Fossil Arthropods of Great Britain

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Chapter 2

Pre-Carboniferous Fossil Arthropods

PRE-CARBONIFEROUS GEOLOGICAL HISTORY

D. Palmer

British environments of sediment deposition, and their related arthropod faunas, have a successive contiguity from Silurian to Devonian times, reflecting the underlying tectonic processes associated with the closure of the Iapetus Ocean and the Caledonian Orogeny that built the Caledonian mountains and led to the creation of the 'Old Red Sandstone Continent'. However, there is a significant gap in the fossil record between the youngest Devonian GCR arthropod site (Rhynie, *c.* 410 Ma) and the oldest Carboniferous arthropod GCR site (Foulden, *c.* 348 Ma), which is also a reflection of wide-ranging geological processes of crustal motion and erosion. Consequently, the Carboniferous arthropod sites are treated separately as an Upper Palaeozoic (post-Devonian) group in the British fossil record for the purposes of the GCR.

The earliest arthropods to be considered in this GCR volume are those which lived in aquatic environments of Silurian age, such as the extinct eurypterids and xiphosurans. Both groups are chelicerate arthropods with evolutionary histories that extend back into mid Ordovician and Cambrian times respectively. However, in the context of their fossil record in the British Isles, they only become relatively abundant in shallow water and marginal marine environments of Silurian age. The development of these depositional environments is particularly interesting and important as they also record the early terrestrialization of plant and animal life.

The British stratigraphical succession has an unusually good record of these environments and the events they record because of its tectonic and palaeogeographical setting and development at the time (see Figure 2.2). The earliest fossil record of animal life within the continental environment of Britain dates back to late Ordovician (Caradoc) times, some 455 Ma. Shallow-water volcaniclastic sediments within the Borrowdale volcanic rocks of the Lake District have been found to contain some distinctive arthropod related trace fossils (Johnson *et al.*, 1994), which consist of closely spaced parallel tracks with repeated individual, but identical, imprints just a few millimetres in size (Figure 2.1). Detailed analysis of the tracks

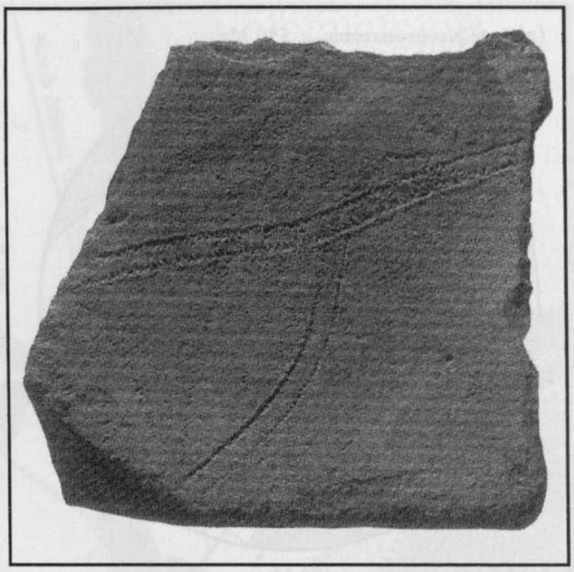


Figure 2.1 Remarkably well-preseved centimetre-wide myriapod tracks in Caradoc shallow-water volcaniclastic sediments. (From Johnson *et al.*, 1994.)

suggests that they were made by elongate aquatic myriapod arthropods with numerous paired walking legs similar to the living centipedes and millipedes. Unfortunately, no associated body fossils have been found in these strata.

At the time the Lake District was an active volcanic arc on the north-western flank of Avalonia as it approached North America and subducted the intervening Iapetus Ocean (Figure 2.2). In between the subaerial volcanoes was a subtropical landscape of lava plateaux and lake basins. Clearly these myriapod arthropods were still aquatic but had moved from the seas into freshwaters by this time – an essential pre-adaptive step on the road to full terrestrialization.

From Caradoc times onwards, as the Iapetus Ocean was in the final stages of subduction and the arc volcanicity was waning, Eastern Avalonia (southern England, Wales and southern Ireland) came increasingly under the influence of its larger neighbours – Laurentia (North America plus Scotland and northern Ireland) and Baltica. Marine organisms from continental shelf environments of Laurentia and Baltica invaded the waters of Eastern Avalonia. Then sedimentary debris flooded into the region. These deposits were compressed between the converging continental crust margins and effectively welded Eastern Avalonia to Laurentia and Baltica

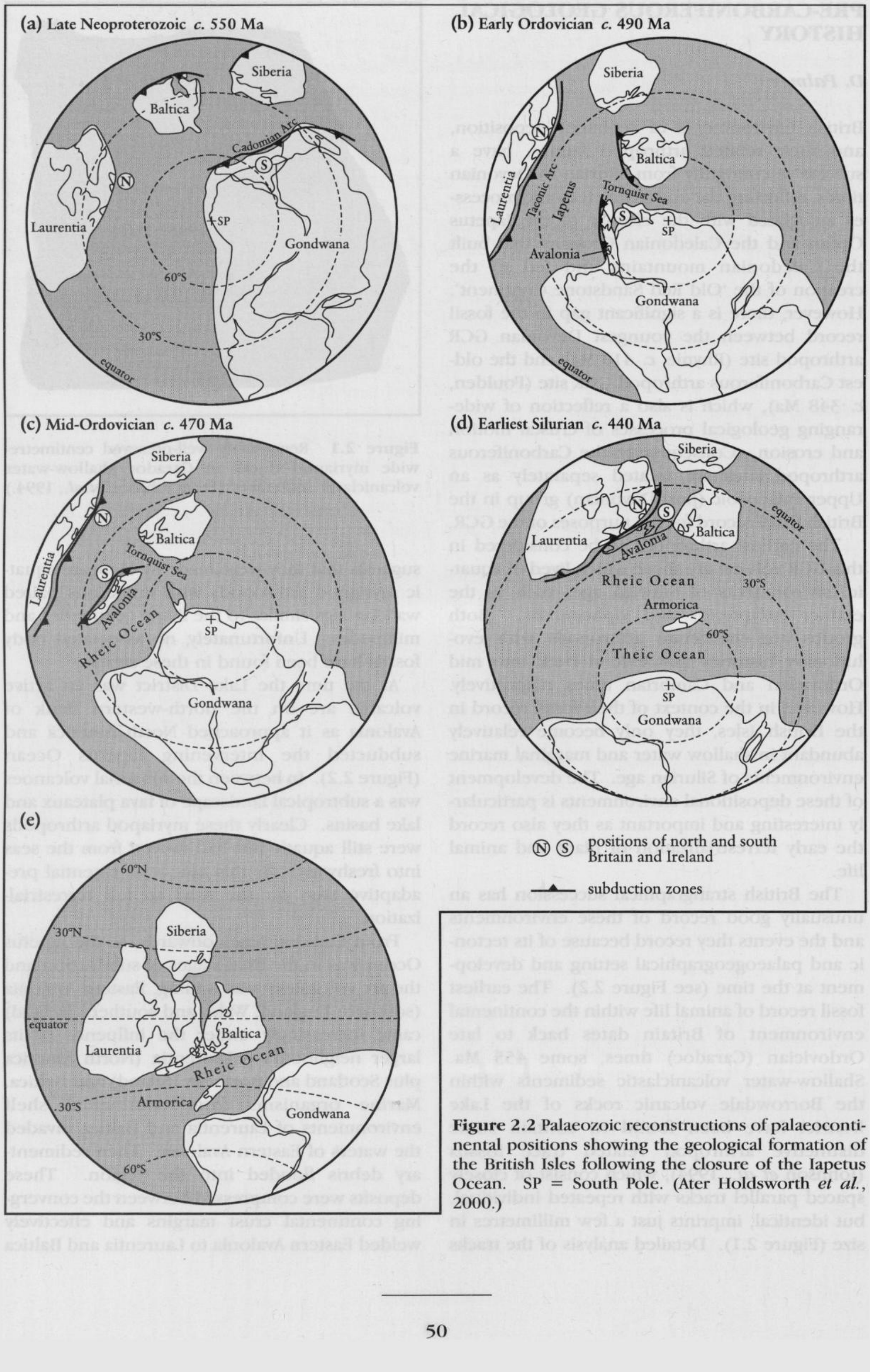


Figure 2.2 Palaeozoic reconstructions of palaeocontinental positions showing the geological formation of the British Isles following the closure of the Iapetus Ocean. SP = South Pole. (Ater Holdsworth *et al.*, 2000.)

