs after halite in this facies, suggesting marginal marine or playa-lake conditions. The intercalated dolomiticrites are mostly nodular, displacing early diagenetic cementstones recording poorly oxygenated, brackish conditions (estuaries or tidal flats). Cryptalgal laminated dolostones with fenestrae and desiccation cracks are also present, consistent with a stressful, periodically emergent coastal setting. The thin, ripple-laminated, silty sandstones are interpreted as crevasse-splay deposits derived from nearby river channels into low-lying interfluvial areas. The fining-upward

part of Sandstone Unit 1 (Figure 3.13) is a typical point-bar deposit formed by lateral accretion. The coarse-grained lags are channel-base scour-fills. The wavy-laminated fine-grained sandstone capping this unit may be a crevasse-splay deposit formed after further subsidence of the flood-plain. The coarse upper part of Sandstone Unit 1 has an undulating, wave-rippled top and may represent a lacustrine storm deposit. During an initial storm-flood phase, sand and plant debris were carried into a shallow-water body. The deposit was partially re-worked by wave action during the waning storm stage. Sandstone Unit 2 consists of two separate shallow-water storm deposits similar to that described above. Coastal plain dolomitic mudrocks and splay sandstones cap the sequence, followed by a c. 4 m gap, and then over 3 m of coarse sandstones. Leeder (1974, plate 17, fig. 1) recorded a 1–5 m gap followed by 10 m of sandstones at this level. The sand body consists of upward-fining units; the thickness and coarseness of the trough cross-bedded units suggests that they were deposited in a major fluvial channel system, such as a distributary river crossing the coastal plain. The abundance of fluvial deposits, the lack of marine reworking (e.g. beach deposits) and of derived marine fossils indicates that most of the Tarras Water Foot sequence was deposited on an upper coastal plain beyond marine influence. However, in the absence of any apparent non-marine sulphate supply, the presence of pseudomorphs after halite (Leeder, 1974), cementstones and cryptalgal laminated dolostones is also consistent with raised salinities in the lower part of the section that may record limited marine influence.

The arthropod fauna

The arthropod fauna at Glencartholm is significant because the shrimp fauna (Figure 3.14) is the most prolific and diverse of all those in the Dinantian strata of northern Britain and the chelicerates include some unique and rare scorpions and bizarre eurypterids, and other forms.

Phylum ARTHROPODA

Subphylum Chelicerata

Order Xiphosura

Rolfeia fouldenensis Waterston, 1985

?*Euproops* sp.

Order Eurypterida

Adelophthalmus perornatus (Peach, 1882b): HOLOTYPE

?*Pterygotus* sp.

Woodwardopterus scabrosus

(Woodward, 1887): HOLOTYPE

unidentified eurypterids

Order Cyrtoctenida

**Cyrtoctenus peachi* Størmer & Waterston, 1968

Order Scorpiones

Anthracochaerilus palustris Kjellesvig-Waering, 1986: HOLOTYPE

Archaeoctonus glaber (Peach, 1882b): HOLOTYPE

Centromachus euglyptus (Peach, 1882b): HOLOTYPE

Eskiscorpio parvus Kjellesvig-Waering, 1986: HOLOTYPE

Gigantoscrapio willsi Størmer, 1963: HOLOTYPE

Loboarchaeoctonus squamosus Kjellesvig-Waering, 1986: HOLOTYPE

Pseudoarchaeoctonus denticulatus Kjellesvig-Waering, 1986: HOLOTYPE

?*Trachyscorpio* sp. Kjellesvig-Waering, 1986

unidentified scorpions

Subphylum Crustacea

Class Ostracoda

Bairdia sp.

?*Beyrichiopsis*

Tribolbina carnegiei Latham, 1932
cyprinidoidean myodocopid

Class Malacostraca

Subclass Phyllocarida

Sairocaris elongata (Peach, 1882a): LECTOTYPE

Subclass Hoplocarida

Bairdops elegans (Peach, 1908): LECTOTYPE

Crangopsis eskdalensis (Peach, 1882a): LECTOTYPE

Joanellia elegans (Peach): LECTOTYPE

Perimecturus parki (Peach, 1882a): LECTOTYPE

Subclass Eumalacostraca

Anthracocaris scotica (Peach, 1882a): LECTOTYPE

Anthracophausia dunsiana Peach

Belotelson traquairi (Peach, 1882a): LECTOTYPE

**Pseudogalathea macconochiei* (Etheridge, 1879)

Pseudotealliocaris etheridgei (Peach,

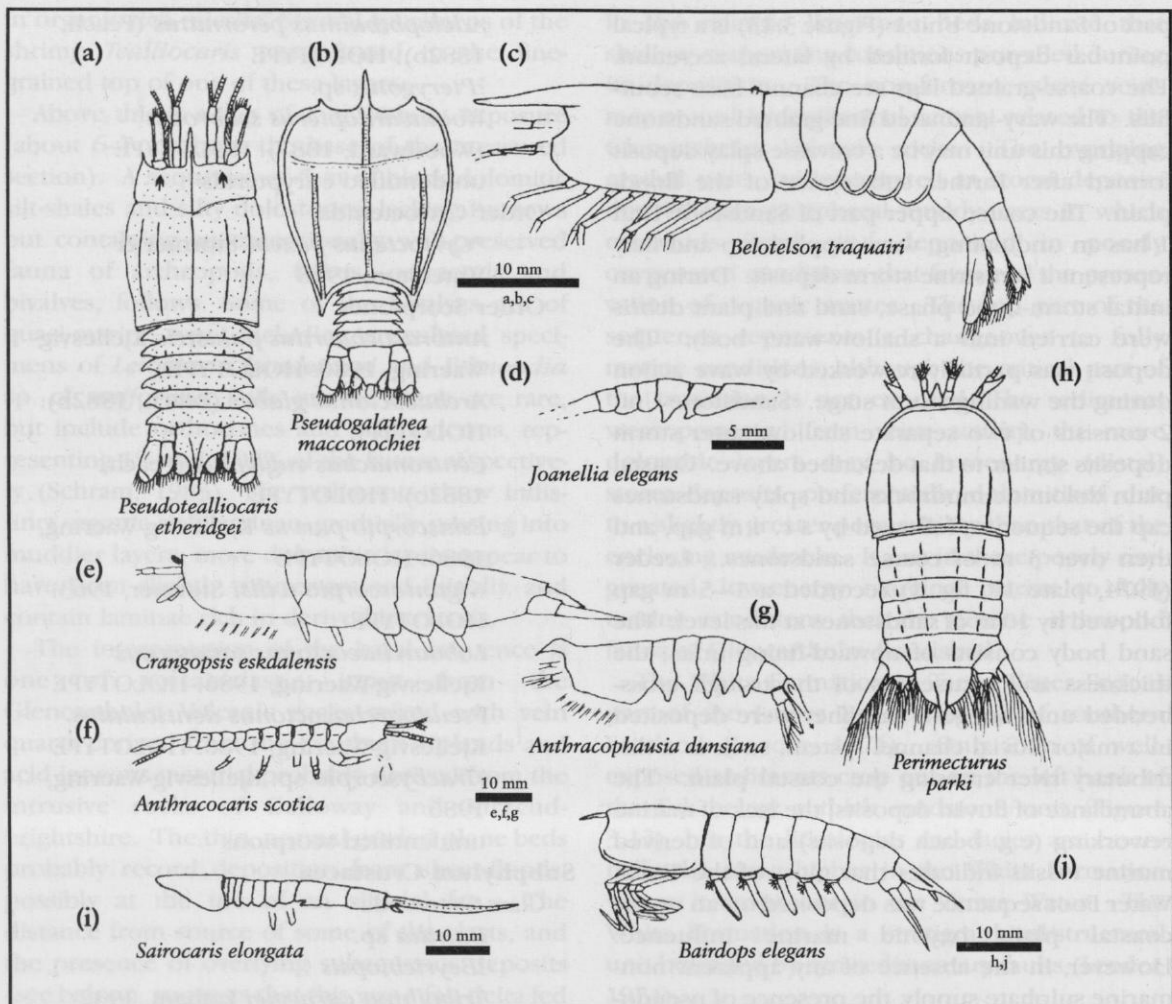


Figure 3.14 Fossil shrimps from Glencartholm. (After Schram, 1981.)

1882a: LECTOTYPE

†*Tealliocaris* (Peach, 1908)

unidentified malacostracans

Class Maxillopoda

Subclass Halicyna

Cyclus testudo Peach

*Also at Tarras Water Foot

† Only at Tarras Water Foot

Interpretation

The Glencartholm eurypterid fauna was first mentioned by Peach (1882b), who described *Adelophthalmus perornatus*, as a scorpion in the new genus *Glyptoscorpius*. However, because the genus was based on a suite of spec-

imens in different species, and the characters were either poorly preserved or meaningless, some confusion ensued in later revisions (see review in Størmer and Waterston, 1968). Bell (1922) recognized that another *Glyptoscorpius* species, *G. kidstoni* Peach, 1888, from Radstock, Somerset, was a eurypterid, and Waterston (1957) referred the genotype, *G. perornatus* from Glencartholm, and other species to the Eurypterida. Some specimens referred to *Glyptoscorpius* by Peach (1882b) from Glencartholm belong to *Gigantoscorpio* Størmer (1963) and to *Cyrtoctenus* Størmer & Waterston, 1968 (see below). Thus, *Glyptoscorpius* Peach, 1882b, is a junior synonym of *Adelophthalmus*, and its included species have all found better homes elsewhere.