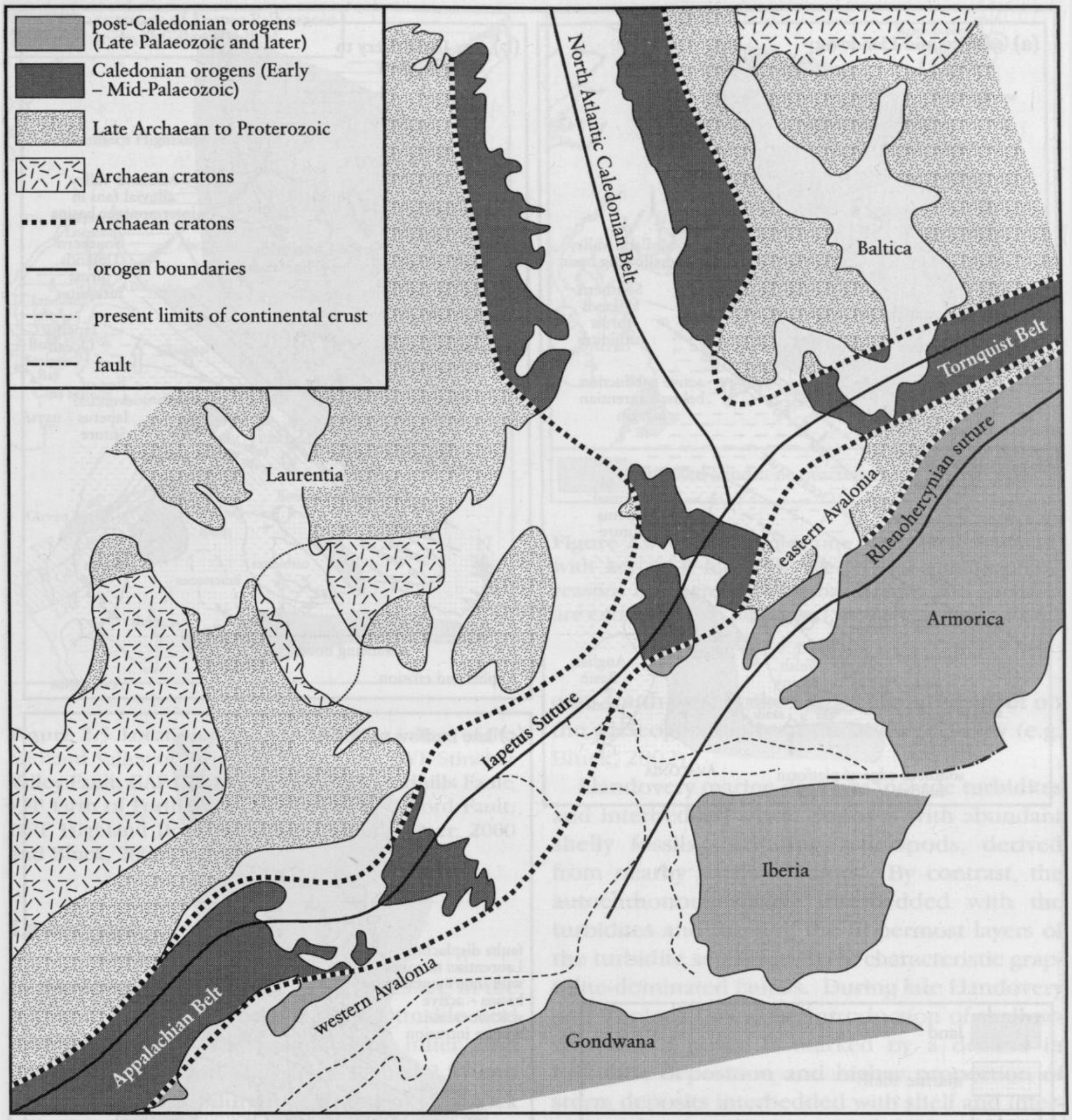


Figure 2.3 A pre-Atlantic Ocean reconstruction of the palaeocontinental areas around 'Britain'. (After Woodock and Strachan, 2000.)

along the line of the Caledonian mountains (Figure 2.3).

This process of plate convergence transformed the overall palaeogeography and environments of deposition within the regions of the British Isles (Figure 2.4). Silurian marine basins of deposition had been accumulating sediment and fossil remains on both the 'Scottish' margin of Laurentia (now represented by Southern Upland and Midland Valley strata) and Eastern Avalonia (now represented by the Welsh and Lake District strata). During late Silurian times all these basins shallowed with the development of regressive sequences forming the Old Red Sandstone facies which also developed over large areas of Laurentia and Baltica but the timing varied from place to place.

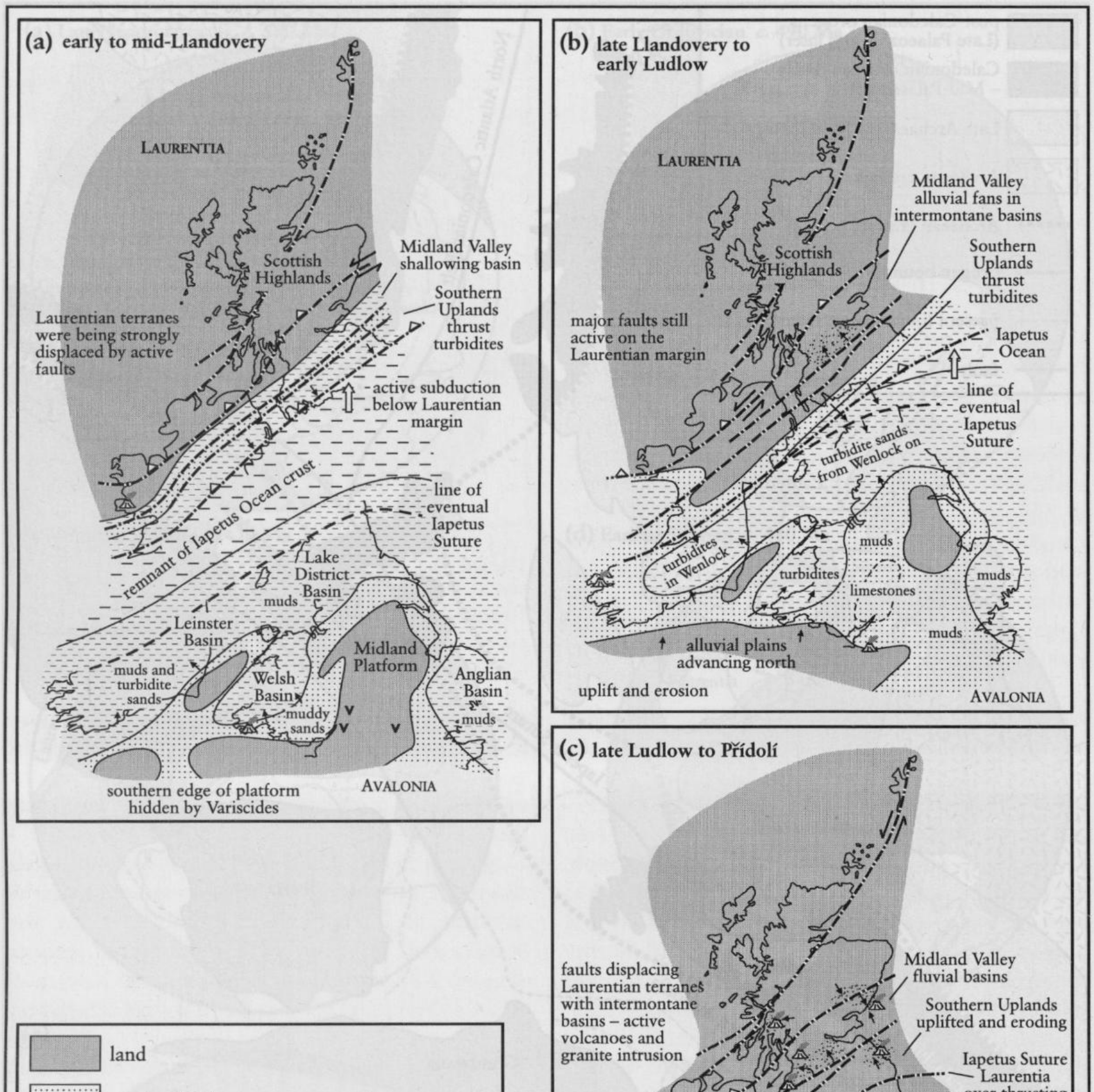


Figure 2.4 Palaeogeographical maps of Britain for three intervals of Silurian time (a) early to mid-Llandovery; (b) late Llandovery to early Ludlow and (c) late Llandovery and Přídolí. (After Aldridge *et al*., 2000.)

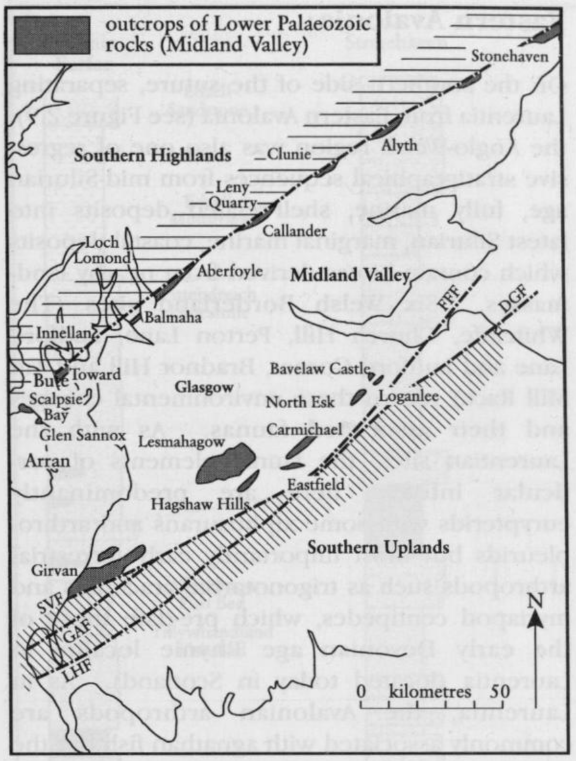


Figure 2.5 Location of the main Silurian inliers of the Midland Valley of Scotland, and faults. SVF Stinchar Valley Fault; GAF Glen App Fault; LHF Leadhills Fault; FFF Firth of Forth Fault; DGF Dunbar–Gifford Fault; HBF Highland Boundary Fault. (After Palmer, 2000 and Bluck, 2002.)

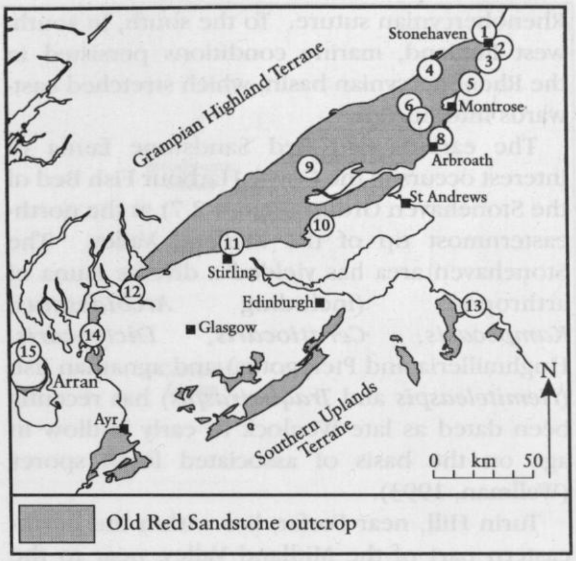


Figure 2.6 Old Red Sandstone outcrops in Scotland, with key GCR localities selected for stratigraphical reasons numbered. Note that Orkney and Shetland are excluded from this map. (See Barclay *et al.*, 2005.)