Størmer and Waterston (1968) erected the new order Cyrtoctenida, type genus *Cyrtoctenus*, for some strange, eurypterid-like arthropods with comb-like appendages on the abdomen. One specimen from Glencartholm belongs to *C. peachi* Størmer & Waterston, 1968. Waterston *et al.* (1985) referred cyrtoctenids to Eurypterida: Hibbertopteroida, and this assignment was followed but Jeram and Selden (1994), but in the most recent systematic review of eurypterids, Tollerton (1989) recognized the order Cyrtoctenida as distinct from Eurypterida. The family Woodwardopteridae was erected by Kjellesvig-Waering (1959) for the Glencartholm eurypterid *Woodwardopterus scabrosus* (Woodward, 1887). Just recently, excavations by S. P. Wood adjacent to the Glencartholm site have yielded a number of specimens of *Rolfeia fouldenensis*, the earliest known limuloid, previously known only from Foulden (see GCR site report in the present volume).

Scorpions from Glencartholm were first described by Peach (1882b), and later systematic revision was carried out by Petrunkevitch (1949, 1955). *Gigantoscrapio willsi* was described by Størmer (1963) in a fascinating study that included a description of nematodes and other decomposing organisms that had been feeding on the scorpion carcass before fossilization. In his posthumous review of fossil scorpions of the world, Kjellesvig-Waering (1986) re-described the Glencartholm scorpions and erected the new genera and species *Eskiscrapio parvus* Kjellesvig-Waering, 1986, *Loboarchaeoconus squamosus* Kjellesvig-Waering, 1986, and *Pseudoarchaeoconus denticulatus* Kjellesvig-Waering, 1986; he placed the last two genera in a new family, Loboarchaeoconidae Kjellesvig-Waering, 1986. However, re-study of the specimens led Stockwell (1989) to consider that *Loboarchaeoconus* and *Pseudoarchaeoconus* were synonyms of *Archaeoconus*, and that Kjellesvig-Waering's family Loboarchaeoconidae was a junior synonym of Archaeoconidae Petrunkevitch, 1949. In a recent cladistic analysis of early scorpions (Jeram, 1998), the Archaeoconidae is subsumed within the family Proscorpiidae Scudder, 1885, in which *Archaeoconus* is especially interesting because it is one of only two genera in this family (the other being *Labriscrapio* Leary, 1980, from the middle Carboniferous strata of Illinois) which occur in Carboniferous rocks, the others range from late Silurian to mid-Devonian in age.

These genera represent late survivors of the early aquatic scorpions, and the inferred marginal marine environment of the Glencartholm beds in which *Archaeoconus* occurs is in agreement with this. Stockwell (1989) suggested that *Eskiscrapio parvus* Kjellesvig-Waering, 1986, a tiny scorpion from Glencartholm, might be a juvenile of one of the other archaeoconids at the same locality. However Jeram (1994b) could find no trace of typical archaeoconid cuticle on the specimen and included it as *incertae sedis* in the suborder Mesoscorpionina Stockwell, 1989. In the same study, Jeram (1994b) placed the Glencartholm scorpions *Centromachus* and *Gigantoscrapio* in the Mesoscorpionina, so *Eskiscrapio* could represent a juvenile of one of these genera.

Among Crustacea (Figure 3.14), *Sairocaris elongata* is abundant at Glencartholm; a phyllocarid, it is a later representative of an early Palaeozoic diversity of bivalved Crustacea, before the true shrimps appeared in the Devonian Period (Briggs and Clarkson, 1990). *Cyclus*, a relatively common genus in non-marine Carboniferous rocks, has had a chequered systematic history, having been allied at various times with the trilobites, chelicerates, crustaceans, and as a separate subclass of trilobitomorphs (Schram *et al.*, 1997). A recent study of the cycloids of Mazon Creek (Schram *et al.*, 1997) concluded that the cycloids are indeed Crustacea, possibly a sister taxon to the copepods. These authors noted a variety of body forms within the Cycloidea; *C. testudo* from Glencartholm belongs in the *C. rankini* species group of somewhat flattened forms. They found no evidence for a parasitic ('fish louse') mode of life, but suggested that the range of body forms of cycloids compared to that found in the specialisms of Holocene small crabs.

Of the true shrimps (Hoplocarida and Eumalacostraca), *Crangopsis eskdalensis*, *Pseudotealliocaris etheridgei* are abundant, *Bairdops elegans*, *Anthracocaris scotica*, *Perimecturus parki*, *Anthracophausia dunsiana* and *Belotelson traquairi* are common, whereas *Pseudogalathea macconochiei* and *Joanellia elegans* are rare at Glencartholm (Schram, 1983). Briggs and Clarkson (1990) reviewed the radiation of late Palaeozoic shrimps. They concluded that taphonomy was a more important factor than biodiversity in accounting for the fossil record of Devonian-Permian shrimps: fossils were most-often preserved in marginal marine

environments. The oldest-known shrimp occurs in Devonian strata, but in the Lower Carboniferous rocks the diversity exceeded 10 families, indicating a cryptic radiation. The fossil record of Palaeozoic shrimps reveals two major peaks in apparent diversity: Glencarholm (Viséan) and Mazon Creek, Illinois (Westphalian). Thus, Glencarholm represents the most important source of information on the first half of shrimp evolutionary history.

Briggs and Clarkson (1990) discussed the modes of life of Palaeozoic shrimps. The Glencarholm fauna, like those of Bear Gulch (Mississippian, Montana) and the Essex biota of Mazon Creek (Westphalian, Illinois), is dominated by carnivores; 67% of individuals at Glencarholm fall into this feeding category. *Perimecturus parki*, *Bairdops elegans*, *Anthracophausia dunsiana*, *Anthracocaris scotica*, and the phyllocarid *Sairocaris elongata* are rapacious carnivores, *Belotelson traquairi*, *Pseudogalathea macconochiei* and *Tealliocaris etheridgei* are scavengers or low-level carnivores, whereas the others are of uncertain feeding type.

Comparison to other faunas

The Glencarholm section ranges from fan-delta through coastal lagoon to fully marine (Cater *et al.*, 1989). Briggs and Clarkson (1989) discussed Schram's (1981) classification of Carboniferous crustacean communities. The near-shore marine community was characterized by Schram (1981) on the basis of Glencarholm, Bear Gulch, and the Essex fauna of the Mazon Creek biota. These faunas include the highest diversity of Carboniferous shrimps and the similarity between the crustacean assemblages is striking. Sedimentological evidence, however, indicates that the environment may have experienced more freshwater influence than formerly suggested. The Glencarholm section shows the greatest marine influence of all those yielding shrimps in the Dinantian rocks of Britain (Cater *et al.*, 1989), but fully marine taxa are rare (see above). This suggests that salinities fluctuated within brackish to near-normal marine. The Bear Gulch Limestone was deposited in a low-energy shallow water tropical basin (Williams, 1983; Factor and Feldmann, 1985). Although benthic organisms (including articulate brachiopods) are common, many normal marine taxa (e.g. corals, bryozoans and echinoderms)

are absent. Lack of bioturbation indicates low oxygen levels below the sediment-water interface, and the proximity of non-marine and brackish-water deposits suggests a large freshwater input (Williams, 1983). Likewise, the Essex fauna lacks a number of typical stenotypic groups, although polychaetes are relatively abundant. Fusulinid foraminiferans, sponges, articulate brachiopods, anthozoan corals, bryozoans, crinoids and cephalopods are all absent or very rare (Baird *et al.* 1985, p. 264). In this case the assemblage probably occupied a semi-restricted estuarine embayment and salinities were lowered due to the influence of rivers (Baird *et al.*, 1985, p. 277). Thus, the three most complete examples of Schram's (1981) near-shore marine community, Glencarholm, Bear Gulch, and the Essex fauna, all represent conditions where salinity was probably lower than normal marine levels (Briggs and Clarkson, 1989).

Because of the Lower Carboniferous age of Glencarholm, this Fossil-Lagerstätte constitutes an important window on the evolutionary history of scorpions and eurypterids, which are otherwise sparsely represented in rocks of this age. This is especially true for the scorpions, which included both aquatic and terrestrial forms living together at this time (Jeram, 1994a).

Conclusions

Glencarholm has yielded the greatest diversity of Lower Carboniferous shrimps in the world, which, together with the younger Mazon Creek fauna of Illinois, represent the main source of information on shrimp evolution in the Palaeozoic Era. Seventeen crustaceans have been recorded, for half of which this site is the source of the type specimens; several are known only from Glencarholm. For the Chelicerata, especially scorpions and eurypterids, Glencarholm is scarcely less important. Fifteen species are known, for nine of which (all those identified to species level) this site is the source of the type specimens. Many of the collections are Victorian in age, but substantial excavations were carried out in the 1930s and 1960s. Exploratory trenching in the 1980s allowed a modern stratigraphical and sedimentological study to be carried out. Thus the palaeoecology and preservation of the arthropods is well known. This has led to good understanding of the environmental and ecological context of the

faunal, and places it into a framework of Carboniferous arthropod faunas worldwide. Glencartholm is a major source of information in this context. The 1980s excavations also showed further potential of the site for more finds of fossil arthropods and more detailed palaeoecological research at this internationally rich and important fossil site.

GRANTON SHORE, LOTHIAN (NT 245 771)

Introduction

Foreshore exposures near Granton Harbour, near Wardie, along Edinburgh's Firth of Forth shoreline in East Lothian, Scotland (Figures 3.9 and 3.15) expose a sequence of Upper Viséan strata of Lower Carboniferous (Asbian, c. 332 Ma) age. These include the internationally famous Granton 'Shrimp Bed', renowned mainly for fossils of the conodont animal found here but it also has an important arthropod fauna of eumalacostracan crustaceans, especially the shrimps *Tealliocaris woodwardi*, *Waterstonella grantonensis* and *Crangopsis socialis*.

The Granton 'Shrimp Bed' was discovered in 1919 by D. Tait and its lithology and regional setting were first described by him in 1925. He also listed the fauna and figured a slab covered with many of the small crustacean fossils and reported that they were considered to belong to the genus *Tealliocaris* by B.N. Peach 'but that some of the species are new to science'. According to Briggs and Clarkson (1983) the Harvard palaeontologist P.E. Raymond subsequently collected material from the site with Tait and apparently prepared a description of the most abundant crustacean, which he considered to be a new species; the paper was never published. Not until 1979 was the common crustacean species, *Waterstonella grantonensis*, named and described by Schram.

The discovery in the early 1980s of the fossilized traces of soft tissues associated with conodont assemblages from the 'Shrimp Bed' at Granton (Briggs *et al.*, 1983) co-incided with a wider project on Scottish Carboniferous Crustacea and revitalized interest in all aspects of the 'Shrimp Bed'. As a result a detailed account of its lithology and palaeontology was published by Briggs and Clarkson in 1983.

Description

The Granton 'Shrimp Bed' of Upper Viséan (Asbian) age lies within the Granton Sandstones of the Lower Oil Shale Group (see Figure 3.10) and Calciforous Sandstone Measures. Two units occur within the Granton Sandstone – the lower Craighleith Sandstone (30 m thick) and upper Ravelston Sandstone (110 m thick) separated by about 100 m of shale within which lies the 'Shrimp Bed'. The Granton Sandstones underlie the Wardie Shales that are exposed to the east of Granton Harbour and have yielded a well-known fish fauna (Dineley and Metcalf, 1999).

The Wardie Shales lie within the Lower Oil Shale Group whose oil shales are largely of non-marine origin and were deposited in a large fresh or brackish water lake that covered the eastern end of the Midland Valley of Scotland. The lake was intermittently flooded by marine incursions from the east and the 'Shrimp Bed' lies within a lime-rich layer deposited during such an incursion.

The 'Shrimp Bed' was originally found by Tait in two locations of which the more easterly, the old Granton land and sea quarries have been lost due to infilling associated with land reclamation. Much of the second, westerly outcrop along the Muirhouse shore has been covered up more recently by construction of an esplanade and breakwater. Only two small exposures remain and these were re-discovered by S.P. Wood in 1978 and J.G. Sharp in 1981.

Some 20 m of the Wardie Shales are exposed at Granton Shore and within them is a 45 cm interval that includes three thin bands of laminated limestone. The lower Bands 1 and 2 (each around 4cm thick) (Figure 3.15), are lithologically similar but more fissile and less limy than the upper Band 3, which is significantly thicker (14–20 cm). All three bands appear to be largely of algal origin and consist of alternating dark and light laminae that pass laterally into microbreccias.

Band 3 is by far the most fossiliferous and has yielded all the material recorded by Briggs and Clarkson (1983) and is considered by them to have also been the source of Tait's specimens as they share the same distinctive lithology. The abundant crustaceans are confined to four bedding planes within Band 3 but other elements of the fauna (worm-like forms and branching organisms) occur throughout the Band.

Post-Devonian fossil arthropods

The limestones are predominantly dolomitic with alternating layers of calcareous mud and dark brown-black carbonaceous material up to 1 mm thick with some of the latter preserving algal filaments. Shrinkage cracks on bedding planes, microbreccias and pull-apart structures suggest dewatering or dessication, perhaps linked with intermittent subaerial exposure. The crustacean fossils are generally well preserved and are normally found on undisturbed laminae.

The detailed characteristics of the Granton Shore laminated limestones have been found to compare closely with other fossil and Holocene tidal-flat stromatolite successions. Such characteristics suggest that the Granton assemblage, with its associated dolomitization and evidence of dessication, was deposited and preserved in similar intertidal algal mat environments.

Palaeontology

Although the most common fossils within the Granton 'Shrimp Bed' are eumalacostracan crustaceans, other faunal elements have been found. Two poorly preserved palaeoniscid fish are known along with an unidentifiable coiled nautiloid and bivalve, but Tait's record (1925) of rare gastropods cannot be verified. Similarly, two worm-like forms are unidentifiable. More common are abundant branching organisms that are considered by Briggs and Clarkson (1983) to be the remains of hydroids but could alternatively be algal or bryozoan in origin.

The most famous fossils from the Granton Shore 'Shrimp Bed' are undoubtedly those of the conodont animal. Small tooth-like isolated conodont elements have been described since the early decades of the 19th century, but their biological affinities were debated and disputed

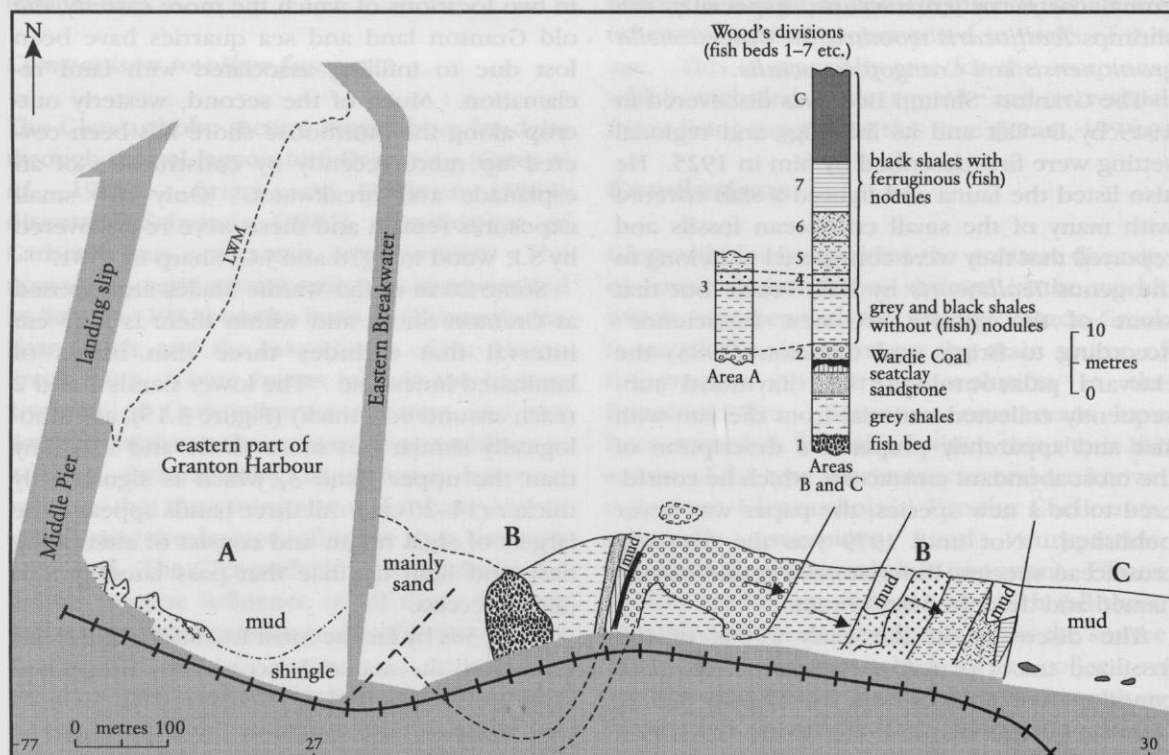


Figure 3.15 Sketch map and geological section at the Granton Shore GCR site, East Lothian. (After Wood, 1975.)

until the 1980s and the discovery of the first fossilized conodont animal from the Granton 'Shrimp Bed' (for a review of the history of investigation of conodonts see Sweet and Donoghue, 2001). The first specimen to be found was unbeknowningly recovered many years ago, probably by Tait. It lay unrecognized in the collections of the Institute of Geological Sciences (now the British Geological Survey) until 1982. Since then, several other specimens have been found and described (Aldridge *et al.*, 1993), now the only dispute concerns the exact position of the group as primitive vertebrates.

The crustaceans are all preserved in the dark organic-rich (?algal) layers and are generally very obvious as they contrast with the sediment background being preserved in whitish fluorapatite. It is not clear whether the mineral is replacing the cuticle or is an infill of the body cavity.