Laurentia

In the present context, the oldest sites are in the Midland Valley of Scotland with Dunside and Slot Burn within the Lesmahagow inlier, and within the Pentland Hills, (see Figure 2.5) and are of early-mid Silurian (Llandovery–Wenlock age, 430–426 million years ago). Two further sites (Rhynie and Turin Hill, see Figure 2.6) are of early Devonian age (*c.* 411–410 million years ago) but only Turin Hill lies within the Midland Valley near Forfar, Rhynie lies to the north, across the Highland Boundary Fault within the Grampian Highland terrane.

Initially, in the Midland Valley, there is a marine sequence with a diverse fauna of shelly invertebrates accompanied by agnathan fish and a diversity of eurypterids. Faunal relationships are stronger with the contemporary fossils of the Baltic region (and the west of Ireland, Palmer *et al.*, 1989) than with contemporary biotas to the south. This reflects a significant north-east–south-west strike slip structural control on the palaeogeography of the Midland Valley (e.g. Bluck, 2002).

Llandovery marine deposits include turbidites and interbedded storm deposits with abundant shelly fossils, including arthropods, derived from nearby shallow waters. By contrast, the autochthonous shales, interbedded with the turbidites and forming the uppermost layers of the turbidite sequences have characteristic graptolite-dominated faunas. During late Llandovery and Wenlock times, the introduction of shallower water deposits is marked by a decline in turbiditic deposition and higher proportion of storm deposits interbedded with shelf and intertidal sediments and their accompanying shelly faunas (see Figure 2.11 in the GCR site report for Dunside). The development of lagoons and lakes within these marginal marine environments resulted in the deposition of fine-grained and finely laminated sediments that preserve some distinctive faunas in excellent detail. Most significant here are the diversity of arthropods and agnathan fish that seem to have been tolerant of changing salinities, oxygen levels and water depths.

By early Devonian times, Scotland was part of the Old Red Sandstone continent of Euramerica, which included North America, Greenland and Northern Europe to the north of the

Rhenohercynian suture. To the south, in south-west England, marine conditions persisted in the Rhenohercynian basin, which stretched eastwards into Europe.

The earliest Old Red Sandstone fauna of interest occurs in the Cowie Harbour Fish Bed of the Stonehaven Group (Figure 2.7) at the north-easternmost tip of the Midland Valley. The Stonehaven area has yielded a diverse fauna of arthropods (including *Archidesmus*, *Kampecaris*, *Ceratiocaris*, *Dictyocaris*, Hughmilleria and Pterygotus) and agnathan fish (*Hemiteleaspis* and *Traquairaspis*) has recently been dated as late Wenlock to early Ludlow in age on the basis of associated fossil spores (Wellman, 1993).

Turin Hill, near Forfar, lies within the north-eastern part of the Midland Valley, near to the Highland Boundary Fault (Figure 2.6). Here, the Old Red Sandstone facies is represented by the fluviatile sandstone and lacustrine siltstones of the Arbuthnott Group of early Devonian age (*c.* 410 million years old, Figure 2.7). These freshwater sediments contain an important flora of early vascular and other primitive plants accompanied by fish and arthropods. To the north, across the Highland Boundary Fault, the Grampian Terrane with the early Devonian locality of Rhynie was part of Euramerica. Palaeogeographically, the region generally lay in a semi-arid belt about 30° South (Figure 2.8) and the high rates of sedimentation were related to the uplift of the Caledonian mountains. However, the fluviatile and lacustrine sediments of the Arbuthnott Group and similar facies at Rhynie indicate that there were also phases of wetter and cooler climates.

Rhynie is internationally renowned for the high-quality preservation of one of the earliest land communities of plants and arthropods. The chert deposits were originally laid down around a hot mineral rich spring with its bog-like growth of primitive plants (such as *Rhynia*, *Aglaophyton*, *Nothia*, *Asteroxylon*, *Horneophyton* plus algae, fungi and cyanobacteria) which have been silicified. The plants supported a microarthropod community fossils of which include a crustacean, trigonotarbid arachnids, a harvestman arachnid, a mite, a myriapod and a collembolan. Some of these fossils represent the earliest known fully terrestrial animals.

Eastern Avalonia

On the southern side of the suture, separating Laurentia from Eastern Avalonia (see Figure 2.9), the Anglo-Welsh region was also one of regressive stratigraphical sequences from mid-Silurian age, fully marine, shelf-related deposits into latest Silurian, marginal marine, coastal deposits which contain biotas derived from nearby landmasses. Six Welsh Borderland sites (The Whitcliffe, Church Hill, Perton Lane, Ludford Lane and Ludford Corner, Bradnor Hill and Tin Mill Race) record these environmental changes and their associated faunas. As with the Laurentian sites, the faunal elements of particular interest here are predominantly eurypterids with some xiphosurans and arthropleurids but most importantly early terrestrial arthropods such as trigonotarbid arachnids and myriapod centipedes, which pre-date those of the early Devonian age Rhynie locality in Laurentia (located today in Scotland). As in Laurentia, the Avalonian arthropods are commonly associated with agnathan fish but the taxa are different, reflecting the palaeogeographical separation of the two regions.

There were three factors influencing the changing palaeogeography of the Anglo-Welsh region. The convergence of Eastern Avalonia and Laurentia progressively restricted the flow of seawater and its accompanying biota to and fro between the open ocean and the marginal marine basins. Eustatic rise in sea level that flooded much of the Midland Platform slowed down (during late Ludlow to Přídolí times, Figure 2.10). But at the same time local crustal extension led to basin subsidence in the Welsh region and the western flank of the Midland Platform which accommodated increased sedimentation. Consequently, the overall dynamic evolution of the region was complex with pulsed regression producing a progressive transformation of both basin and shelf into environments of non-marine deposition.

The timing of the transition varies from place to place with marginal marine conditions first appearing in south-west Wales by early Ludlow time, moving into north and mid-Wales by early Přídolí time, north-west England in late Přídolí time and finally early Devonian times in eastern England. Subsequent burial, tectonism and re-exhumation preserved and then revealed narrow strips of outcrop from south-west Wales through the Welsh Borderlands. It is from the

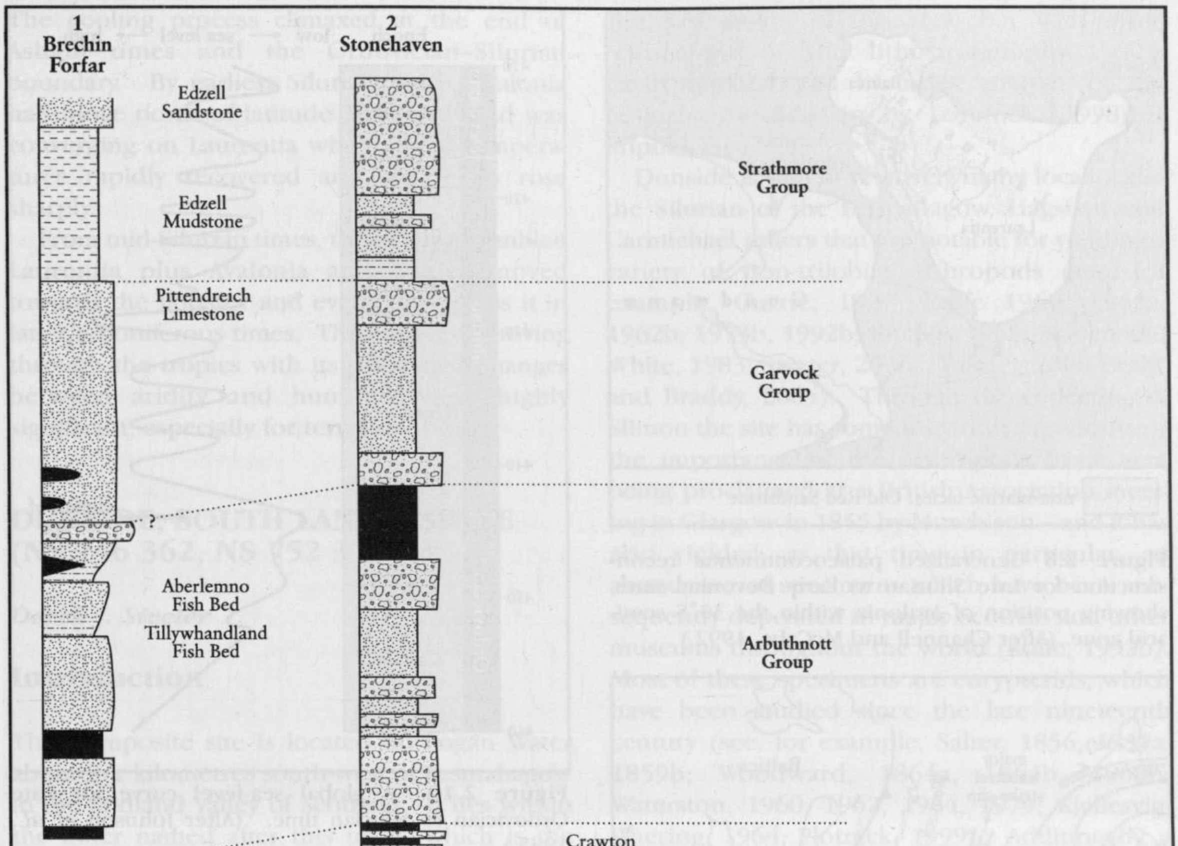


Figure 2.7 Selected sections of Lower Old Red Sandstone in the northern Midland Valley. (After Mykura, 1991.)