The commonest crustacean in the 'Shrimp Bed' is *Waterstonella grantonensis* and is normally found as complete laterally compacted specimens although disarticulated specimens are common on some bedding planes and probably represent exuviae. Most entire specimens preserve all the appendages, even the long delicate antennae and some retain traces of the gut, all of which suggests that the fossil remains are those of carcasses.

Crangopsis, represented by two forms that may be separate species, is also present in some abundance at certain horizons in the 'Shrimp Bed'. The smaller form can easily distinguished from *Waterstonella* in being smaller (14–22 mm in length) but with a thicker cuticle and more robust morphology. It has been found to occur in similar numbers on three horizons. The larger form of *Crangopsis* (up to 50 mm long) occur rarely in Band 3 and has been identified by (Schram, 1979) as *Crangopsis socialis* (Salter, 1861), a species that is common elsewhere in the shrimp bearing sequences of the Midland Valley of Scotland. Both *Crangopsis* and *Waterstonella* were probably filter feeders.

Although Peach thought that the 'shrimp' fossils collected by Tait (1925) were *Tealliocaris*, only four poorly preserved specimens are now recognized from the Granton 'Shrimp Bed'. Slightly more common is the much larger genus *Anthracophausia* that was first named and described by Peach in 1908. The presence of a raptorial second antenna in this genus shows that it was an active predator.

The preservation of the 'Shrimp Bed' crustaceans, which dominate the fauna, is unusual. If the stromatolites were intertidal, it may be that the crustaceans were concentrated in intertidal pools where they died as the pools dried out. The completeness of so many of the fossils indicates that they must have been rapidly covered with algal films and sediment.

The relative occurrence of the most abundant species is somewhat puzzling. *Waterstonella* only occurs at Granton suggesting a particular kind of restricted environment, perhaps hypersaline. However, *Crangopsis* occurs elsewhere and must have been tolerant of a wider range of salinity conditions. Briggs and Clarkson (1983) suggest as an alternative explanation that preservation of the lightly sclerotized *Waterstonella* requires the exceptional conditions that are only present in the 'Shrimp Bed' at the Granton Shore GCR site.

Comparison of Lower Carboniferous 'shrimp' (eumalacostracan) bearing successions in Scotland and Northern England (Cater *et al.*, 1989) shows common features that can be interpreted as indicative of particular environments of deposition. Twelve shrimp-bearing localities were compared by Cater *et al.* (1989) and most were found to have been deposited in coastal delta-plain or interdistributary bay environments with transitional salinity. None of the shrimp beds was deposited under fully marine conditions but most sequences show some evidence of marine influence. Crustacean diversity is known to increase with salinity and the relatively low diversity (compared with Glencarholm) seen at Granton probably reflects deposition in a brackish water interdistributary bay.

Conclusion

The remaining foreshore exposures of the Granton 'Shrimp Bed' near Granton Harbour in East Lothian are of considerable importance for their fossil eumalacostracan 'shrimps', especially as there is a unique endemic element to the fauna – *Waterstonella grantonensis*. The site is part of a network of other Scottish Lower Carboniferous Oil Shale sites that includes Glencarholm and Foulden. The Granton site is also of international renown for the co-occurring primitive vertebrate conodont animal *Clydagnathus*.

EAST KIRKTON, LOTHIAN (NS 990 690)

Introduction

The East Kirkton site, near Bathgate in West Lothian is a disused limestone quarry, some 27 km west of Edinburgh (Figure 3.9) where Lower Carboniferous limestones have been worked as a building stone since the 19th century (Rolfe *et al.*, 1994). Some plant and invertebrate fossils were recovered from here during the latter part of the 19th century but it was not until the 1980s and the pioneering excavations of Mr S.P. Wood, a professional fossil collector, that the true fossil riches of these strata were revealed. Since then, intensive collecting by international experts has uncovered a remarkably well-preserved terrestrial fauna and flora that offers unique insights into an early Carboniferous (Upper Visean, Brigantian) age freshwater lake ecosystem, some 328 million years old. The fossils include a primitive reptile-like tetrapod, some of the earliest-known temnospondyl amphibians, fishes and a variety of arthropods which are the main concern here – namely eurypterids, myriapods, scorpions and the earliest-known harvestman (opilionid).

It was the discovery at East Kirkton in 1984 of the almost complete and articulated skeleton of reptile-like tetrapod *Westlothiana lizziae* (Smithson and Rolfe, 1991) by Mr S.P. Wood that prompted a detailed investigation of the strata in and around this quarry. At the time it was thought that *Westlothiana* was perhaps one of the oldest known true amniotes and this generated a great deal of interest in the fossil potential of the site. From 1987 systematic investigation of the site was carried out under the auspices of the National Museums of Scotland and the results were published in a special volume by the Royal Society of Edinburgh (Rolfe *et al.*, 1994).

Description

The East Kirkton Limestone lies at the top of the West Lothian Oil Shale Formation and within the quarry site there is a highly variable and well-stratified succession of shales and tuffs overlying a distinctively laminated sequence of thin cherty limestones and underlain by further shales and tuffs, altogether some 15 m of strata. The succession of carbonate laminites and volcanoclastic

lithologies has been logged and extensively sampled with the identification of some 88 separate lithological units (Whyte, 1994).

The exposed 11m thick East Kirkton Limestone sequence consists, in ascending order, of calcareous tuffs (Units 88–83), an important tetrapod-bearing black shale (Unit 82), laminated cherty beds (Units 81–76), massive spherulitic limestones (Units 75–4), a series of intermediate beds (Units 73–70) then the characteristic laminated spherulitic limestones of East Kirkton (Units 69–36). Tuffs are present throughout the succession, but are especially abundant between units 76 and 72. The overlying strata are some 4 m thick of which the lower part consists of the 2m thick Little Cliff Shale (Units 36–32) and terminates with the overlying Geikie Tuff (4 m thick, Units 31–1), capped with a 2 m thick basalt lava.

Typically, the East Kirkton Limestone is a carbonate–organic laminite in which radially fibrous calcite spherules are abundant at many levels. In addition there are larger stromatolite-like accretions of laminated botryoidal radially fibrous calcite (RFC). The common inclusion of cyanophyte and chlorophyte remains within the RFC indicates a close association in the development of the RFC with microbial cyanophyte mats that spread over the sediment substrate and in some instances they may have been contemporaneous (Walkden *et al.*, 1993). The larger botryoidal accretions often enclose elements of the micro- and meio-fauna. Stable isotopes from the calcite are similar to those of present-day freshwater precipitates and whereas precipitation may have been microbiologically mediated, the spherules and botroids are regarded as passive lake-floor cements.

The siliceous 'cherty' laminae of Units 80–79 have also been analysed in detail (McGill *et al.*, 1993) using stable isotopes. Oxygen isotopes show that the silica was deposited from meteoric water at a temperature of around 60°C. This is consistent with Geikie's claim (1861) that the silical laminae are a primary feature and result from hot-spring influence in a lake-type environment.

The tuffs are all of basaltic origin and may have been debris flows with perhaps some lahars but they have all been re-deposited. None are air-fall tuffs and so their presence does not necessarily indicate active volcanicity during deposition of the succession.

The East Kirkton Limestone is the lowest of

five carbonate sequences within the Bathgate Hills Volcanic Formation and can be correlated with the Hopetoun Member of the West Lothian Oil-Shale Formation. Indeed a black shale near the base of the limestone sequence at East Kirkton has been found to be kerogenous with a high hydrocarbon-yield exceeding that of some of the Lothian Oil Shales. The succession correlates with the lower part of the Brigantian Stage at the top of the Visean Series of the Lower Carboniferous strata.

Palaeontology

An extensive flora and fauna was recovered in the 1980s during intensive collecting by teams of experts. Most publicity has been attached to the discovery of the new terrestrial vertebrates which apart from the reptiliomorphs such as *Westlothiana* (Smithson *et al.*, 1993), *Silvanerpeton* (Clack, 1993) and *Eldeceeon* (Smithson, 1993) includes some important new specimens of some of the earliest temnospondyl amphibians known, especially *Balanerpeton* (Milner and Sequeira, 1993), which is known from more than 30 complete or nearly complete specimens. In addition, numerous acanthodian and actinopterygian fish together with some hybodont sharks have been found (Coates, 1994) and also a diversity of invertebrate and plant fossils.

Different groups of the fossil biota tend to have particular distributions within the overall sequence although plant and arthropod material does tend to occur throughout. Even so plants are most common within certain units (see Scott *et al.*, 1994, for details). The lower part of the succession (Units 88–72) is dominated by the transported remains of arborescent gymnosperms that grew in warm, fairly dry conditions. The presence of charcoal at certain levels is indicative of a prevalence of periodic forest fire, especially in the lower part of the East Kirkton Limestone (Units 88–81). Higher up Units 51–39 are dominated by pteridosperm fronds and small fern leaves that were perhaps transported further into the lake environment. The plants of the overlying Little Cliff Shale show a dramatic change to a lycopod flora adapted to rooting in permanently damp soils and may reflect the onset of wetter climate conditions.

Tetrapod and fish fossils have been found within the Little Cliff Shale (Units 38–26) and the fish predominate in the upper part reflecting a

passage from terrestrial to aquatic environments. Tetrapods have also been found in the East Kirkton Limestone lower in the sequence (Units 82–70), especially in the black shale Unit 82.

Ostracods have been found sporadically throughout the East Kirkton Limestone and tend to occur in monospecific swarms, for example *Carbonita* sp., which were bottom-dwelling primary consumers that fed on the lake-floor microflora. In addition, poorly preserved bivalves have been found within the Little Cliff Shale.

Of most concern here is the remarkable and diverse arthropod fauna of eurypterids, scorpions, myriapods and a single important specimen of a harvestman (opiolinid), the oldest known fossil representative of this group.

Eurypterids

Unfortunately, the horizon that, in the 19th century, provided the spectacular large three-dimensional specimens of *Hibbertopterus* (originally referred to in the Scots vernacular as 'Scouler's heids') has not yet been relocated. *Hibbertopterus scouleri* (Hibbert, 1836) was the first animal fossil to be described from East Kirkton and was the first-known British eurypterid to be found and described, although it was not initially recognized as such since eurypterids as a distinct group of extinct arthropods were only recognized in 1825 in America.

However, plenty of flattened and fragmentary eurypterid material has been found recently and from this the remains of another two genera of hibbertopteroids, *Dunsopterus* and *Cyrtoctenus*, have been identified. Nevertheless, nearly all the identifiable material from East Kirkton is attributable to *Hibbertopterus scouleri*.

Typically hibbertopteroids are short-bodied eurypterids with a large, domed prosomal shield (carapace) and with specialized food-gathering structures on the second, third and fourth pairs of prosomal appendages. New material from East Kirkton revealed that the posterior legs and telson of *Hibbertopterus scouleri* more closely resemble those of cyrtoctenids than previously thought. This observation has prompted Jeram and Selden (1994) to postulate that *Hibbertopterus*, *Dunseropterus* and *Cyrtoctenus* are separate growth morphologies of a single species. A new investigation of the supposed giant spider *Megarachne*, from the uppermost Carboniferous strata of Argentina showed that this animal was also a large eurypterid related to

the hibbertopteroids (Selden *et al.*, 2005), specifically confamilial with *Woodwardopterus scabrosus* of Glencartholm (see GCR site report). When comparing *Megarachne* with *Hibbertopterus*, Selden *et al.* (2005) noted that the supposed genital plate beneath the metastoma in one specimen of *Hibbertopterus* figure by Waterston (1957), which resembles a similar plate seen on the ventral surface of *Megarachne*, could represent fused coxae VI. Thus the eurypterids of East Kirkton are an important component of the worldwide fauna of bizarre, giant eurypterids of Carboniferous times.

Scorpions

Articulated scorpion specimens are rare at East Kirkton, most of the scorpion fossil material consists of fragmentary cuticle. But when isolated from the matrix, the cuticle is beautifully preserved, better than any other Carboniferous material and has allowed the fauna to be described in considerable detail (Jeram, 1994). The most common scorpion at East Kirkton is *Pulmonoscorpius kirktonensis* and it is the oldest scorpion that is known to have been fully terrestrial.

The discovery of some exceptionally well preserved material here has allowed Jeram and Selden (1994) to identify the presence of true book-lungs in this genus. Book-lungs are an essential adaptation for land living and the intake of oxygen directly from air. Although most of the known specimens from East Kirkton are tiny juveniles there are rare larger individuals including a probable adult with the considerable maximum length of around 70 cm, much larger than any living scorpions, this extinct giant genus has been interpreted as a fully terrestrial top carnivore of the forest and lake-shore. With large lateral compound eyes, vision may have played a significant role in prey capture and it probably hunted by day, compared with nocturnal hunting typical of modern scorpions. The gigantism of this Carboniferous scorpion may have been due to the lack of even larger tetrapod predators and/or the more oxygen-rich Carboniferous atmosphere.

Myriapods

Fossil myriapods are uncommon at East Kirkton and what few specimens that have been recovered are not particularly well preserved but are nevertheless palaeontologically important as shown by Shear (1994). One of them, a milli-

pede, preserves the oldest known ozopores (openings of repugnatorial glands) and spiracles, thus providing unequivocal evidence of a fully terrestrial mode of life.

The fossils were found in Unit 47 of the East Kirkton Limestone and represent at least three ecomorphotypes that were specialized for different forest microhabitats. One 'bull-dozer' its way through the litter of the forest floor, another's body has lateral knobs that enabled it to traverse through tunnels.

The fossil record of myriapods extends back at least into Silurian times and perhaps much earlier as suggested from trace-fossil evidence (Wilson and Anderson, 2004) making them some of the earliest known terrestrial arthropods. However, there is a significant gap of some 60 million years in the post-Devonian record until these East Kirkton fossils, which are the oldest known from Carboniferous times.

Opilionid

A remarkably modern-looking opilionid (harvestman) from the East Kirkton Lagerstätte was reported by Wood *et al.* (1985), and formally described by Dunlop and Anderson (2005) as *Brigantibunum listoni*. Opiliones branched relatively early in their history into the modern clades; the earliest described harvestman is from the Early Devonian Rhynie Chert (see GCR site report), and this animal shows affinities to the modern Euponi clade. *Brigantibunum* was also provisionally assigned to Eupnoi by Dunlop and Anderson (2005). Thus, the East Kirkton harvestman adds evidence to the theory that the crown-group taxa of Opiliones evolved earlier than those of other arachnids, and that harvestmen are possibly fairly basal within the Arachnida (Giribet *et al.*, 2002).

Interpretation

The East Kirkton deposits have been interpreted as those of a predominantly shallow freshwater-lake basin, spasmodic ash falls and occasional marine incursions. The depositional environment was situated close to the West Lothian volcanic centre and may have extended from West Lothian to the Glasgow district either as a single water body (sometimes referred to as 'Loch Baldernock', Whyte, 1994, p.245) in a region that lay within a humid tropical climate regime. The water body may have resulted from the

development of volcanic activity impacting upon the local palaeogeography.

Whyte (1994, p. 246) pointed out that the environmental interpretation of the limestones as deposits in freshwater has been largely based on the lack of marine fossils and the presence of terrestrial fossils. However, many of the aquatic fossils belong to groups that can tolerate brackish conditions such as the ostracods, spirorbids and fishes.

The rich terrestrial flora and fauna is remarkably well preserved and offers a unique view of an early Carboniferous ecosystem in a volcanic setting with a wet tropical climate. Apart from the internationally important tetrapods and abundant fish and plant fossils, a variety of invertebrates have been recovered, largely arthropods such as harvestman 'spiders', millipedes, scorpions and large eurypterids.

Whereas the tetrapods may have been dependent on aquatic food sources, the aistopod amphibian may have occupied a terrestrial niche comparable to that of some recent snakes, living within the plant litter or even burrowing in the soil. Its few large teeth suggest that it preyed on organisms almost as large as the gape of its own jaws. These prey would have almost certainly included arthropods and small or larval tetrapods.

A gymnosperm-pteridosperm dominated forest surrounded the water body for much of its existence and would have supported a diversity of terrestrial organisms. Some at least of these have been preserved in the lake bed sediments and some of them may have been driven into the lake environment during forest fires, especially the large scorpions and millipedes. The amphibious hibbertopterid eurypterids must have occupied the lake at those times when the lake waters supported sufficient organisms for a food chain to be established.

Conclusion

This internationally important site has a unique and diverse biota which is exceptionally well preserved and has recently been studied in considerable detail by an international team of experts. The fossil arthropods have been shown to form an integral part of evolving land communities and early terrestrial environment with their mixture of terrestrial and aquatic deposits. There is the good potential for further excavation.

WRITHLINGTON, AVON (ST 703 553)

Introduction

The Radstock coal basin of the Bristol-Somerset Coalfield in south-west England (Figure 3.16) has been long recognized (Woodward 1729; von Sternberg 1820-1838; Brongniart 1828-1838) for the exceptional preservation of its Upper Carboniferous plant fossils. Numerous holotypes and important illustrations of fossil plants were chosen from Radstock basin examples (see Thomas and Cleal, 1994). The last mines closed in the 1970s, but reworking of the tips for coal from 1984 to 1986 exposed fresh Roof Shale (mainly mudstone) and attracted the interest of fossil collectors.

Through co-operation between the site owner, local geological and conservation groups and the enthusiasm of palaeontological societies and individuals, some 3000 tons of spoil from the old colliery tip was set aside in a fenced conservation area and in 1987 the site became a geological nature reserve – the Writhlington GCR site (Figure 3.17). The result has been one of the most successful and innovative, palaeontological site-based conservation initiatives of recent years.