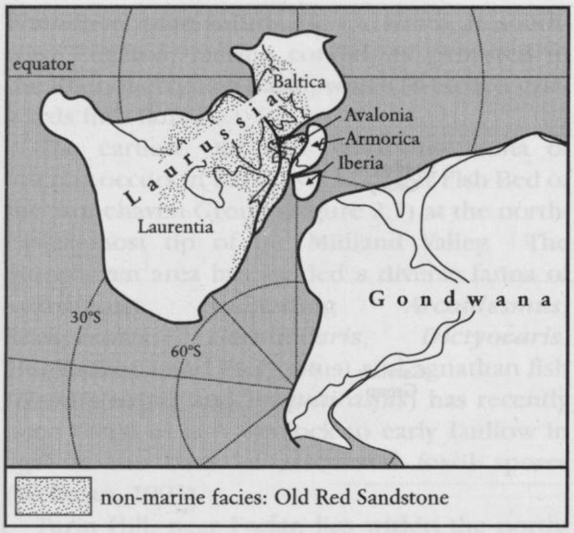


Figure 2.8 Generalized palaeocontinental reconstruction for Late Silurian to Early Devonian time, showing position of Avalonia within the 30°S semi-arid zone. (After Channell and McCabe, 1992.)

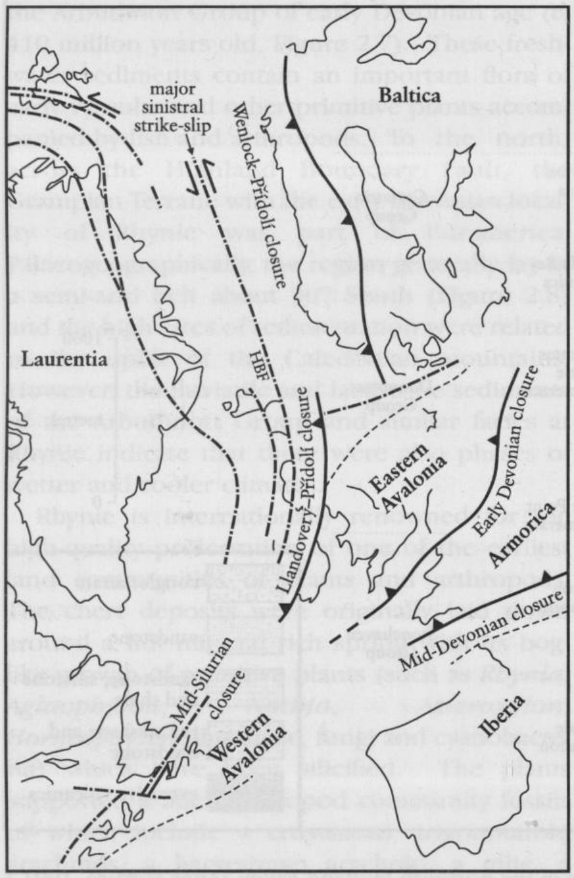


Figure 2.9 Palaeocontinental positions during Early Devonian time showing effects of major sinistral strike-slip faults on palaeogeography of 'Scotland'. HBF: Highland Boundary Fault. (After Soper *et al.*, 1992.)

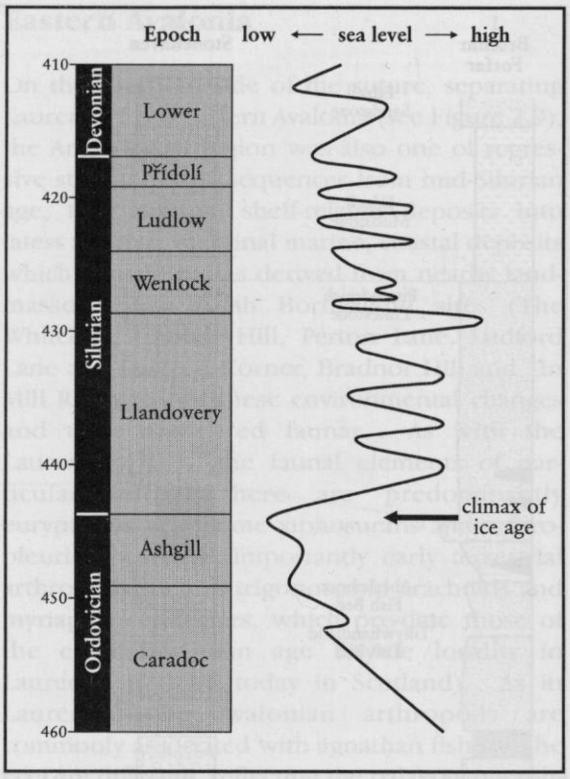


Figure 2.10 A global sea-level curve for Late Ordovician to Silurian time. (After Johnson *et al.*, 1985.)

latter that a network of six sites has been chosen for the GCR that record the role played by arthropods in this environmental transition and the terrestrialization of life.

Of these Borderland localities, that of Ludford Lane and Ludford Corner is perhaps the most important in this context. The site is internationally renowned for the appearance of terrestrially derived vascular plants and animals (trigonotarbid and centipede remains) mixed in with marine fossils and euryhaline arthropods such as eurypterids in late Silurian age (*c.* 418 million year old) near-shore deposits.

Climate

A combination of global climate change and plate tectonic movement played a significant role in the evolution of Ordovician to Devonian environments for life within both Laurentia and Avalonia. In early Ordovician times, Avalonia, as part of Gondwanaland, was much closer to the South Pole than Laurentia and North America. However, by late Ordovician times, Avalonia was moving towards Laurentia and global climates descended into an ice age and sea levels fell.

The cooling process climaxed at the end of Ashgill times and the Ordovician–Silurian boundary. By earliest Silurian times, Avalonia had move north of latitude 30° South and was converging on Laurentia when global temperatures rapidly recovered and sea levels rose sharply.

From mid-Silurian times, the newly assembled Laurentia plus Avalonia and Baltica moved towards the Equator and eventually across it in late Carboniferous times. The impact of moving through the tropics with its associated changes between aridity and humidity were highly significant, especially for terrestrial biotas.

DUNSIDE, SOUTH LANARKSHIRE (NS 746 362, NS 752 371)

Derek J. Siveter

Introduction

This composite site is located on Logan Water about five kilometres south-west of Lesmahagow in the Midland Valley of Scotland. It lies within the inlier named after this town, which is the largest of four Silurian inliers in the central part of the Midland Valley, the others being the Hagshaw Hills, Carmichael and Eastfield (see Figure 2.5). Devonian and Carboniferous strata surround the inlier. The Silurian at Lesmahagow is disposed into an asymmetrical anticline and comprises sediments of at least Llandovery and Wenlock age, the Dunside site exposing rocks of the Llandovery Series, some 430 Ma.

Murchison (1856), in connection with the arthropod discoveries at Lesmahagow of Robert Slimon, gave some observations on the geology of the area, as did Woodward (1970). Peach and Horne (1899) produced a more detailed account later in the 19th century, in which they specifically referred to the Logan Water exposures that form the Dunside site, and gave lists of fossils that occur there. However it was Jennings (1961), through his mapping of the inlier, who established a modern stratigraphy for it. All subsequent authors who have published on the geology or palaeontology of Lesmahagow, for example Rolfe (1973b, 1992b), Ritchie (1968, 1985), Walton and Oliver (1991), and Dineley (1999a), have used his stratigraphical scheme. Armstrong *et al*. (1995) and Paterson *et al*. (1998) also essentially did so in their re-mapping and assessment of the area, but with some refinement of the lithostratigraphy. The environmental and biofacies analysis of the Lesmahagow Silurian by Lovelock (1998) is unpublished.