Particularly through the efforts of Dr E. Jarzembowski and the many volunteers, both professional and amateur, a vast fossil fauna was assembled from the site (Jarzembowski, 1989) including vascular plants, arthropods (insects, arachnids, xiphosurans, conchostracans, giant millipedes and a eurypterid), nematodes,

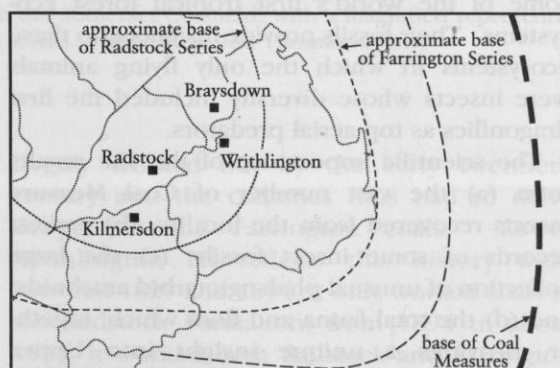


Figure 3.26 The Radstock Coal Basin of the Bristol-Somerset Coalfield, sketch map.

Post-Devonian fossil arthropods

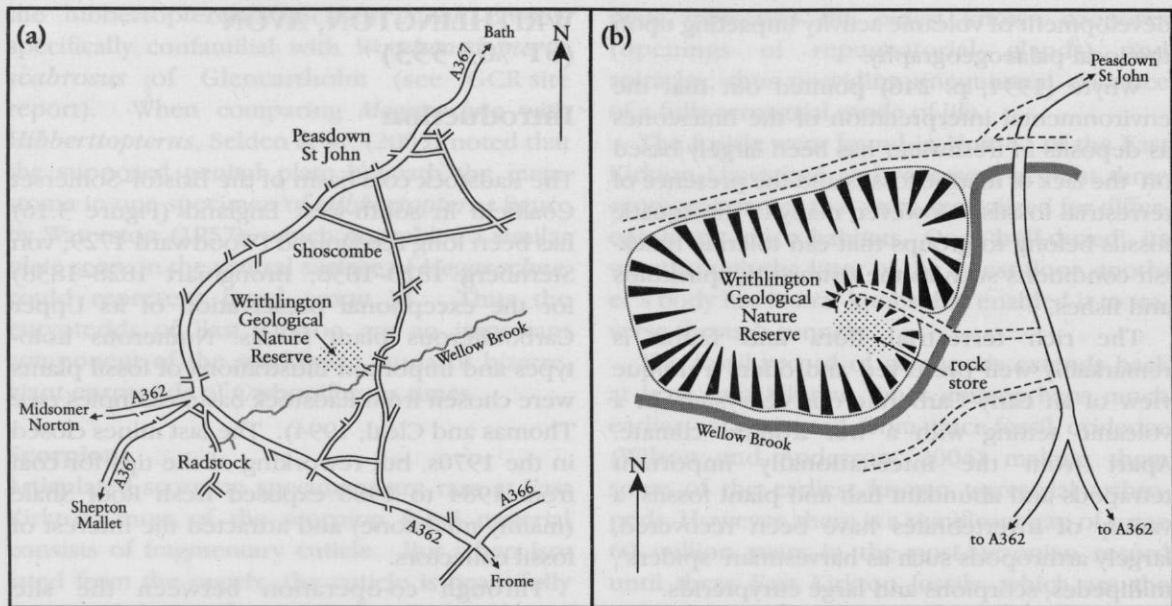


Figure 3.17 Sketch maps showing the location of the Writhlington geological nature reserve and the rock store. (After Jarzembowski, 1989b.)

bivalves, fishes and reptiles in order of descending abundance. The collection includes the largest collection of fossil insects in the UK, more than 1200 specimens, including the oldest known damselfly (Jarzembowski and Nel, 2002), and the greatest number of phalangiotarbid arachnids in Britain. The fossil material is derived from Farrington Formation shales of late Westphalian D age (*Dicksonites plueckeneti* Subzone), some 307 million years old (Todd, 1991).

These Upper Carboniferous coals and associated sediments accumulated close to the palaeoequator and are therefore deposits of some of the world's first tropical forest ecosystems. Their fossils provide insights into these ecosystems in which the only flying animals were insects whose diversity included the first dragonflies as top aerial predators.

The scientific importance of the site results from (a) the vast number of Coal Measure insects recovered from the locality; (b) earliest records of some insect fossils; (c) the large collection of unusual phalangiotarbid arachnids; and (d) the total fauna and flora which, together, provides a unique insight into Upper Carboniferous terrestrial life on a delta plain (forested floodplain with freshwater wetland and waterways) in Britain (Todd, 1991).

Description

Writhlington lies in the southern part of the Bristol–Somerset Coalfield. Upper Carboniferous strata in this part of the coalfield form a broad structural basin known as the 'Radstock Syncline', which is truncated on the north side by the Farmborough Fault that was activated during the Hercynian (Variscan) orogeny. Apart from some exposure near Paulton, and in the Nettlebridge Valley, Upper Carboniferous rocks are concealed below a maximum of 150 m of Mesozoic cover (mainly Triassic and Middle Jurassic in age). Consequently, most of what is known of the geology of these strata is based on old mining records (e.g. Moore, 1937; Kellaway and Welch, 1948; Kellaway, 1970; Green, 1992).

Strata in the Radstock Syncline is mainly of Westphalian age, probably lying unconformably on Viséan Carboniferous Limestone. The interval can be divided into three main units (Figure 3.18). The lowest (Langsettian to middle Bolsovian) consists of about 1700 m of mudstones, thin sandstones and coals of the Vobster and New Rock groups (Moore and Trueman, 1937, 1942). These are overlain by some 3600 m of Pennant-like sandstones (upper Bolsovian to lower Westphalian D), which Kellaway (1970) referred to as the Downend and Mangotsfield

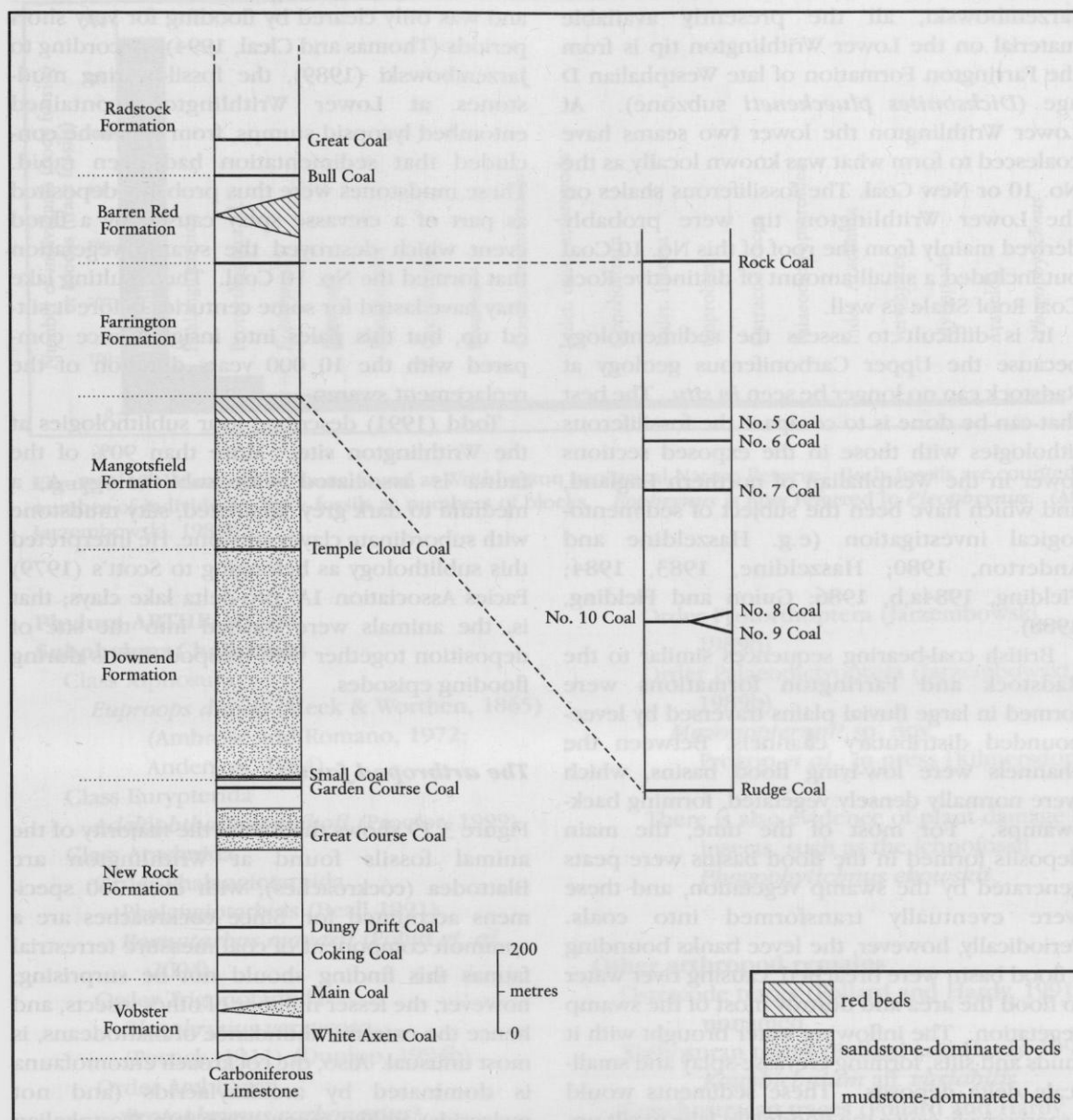


Figure 3.18 Generalized stratigraphical section through the Somerset Coalfield, with a magnified representation of the Farrington Formation showing the main coal seams. (After Cleal and Thomas, 1994.)

groups. These sandstones are, in turn, overlain by about 2500 m of mudstones and thin sandstones, which include most of the coals exploited in the Radstock area.