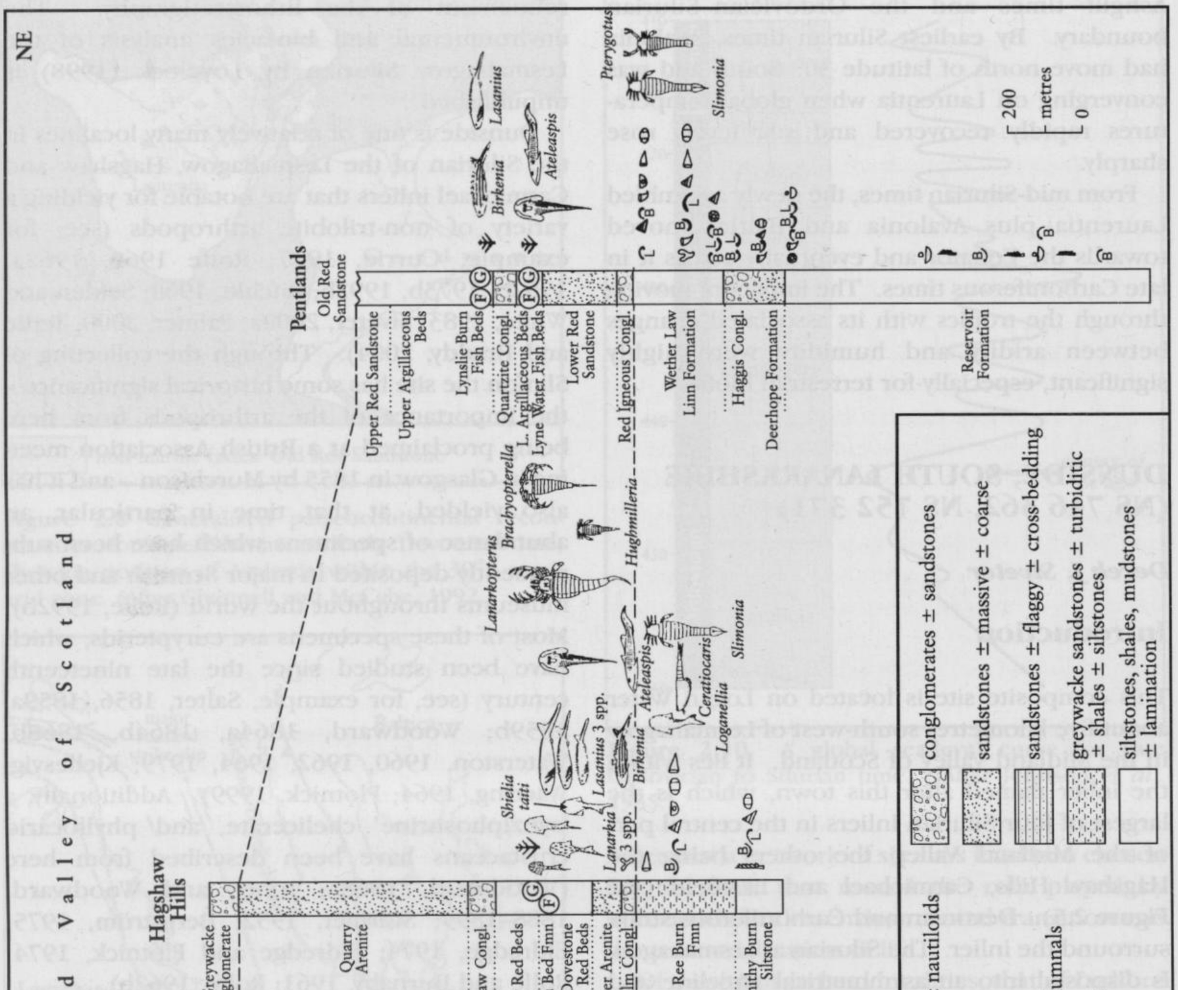
Dunside is one of relatively many localities in the Silurian of the Lesmahagow, Hagshaw and Carmichael inliers that are notable for yielding a variety of non-trilobite arthropods (see, for example, Currie, 1927; Rolfe 1960, 1962a, 1962b, 1973b, 1992b; Ritchie, 1968; Selden and White, 1983; Siveter, 2000a; Palmer, 2000; Tetlie and Braddy, 2004). Through the collecting of Slimon the site has some historical significance – the importance of the arthropods from here being proclaimed at a British Association meeting in Glasgow in 1855 by Murchison – and it has also yielded, at that time in particular, an abundance of specimens which have been subsequently deposited in major Scottish and other museums throughout the world (Rolfe, 1992b). Most of these specimens are eurypterids, which have been studied since the late nineteenth century (see, for example, Salter, 1856, 1859a, 1859b; Woodward, 1864a, 1864b, 1868b; Waterston, 1960, 1962, 1964, 1979; Kjellesvig-Waering, 1964; Plotnick, 1999). Additionally, a 'synziphosurine' chelicerate, and phyllocarid crustaceans have been described from here (Woodward, 1868a; Jones and Woodward, 1888–1899; Størmer, 1952; Bergström, 1975; Eldredge, 1974; Eldredge and Plotnick, 1974; Rolfe and Burnaby, 1961; Rolfe, 1962b).

Dunside also has significance for early vertebrates, and has been selected for inclusion in the GCR volume on fossil fishes (Dineley and Metcalf, 1999).

Description

The Silurian succession of the Lesmahagow Inlier was divided by Jennings (1961) into, in ascending order, Priesthill, Waterhead and Dungavel groups, each comprising various formations and above which are Old Red Sandstone conglomerates and sandstones of Devonian age (Figure 2.11). Paterson *et al*. (1998) introduced the Ponesk Burn Formation for those strata

Figure 2.11 (overleaf) Stratigraphy and faunas of the main Silurian inliers of the Midland Valley of Scotland. (Modified from Palmer, 2000, after Wellman and Richardson, 1993.)


SW
NE
Lesmahagow
Midland Valley of Scotland
Hagshaw Hills
Pentlands
Wenlock
Llandovery
Greywacke Conglomerate
Plewland Sandstone Formation
Middlefield Conglomerate
Logan Formation
Slot Burn Fmn
Monument Fmn
Dippal Burn Fmn
Birkenhead Sandstone Fmn
Leaze Formation
Dunside Fmn
Blaeberry Fmn
Kip Burn Formation
Castle Fmn
Patrick Burn Formation
Ponesk Burn Formation
Greywacke Conglomerate
Quarry Arenite
Hareshaw Congl.
Gulley Red Beds
Fish Bed Fmn
Dovestone Red Beds
Douglas Water Arenite
Parishholm Congl.
Ree Burn Fmn
Smithy Burn Siltstone
Old Red Sandstone
Upper Red Sandstone
Upper Argillaceous Beds
Lynslie Burn Fish Beds
Quartzite Congl.
L. Argillaceous Beds
Lyne Water Fish Beds
Lower Red Sandstone
Red Igneous Congl.
Wether Law Linn Formation
Haggis Congl.
Deerhope Formation
Reservoir Formation
Lanarkia 3 spp.
Lasanius 3 spp.
Birkenia
Ateleaspis
Lanarkopterus
Brachyopterella
Hughmilleria
Shielia taiti
L. scotica
Birkenia 2 spp.?
Pterygotus
Ceratiocaris
Jamoytius
Ainiktozoon
Loganellia scotica
Slimonia
Cyamocephalus
Loganellia
Lasanius
'Glauconome'
corals
bryozoa
brachiopods
lamellibranchs
gastropods
orthoconic nautiloids
ostracods
trilobites
crinoid columnals
graptolites
fish bed
conglomerates ± sandstones
sandstones ± massive ± coarse
sandstones ± flaggy ± cross-bedding
greywacke sandstones ± turbiditic ± shales ± siltstones
siltstones, shales, mudstones ± lamination
200
metres
0

originally comprising the lower part of the Patrick Burn Formation of the Priesthill Group. These authors also slightly changed the boundaries of the Castle, Kip Burn and Blaeberry formations of this group. Additionally, they did not recognize the Passage Formation of Jennings at the base of the Waterhead Group, with the argillaceous strata in the lower part of this formation being re-assigned to the underlying Dunside Formation at the top of the Priesthill Group, and they arbitrarily took the base of the overlying Waterhead Group at the incoming of red beds into the sequence.

A late Llandovery age is generally accepted for the Priesthill Group, though palynological evidence suggests that beds as old as those of the Patrick Burn Formation, and by implication all younger formations of the Priesthill Group, may be of Wenlock age (Wellman, 1995; Anderson and Moore, 2004). The Waterhead Group has been assigned to the Wenlock Series, and at least part of the Dungavel Group may belong to the Ludlow Series (Cocks *et al.*, 1992; Wellman and Richardson, 1993; Paterson *et al.*, 1998; Palmer, 2000).

The Dunside site consists of two localities along the stretch of Logan Water that runs between the Logan and the Dunside reservoirs. The first of these is represented by exposures close to the outflow from Logan Reservoir, at Shank's Castle (NS 746 362); the second is about 600 m downstream, closer to Dunside Reservoir (NS 752 371).

At Shank's Castle both the Castle and the overlying Kip Burn formations crop out. The Castle Formation here comprises massive siltstone turbiditic flow deposits, sometimes over a metre thick, with load and flute casts, interbedded with bedded grey siltstones. It overlies, regionally, the Patrick Burn Formation, the upper part of the latter containing beds that probably lie within the lower part of Ceratiocaris Beds of Peach and Horne (1899; Rolfe, 1973b, 1992b; Armstrong *et al.*, 1995; Paterson *et al.*, 1998). The Kip Burn Formation comprises grey and olive-grey silty mudstones with dark grey carbonaceous siltstone laminae. At Shank's Castle the carbonaceous siltstones at the base of the unit pass upwards from the massive siltstones and mudstones of the Castle Formation. This locality was specifically noted by Peach and Horne (1899) with respect to the *Ceratiocaris*-bearing strata found there, but it is only one of several localities exposing their Ceratiocaris Beds. The lower part of the Kip Burn Formation, then, includes the uppermost part of their Ceratiocaris Beds.

The Lesmahagow Inlier has some ten species of the phyllocarid *Ceratiocaris* recorded from it. For four of these, *C. angusta* Etheridge, Jones and Woodward, 1886; *C. laxa* Etheridge, Woodward and Jones, 1886; *C. stygia* Salter, 1860; and *C. papilio*, Salter, 1859, the Shank's Castle area probably represents their type locality (Rolfe and Burnaby, 1961; Etheridge *et al.*, 1886). However out of the total of ten species, only *C. stygia* has been regarded as well founded. Other non-trilobite arthropods from Shank's Castle include the eurypterids *Erretopterus* and *Slimonia* and material of the putative phyllocarid *Dictyocaris* (Rolfe, 1973b, 1992b). Also recorded from here, albeit rarely, is the fish *Birkenia elegans*.

At the locality near Dunside that forms part of this site, slightly younger beds than those at Shank's Castle are exposed, belonging to the upper part of the Kip Burn Formation. These are carbonaceous laminated siltstones and they represent the Pterygotus Beds of Peach and Horne (1899; Rolfe, 1973b, 1992b; Paterson *et al.*, 1998). It was from such beds that Slimon amassed his large collection of eurypterids, which are represented (Rolfe, 1973b, 1992b; Plotnick, 1999) by at least the following species: *Pterygotus lanarkensis* Kjellesvig-Waering, 1964, *Slimonia acuminata* (Salter, 1856); *Erretopterus bilobus* (Salter, 1856); *Nanahughmilleria lanceolata* (Salter, 1856), *Carcinosoma scorpioides* (Woodward, 1868), *Paracarsinosoma obesa* (Woodward, 1868) and *Stylonurella spinipes* (Page, 1859) (see Figures 2.12 and 2.13). The very rare synziphosurine species *Neolimulus falcatus* Woodward, 1868, known from just the holotype and possibly one other specimen (see Figure 2.14), and which should probably be referred to *Pseudoniscus*, is also from Dunside (Bergström 1975; Morris, 1980). This locality appears to stand as the type locality for all these species.