These supra-Pennant beds have been assigned to three formations: in ascending order the Farrington, Barren Red and Radstock formations. Much of the early mining in the area concentrated on the stratigraphically higher coals of the Radstock Formation, but these were

largely worked out by the early twentieth century and the collieries thus had to delve deeper to the Farrington coals. Lower Writlington Pit reflects this history well: between 1829 and 1894, it only worked coals in the Radstock Formation; from 1894 to about 1925, it worked both Radstock and Farrington coals; and from about 1925 to its closure in 1973, only Farrington coals were exploited (Jarzembowski, 1989b). According to

Jarzembowski, all the presently available material on the Lower Writhlington tip is from the Farrington Formation of late Westphalian D age (*Dicksonites plueckeneti* subzone). At Lower Writhlington the lower two seams have coalesced to form what was known locally as the No. 10 or New Coal. The fossiliferous shales on the Lower Writhlington tip were probably derived mainly from the roof of this No. 10 Coal but included a small amount of distinctive Rock Coal Roof Shale as well.

It is difficult to assess the sedimentology because the Upper Carboniferous geology at Radstock can no longer be seen *in situ*. The best that can be done is to compare the fossiliferous lithologies with those in the exposed sections lower in the Westphalian of northern England, and which have been the subject of sedimentological investigation (e.g. Haszeldine and Anderton, 1980; Haszeldine, 1983, 1984; Fielding, 1984a,b, 1986; Guion and Fielding, 1988).

British coal-bearing sequences similar to the Radstock and Farrington formations were formed in large fluvial plains traversed by levee-bounded distributary channels. Between the channels were low-lying flood basins, which were normally densely vegetated, forming backswamps. For most of the time, the main deposits formed in the flood basins were peats generated by the swamp vegetation, and these were eventually transformed into coals. Periodically, however, the levee banks bounding a flood basin were breached, causing river water to flood the area and destroy most of the swamp vegetation. The inflowing water brought with it muds and silts, forming crevasse-splay and small-scale delta deposits. These sediments would progressively cause the floodplain lake to silt up, until eventually the swamp vegetation could return.

It has been estimated that a 1 m thickness of clastic deposits caused by crevasse-splay flooding could have been generated in as little as five years (Broadhurst *et al.*, 1980). In contrast, Broadhurst and France (1986) estimated that it took some 7000 years to generate the same thickness (1 m) of coal. Applying these figures to the thicknesses of coals and inter-seam sediments of the Farrington Formation given by Moore (1937), it appears that, despite the immediate impression given by the relative stratigraphical thicknesses, the area was covered by swamp vegetation for at least 97% of the time,

and was only cleared by flooding for very short periods (Thomas and Cleal, 1994). According to Jarzembowski (1989), the fossil-bearing mudstones at Lower Writhlington contained entombed lycopsid stumps, from which he concluded that sedimentation had been rapid. These mudstones were thus probably deposited as part of a crevasse splay caused by a flood event which destroyed the swamp vegetation that formed the No. 10 Coal. The resulting lake may have lasted for some centuries before it silted up, but this pales into insignificance compared with the 10 000 years duration of the replacement swamp.

Todd (1991) described four sublithologies at the Writhlington site. More than 90% of the fauna is associated with sublithology A, a medium to dark grey, laminated, silty mudstone with subordinate clayey siltstone. He interpreted this sublithology as belonging to Scott's (1979) Facies Association 1A: pro-delta lake clays; that is, the animals were washed into the site of deposition together with lycopod debris during flooding episodes.

The arthropod fauna

Figure 3.19 shows that by far the majority of the animal fossils found at Writhlington are Blattodea (cockroaches), with over 700 specimens accounted for. Since cockroaches are a common component of coal measure terrestrial faunas this finding should not be surprising; however, the lesser number of other insects, and hence the extreme abundance of blattodeans, is most unusual. Also, the cockroach entomofauna is dominated by archimylacrids (and not mylacrids) unlike many other late Westphalian faunas (Jarzembowski and Schneider, *in press*).

Similarly, amongst Carboniferous arachnids, which in any case are rare, phalangiotarbid are not normally the commonest; normally it is trigonotarbid which turn up most often. However, Beall (1991) has pointed out that where phalangiotarbid do occur (Writhlington, UK, and Mazon Creek, USA), they do supercede all others in number of specimens. The second commonest insect in Writhlington, one-tenth as numerous as the cockroaches, is Protorthoptera; and the second commonest arachnid group, with one-quarter the number of specimens as Phalangiotarbid, is the Trigonotarbid (Figure 3.20).

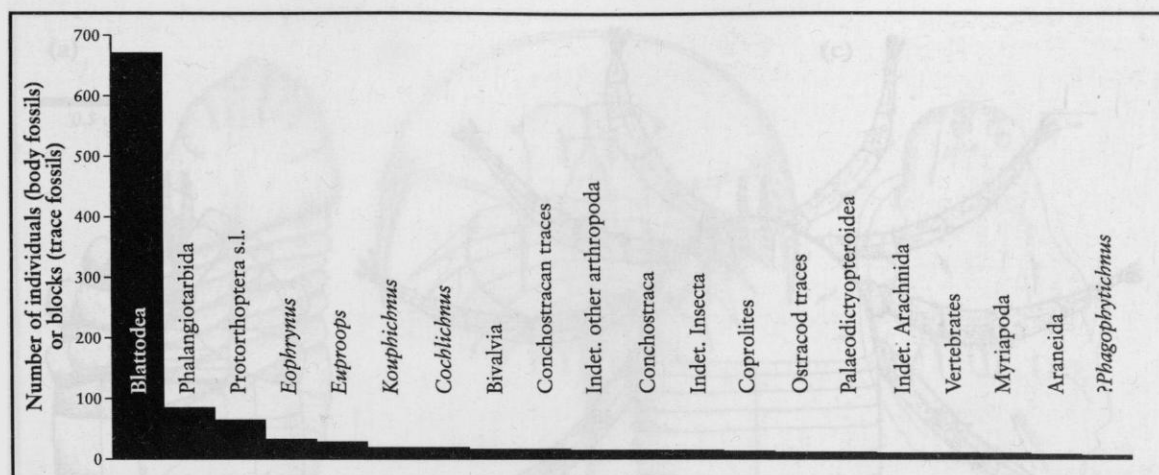


Figure 3.19 Histogram of fauna found at Writhlington geological Nature Reserve. Body fossils are counted as number of individuals; trace fossils as numbers of blocks. *Eophrynus* is now referred to *Pleophrynus*. (After Jarzembowski, 1989b.)

Phylum ARTHROPODA

Subphylum Chelicerata

Class Xiphosura

Euproops danae (Meek & Worthen, 1865)
(Ambrose and Romano, 1972;
Anderson, 1994)

Class Eurypterida

Adelophthalmus imbofi (Proctor, 1999)

Class Arachnida

Order Phalangiotarbida

Phalangiotarbrids (Beall 1991)
Bornatarbus mayasii (Pollitt *et al.*,
2004)

Order Trigonotarbita

Pleophrynus verrucosa
(Pocock, 1911) (Dunlop, 1994b)

Order Amblypygi

Protophrynus carbonarius?
Petrunkevitch, 1913 (Dunlop, 1994a)

Order Araneae

Undescribed mesothel spider (Selden
and Siveter 2001)

Subphylum Hexapoda

Order Odonoptera

Bechlya ericrobinsoni Jarzembowski &
Nel, 2002

Order Blattodea (Jarzembowski, 1989b)

Archimylacris sp. nov. Jarzembowski &
Schneider, in press
Sooblatta spp. Jarzembowski &
Schneider, in press
Phyloblatta? sp. Jarzembowski
& Schneider, in press

Order Protorthoptera (Jarzembowski,
1989b)

Order Palaeodictyoptera (Jarzembowski,
1989b)

Mazonopterum? sp. nov.

Prokop *et al.*, in press [Kilmersdon]

There is also evidence of plant damage by
insects, such as the ichnofossil
Phagophytichnus ekowskii.

Other arthropod remains

Ostracode traces (Pollard and Hardy, 1991)
unnamed

Xiphosuran traces (Pollard and Hardy, 1991)
Kouphichnium aff. *variabilis*

Conchostracan traces (Pollard and Hardy,
1991) unnamed + body fossil:
Anomalonema reumauxi
(Jarzembowski, 2004)

Nematode traces (Pollard & Hardy 1991)
Cochlichnus sp.

Arthropleura armata (Jarzembowski
1989) (Proctor, 1998)

trace fossil: *Diplichnites* cf. *cuithensis*
(Jarzembowski, 2004)

Arthropod coprolites (Jarzembowski, 1989b)

Molluscs (bivalves)

Anthraconaia species
Anthraconauta tenuis

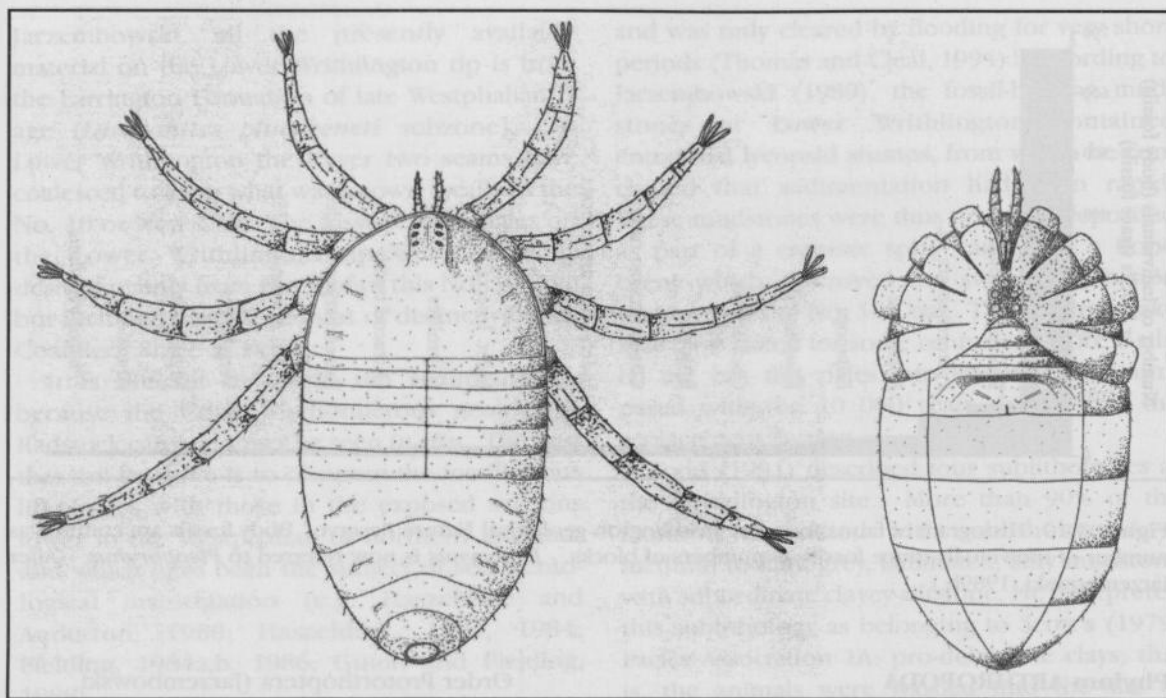


Figure 3.20 Reconstruction of *Pleophrynus verrucosa* (Pocock, 1911) dorsal and ventral views (see Dunlop, 1994b).

Vertebrates

Shark: *Palaeoxyris* cf. *carbonaria* (Jarzembowski, 1989b)

Reptile: cf. *Pseudobradypus* sp. (pelycosaur ichnofossil, Milner, 1994) (Pollard and Hardy (1991) also record cf. *Lunicbnum*).

Interpretation

There are many Coal Measure arthropods known from Britain, but mostly from isolated localities yielding a handful of specimens each; most of the old localities are now destroyed. Writhlington is one of the few to still be reasonably accessible and also to yield an abundance of fossils. Work done so far on the arthropod faunas is as follows.

Ambrose and Romano (1972) described a xiphosuran and a trigonotarbid from the mine tip of Kilmersdon Colliery in the Radstock Coalfield. They named the new xiphosuran taxon *Euproops kilmersdonensis*. Following discovery of additional xiphosuran remains from the Writhlington site, Anderson (1994)

described the Writhlington material in conjunction with a review of the Kilmersdon xiphosuran. He concluded that the animals were conspecific and could be accommodated in the well-known *Euproops danae* (Meek & Worthen, 1865, Figure 3.21). This is not surprising as Kilmersdon and Writhlington deposits are adjoined underground and both mines were working the No. 10 Coal (Jarzembowski, 1989b). The Somerset specimens differed from the type of *E. danae* simply due to taphonomic and tectonic distortion.

The phalangiotarbid arachnids were discussed, but not formally described, by Beall (1991) who distributed the morphologies through three genera. Selden and Siveter (2001) indicated that there is probably only a single species of phalangiotarbid at Writhlington and that the variety of morphologies could be explained by tectonic distortion. Most recently, Pollitt *et al.* (2004) agreed with this conclusion in their redescription of the Writhlington phalangiotarbid fauna and referred the animal to *Bornatarbus mayasii*, a genus and species previously recorded from Germany (Figure 3.21a).

Other arachnids known from Writhlington

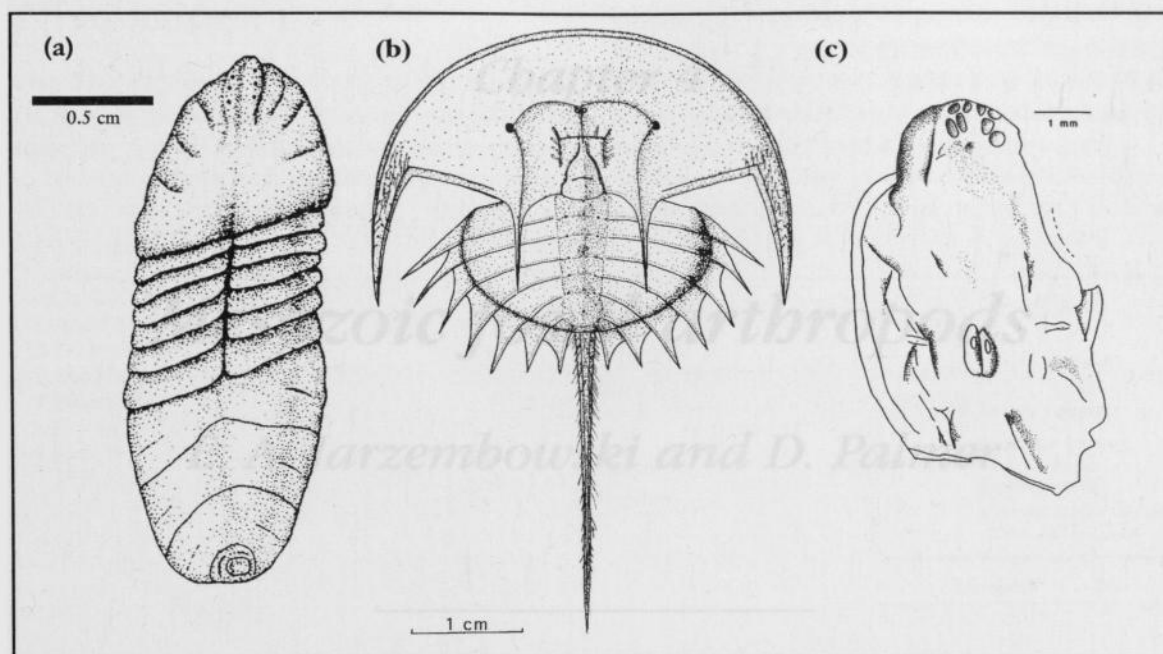


Figure 3.21 Some Writhlington arthropods. (a) A reconstruction of the phalangiotarbid arachnid *Bornatarbus mayasii* (from Pollitt *et al.*, 2004); (b) *Euproops danae* reconstruction, (from Anderson, 1994). (c) carapace of an undescribed spider (original drawing by the author). Note the tectonic distortion shown by the natural specimens (a) and (c).

include one poorly preserved amblypygid (Dunlop 1994a), undescribed spiders carapaces (Selden and Siveter, 2001), and some trigonorbid specimens. The last were described by Dunlop (1994b) as *Pleophrynus verrucosa* (Pocock, 1911). In this paper, he reviewed the specimens of *Eophrynus jugatus* Ambrose & Romano (1972) from Kilmersdon Colliery tip, and concluded that they were conspecific with *Pleophrynus verrucosa* of Writhlington).

General conclusions from these works are that there is much less diversity among Coal Measure arthropod faunas than has hitherto been thought. Previously, each new arthropod locality has produced a new taxon; perhaps it was assumed that new localities should always preserve different species. Critical comparative studies on arthropods from a variety of sites in Britain and the USA have shown that commonly differences in the specimens from these localities can be attributed to different taphonomic histories rather than true morphological dissimilarity. Low diversity of arthropod faunas in the stable environment of the Euramerican

Carboniferous coal swamps fits in well with a similar hypothesis put forward by Milner and Panchen (1973) for vertebrates (Dunlop, 1994b).

Conclusions

The Geological Nature Reserve at Writhlington is an exceptional resource for the study of Upper Carboniferous terrestrial life in Britain. The sheer numbers of fossil cockroaches and the unusual, extinct arachnids called phalangiotarbid, makes this site unique in the world. It can be compared to the other well-known Upper Carboniferous Lagerstätten of Mazon Creek (USA), Montceau-les-Mines (France), and Coseley (UK: now unavailable). Few Upper Carboniferous sites yielding arthropods are still available in Britain, and the saving of Writhlington in 1987 made this the best site for the study of Coal Measures arthropods and their association with other biota, especially the plants, and environments.