About 1.5 km upstream on Logan Water from the Shank's Castle is the separate GCR site of Birk Knowes, where the sediments belong to the slightly older Patrick Burn Formation of the Priesthill Group. Birk Knowes is internationally recognized for yielding the agnathan *Jamoytius kerwoodi*, together with the thelodont *Logania scotica*. However it has also produced the eurypterids *S. acuminata*, *E. bilobus*, *N.*

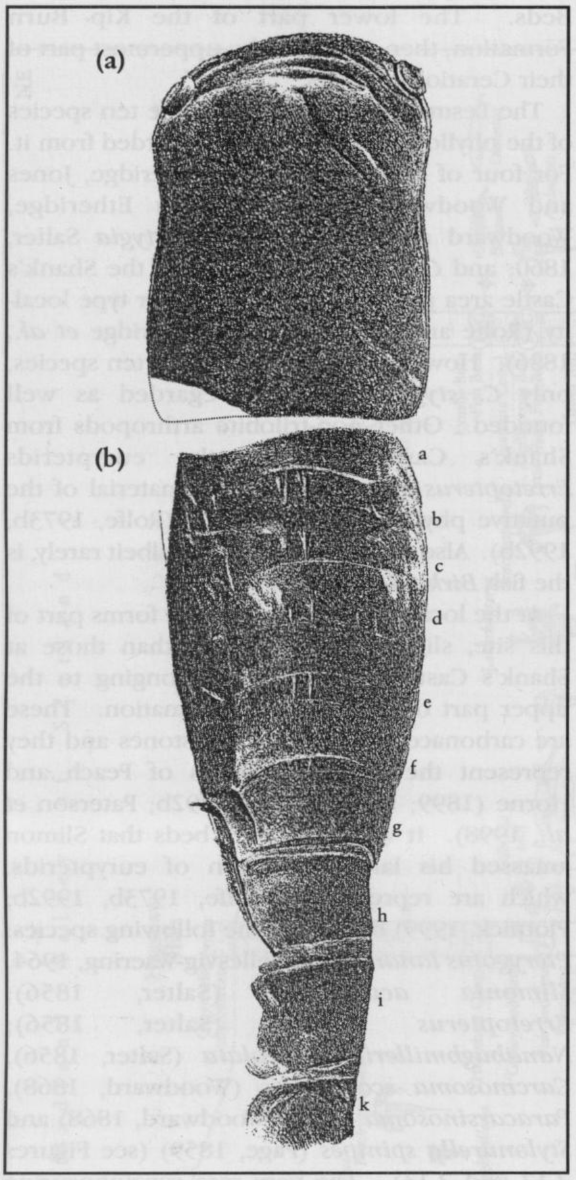


Figure 2.12 *Slimonia acuminata* (Salter, 1856); Llandovery Series, Silurian, Lesmahagow Inlier. (a) 'Carapace'. (b) 'the body of a smaller specimen; the segments a to f have a small double keel, and are probably thoracic; g, h, and k are probably abdominal rings, and are destitute of these ornaments.' (Lithograph from Salter (1859b, plate 2, figs 1a and 10.)

lanceolata, and *Hardieopterus*? *lanarkensis* Waterston, 1979, the chasmataspid *Loganamaraspis dunlopi* Tetlie and Braddy, 2004, the synziphosurids *Cyamocephalus loganensis* Currie, 1927 and a *Pseudoniscus* species, the phyllocarid *Ceratiocaris papilio* Salter, 1859 and the possible thylacocephalan *Ainiktozoon loganense* Scourfield, 1937 (see Currie, 1927; Eldredge, 1974; Waterston, 1979; Ritchie, 1985; Palmer, 2000; and Tetlie and Braddy, 2004). *Archidesmas loganensis* Peach, 1899, also from here and originally described as a myriapod, was later interpreted as a plant fragment (Almond, 1985; Rolfe, 1980, 1992b, Wilson and Anderson, 2004).

Interpretation

The Priesthill group is fully marine in nature in its lower part (Ponesk Burn Formation) and in its upper part (Patrick Burn Formation) it is restricted marine interrupted by turbidite flows (Paterson *et al.*, 1998). The Waterhead Group, comprising red and purple siltsones and sandstones, is of continental origin. The clastic rocks of this latter group are interpreted as being fluvially derived, except for some within the Dippal Burn and Slot Burn formations that were probably deposited when temporary lakes formed. The Dungavel Group sediments are indicative of stable terrestrial conditions and, at least for the conglomerates and pebbly sandstones at its base, high-energy braided river systems. Thus this succession records, as with almost all other Silurian sequences in the Midland Valley, a major regressive episode from the marine Llandovery through into the non-marine environments of post-Llandovery times. The Girvan area witnessed a slight change to this pattern, as marine conditions persisted there into the early Wenlock.

Dunside has particularly close network links with the other Scottish Siluro-Devonian arthropod sites of Slot Burn, Gutterford Burn and Turin Hill. All of these are rich in eurypterids, though the genera and species in each are mostly different. Dunside also has links with the younger, Ludlow through to Přídolí Series Anglo-Welsh arthropod sites of Church Hill, Whitcliffe, Ludford Lane and Ludford Corner, Tin Mill Race, Perton Lane, and Bradnor Hill. All of these sites again have important eurypterid faunas that, however, contrast markedly in their composition to that at Dunside.

Conclusion

This Lesmahagow, upper Llandovery Series (Silurian) site is particularly rich in eurypterids,

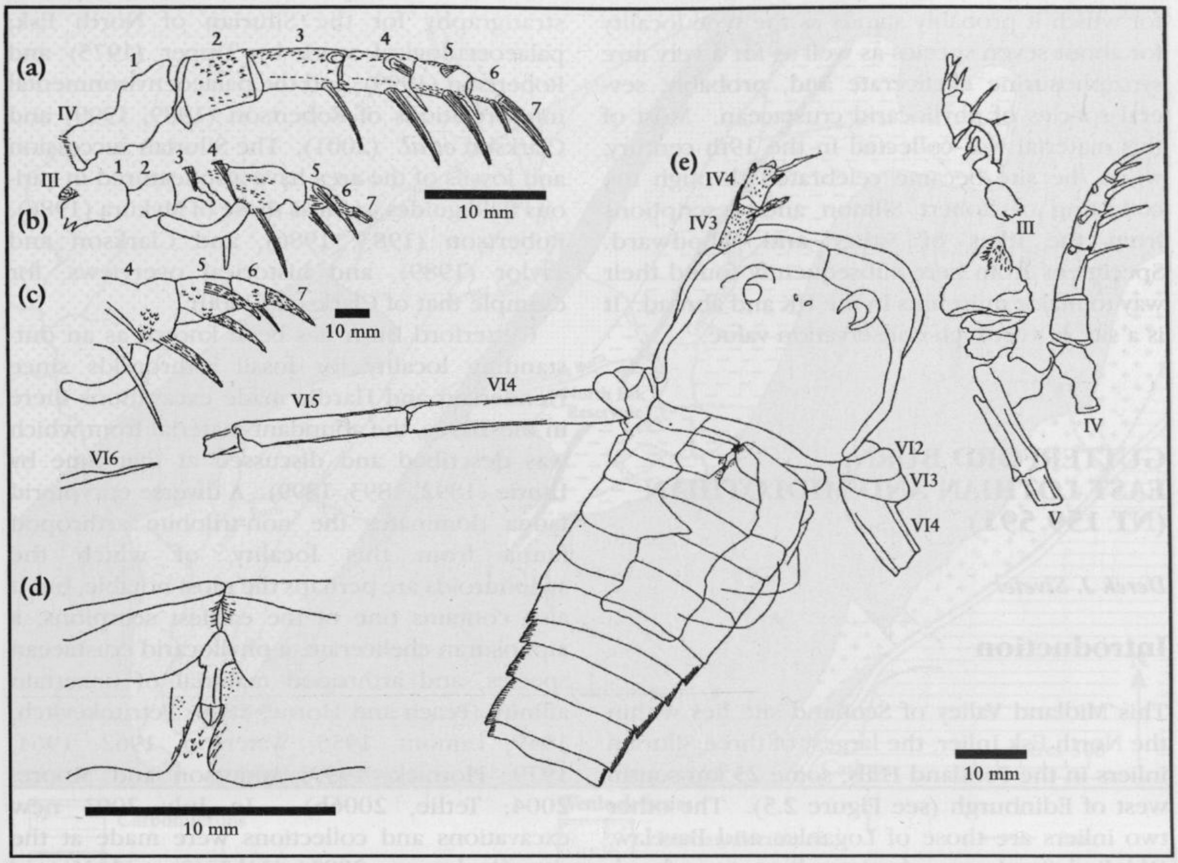


Figure 2.13 *Stylonurella spinipes* (Page, 1859); holotype, British Geological Survey, GSM 87357 and (counterpart) National Museums of Scotland, NMS G.1891.32.33; Kip Burn Formation, Priesthill Group, Llandovery Series, Silurian, Dunside, Lesmahagow Inlier. (a) prosomal appendage IV; (b) prosomal appendage III; (C) distal podomeres of prosomal appendage III; (D) median abdominal appendage; (e) holotype, showing disposition of appendages as preserved. (From Waterston, 1979, text-fig. 12.)

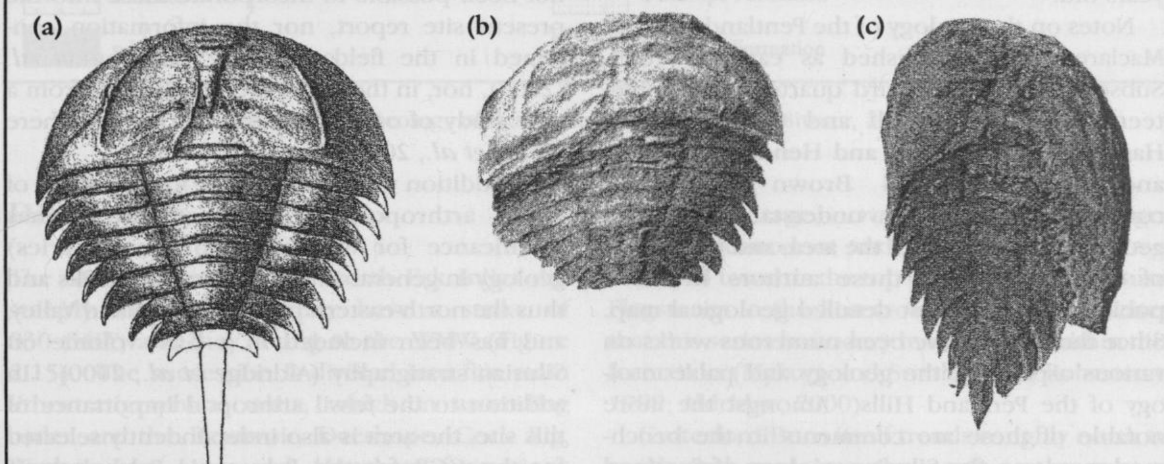


Figure 2.14 *Neolimulus falcatus* Woodward, 1868; holotype, Natural History Museum, London, In.44122; Kip Burn Formation, Priesthill Group, Llandovery Series, Silurian, Dunside, Lesmahagow Inlier. (a) Reconstruction, × 4 (from Woodward, 1868, plate I, fig. 1a.) (b) Photograph, dorsal view, × 3.75 (from Bergström, 1975, plate 1, fig. 2). (c) ? *N. falcatus*, photograph, dorsal view, × 2.8, Natural History Museum, London, In.14724, same horizon and locality as (a) and (b).

for which it probably stands as the type locality for about seven species as well as for a very rare synziphosurine chelicerate and, probably, several species of phyllocarid crustacean. Most of this material was collected in the 19th century, when the site became celebrated through the collecting of Robert Slimon and descriptions from the likes of Salter and Woodward. Specimens from here subsequently found their way to major museums in the UK and abroad. It is a site of very high conservation value.

GUTTERFORD BURN, EAST LOTHIAN AND MIDLOTHIAN (NT 159 591)

Derek J. Siveter

Introduction

This Midland Valley of Scotland site lies within the North Esk Inlier, the largest of three Silurian inliers in the Pentland Hills, some 25 km south-west of Edinburgh (see Figure 2.5). The other two inliers are those of Loganlee and Bavelaw. Old Red Sandstone clastic sediments and volcanic rocks surround the North Esk Inlier, which itself is composed of Llandovery and Wenlock series strata. Gutterford Burn cuts through deposits of Llandovery age, some 428 million years old.

Notes on the geology of the Pentland Hills, by Maclaren, were published as early as 1839. Subsequently, in the third quarter of the nineteenth century, Howell and Geikie (1861), Haswell (1865), Brown and Henderson (1867) and Henderson and Brown (1870) all contributed towards an understanding of the geological succession of the area, and the papers of the last two of these authors included publication of the first detailed geological map. Since then there have been numerous works on various aspects of the geology and palaeontology of the Pentland Hills. Amongst the more notable of these are comments in the benchmark work on the Silurian geology of Scotland by Peach and Horne (1899); the work of Lamont (1947a, 1947b, 1952) who determined much of the sequence here to be Llandovery in age and the youngest rocks to be Wenlock; remapping by Mykura and Smith (1962), and by Tipper (1976) who also established most of the modern lithostratigraphy for the Silurian of North Esk; palaeoecological work by Tipper (1975) and Robertson (1999); and the palaeoenvironmental interpretations of Robertson (1989, 1999) and Clarkson *et al.* (2001). The Silurian succession and fossils of the area have also featured in various field guides, such as those of Mykura (1986), Robertson (1983, 1986), and Clarkson and Taylor (1989), and historical overviews, for example that of Clarkson (2000).

Gutterford Burn has been known as an outstanding locality for fossil arthropods since Henderson and Hardie made excavations there in the 1890s, the abundant material from which was described and discussed at that time by Laurie (1892, 1893, 1899). A diverse eurypterid fauna dominates the non-trilobite arthropod fauna from this locality, of which the stylonuroids are perhaps the most notable, but it also contains one of the earliest scorpions, a xiphosuran chelicerate, a phyllocarid crustacean species, and arthropod material of uncertain affinity (Peach and Horne, 1899; Petrunkevitch, 1949; Lamont, 1955; Waterson, 1962, 1964, 1979; Plotnick, 1999; Anderson and Moore, 2004; Tetlie, 2006b). In July 2003 new excavations and collections were made at the site (Anderson, 2003; Anderson and Moore, 2004). The detailed results of this re-investigation of the Gutterford Burn Eurypterid Bed are contained in a paper by Anderson *et al.* (2007) that was in press at the time of writing, but it has not been possible to incorporate these into the present site report, nor the information contained in the field guide by Clarkson *et al.* (2007), nor, in the main, the conclusions from a new study of one of the eurypterids from here (Tetlie *et al.*, 2007).

In addition to its importance for the study of early arthropods, Gutterford Burn has significance for Silurian (Llandovery Series) geology in general within the Pentland Hills and thus the north-eastern part of the Midland Valley, and has been included in a GCR volume on Silurian stratigraphy (Aldridge *et al.*, 2000). In addition to the fossil arthropod importance of this site, the area is also independently selected for the GCR for the Palaeozoic Palaeobotany, Carboniferous–Permian Igneous Rocks, Carboniferous-Permian Fish/Amphibia and Westphalian selection categories (Cleal and Thomas, 1995, 1996; Dineley and Metcalf, 1999, Stephenson *et al.*, 2003).

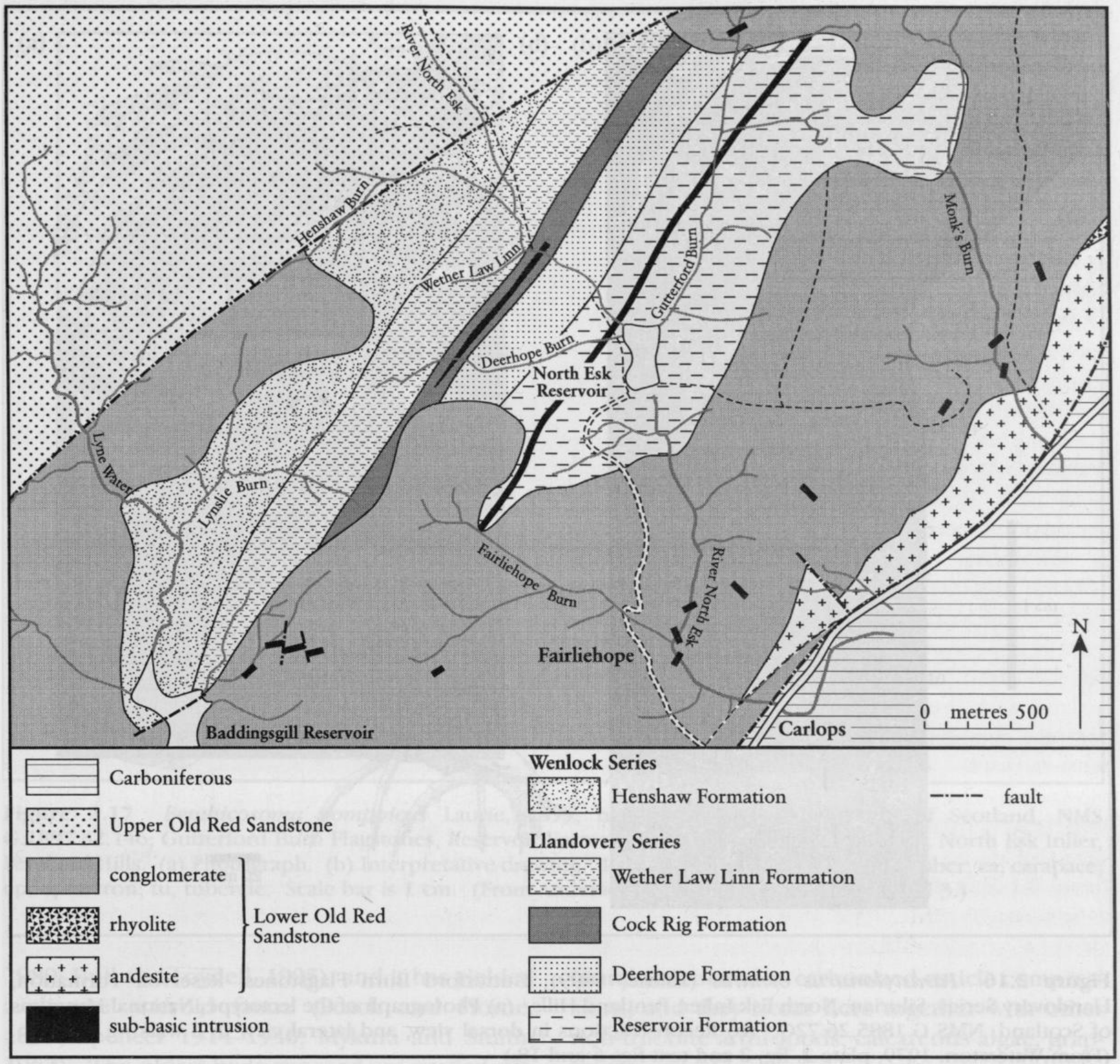


Figure 2.15 Geology of the North Esk Inlier. (After Siveter, 2000b.)

Description

The Silurian strata of the North Esk Inlier dip steeply to vertically, they have a strike of 030–040°, and they young to the WNW (Figure 2.15). The succession is divided into five main lithostratigraphical units, which in ascending order are the Reservoir, Deerhope, Cock Rig, Wether Law Linn and Henshaw formations (Tipper, 1976; Robertson, 1989). The boundary between the Llandovery Series and the Wenlock Series is generally considered to be at the base of the Henshaw Formation or within the top of the Wether Law Linn Formation, with most of the Silurian sequence being of late Llandovery Telychian Stage, *crenulata* Biozone age. However conodont and coral evidence from a shell bed towards the top of the Gutterford Burn Flagstones in the Reservoir Formation indicates that this series boundary may even lie within this formation (Mykura and Smith, 1962; Robertson, 1989; Aldridge, 2000).

Gutterford Burn itself trends roughly north to south and runs into the north-east corner of North Esk Reservoir. The strata of the GCR site lie entirely within the Reservoir Formation, for which it forms part of the type section (Tipper, 1976). Although the base of the formation has not been observed in the inlier, over 1000 m of alternating mudstones and siltstones are

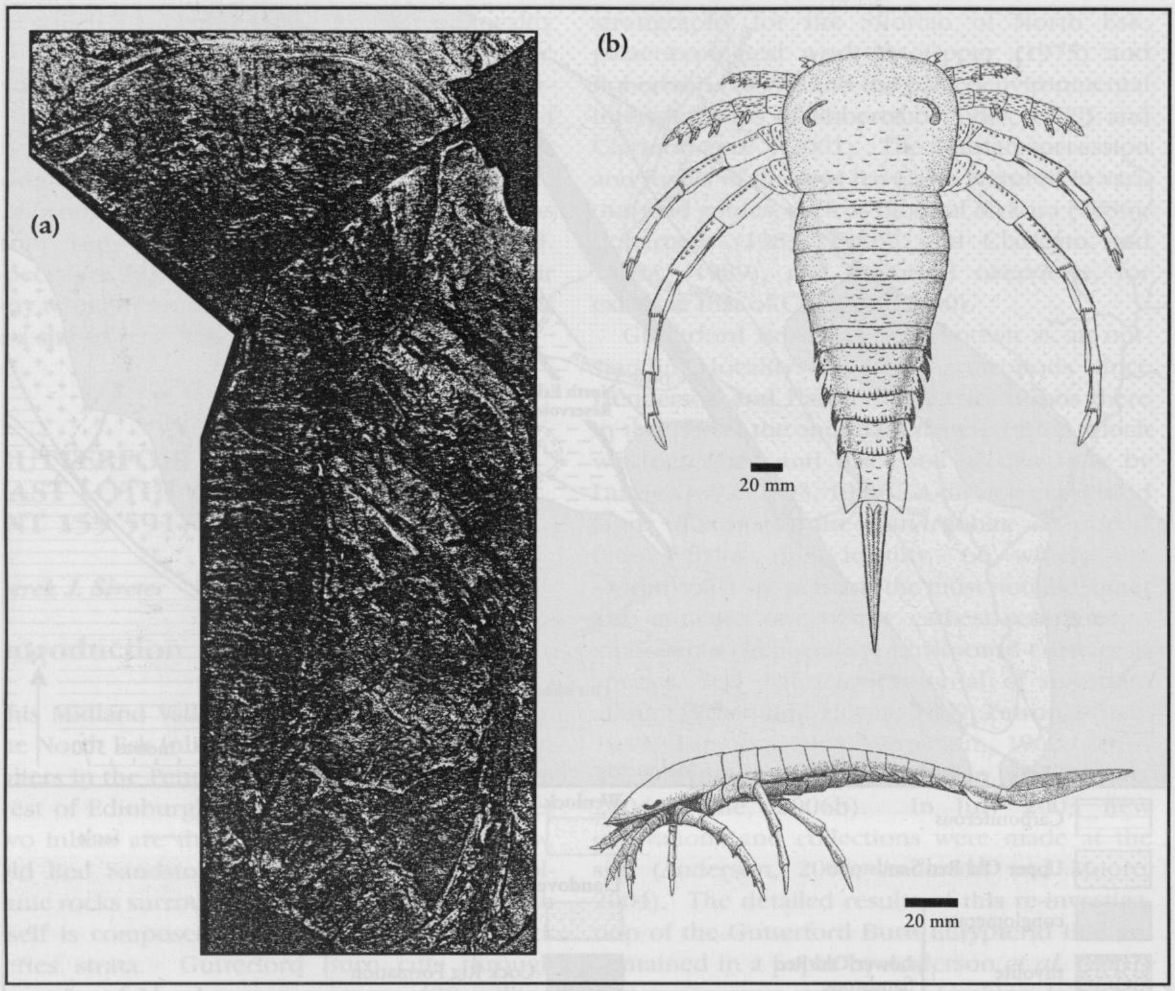


Figure 2.16 *Parastylonurus ornatus* (Laurie, 1899); Gutterford Burn Flagstones, Reservoir Formation, Llandovery Series, Silurian, North Esk Inlier, Pentland Hills. (a) Photograph of the lectotype, National Museums of Scotland, NMS G.1885.26.72G. (b) Reconstructions in dorsal view, and lateral view in a walking position. (From Waterston, 1979, plate 2, fig. 2 and text-figs 6 and 18.)

exposed below the base of the overlying Deerhope Formation. The oldest exposed strata of the Reservoir Formation are found at the south-east corner of the reservoir, stratigraphically above which, along the east margin of the reservoir and in Gutterford Burn, lies (see Mykura and Smith, 1962) the following 500 m thick sequence:

	Thickness (m)
(iv) grey to olive mudstones with laminae of siltstone and thin beds of flaggy sandstone near the base	200 +
(iii) flaggy buff or dark grey grits interbedded with grey mudstones (Gutterford Burn Flagstones)	120
(ii) mudstones and silty mudstones with laminae of siltstone and rare beds of flaggy greywacke (Gutterford Burn Mudstones)	125
(i) fine-grained grits and siltstones in units up to 20 m thick, alternating with units of interlaminated mudstone and siltstone	50 +

Overall, the Reservoir Formation is sparsely fossiliferous but in addition to eurypterids and other arthropods there are some shelly horizons, there are graptolites that have enabled zoning of the formation (Bull, 1987; Robertson,

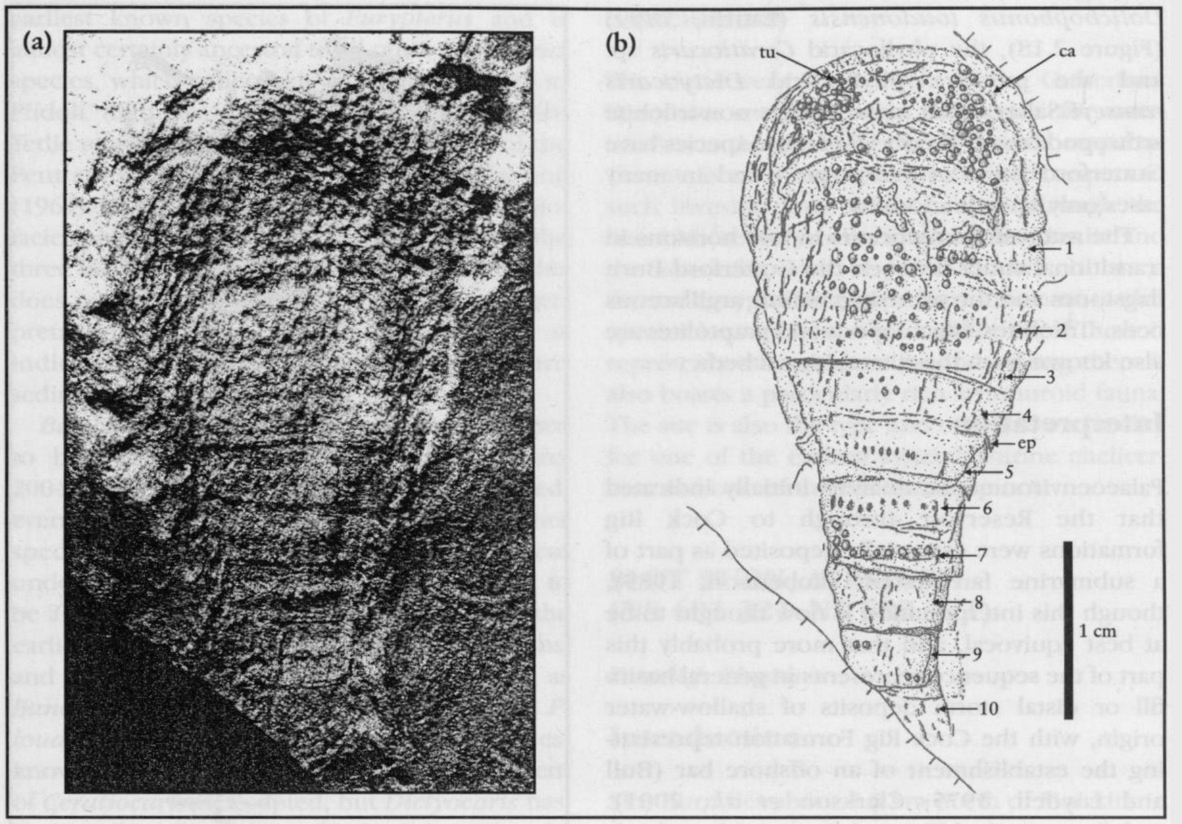


Figure 2.17 *Bembicosoma pomphicus* Laurie, 1899; holotype, National Museums of Scotland, NMS G.1897.32.146; Gutterford Burn Flagstones, Reservoir Formation, Llandovery Series, Silurian, North Esk Inlier, Pentland Hills. (a) Photograph. (b) Interpretative drawing. 1–10, opisthosomal segment number; ca, carapace; ep, epimeron; tu, tubercle. Scale bar is 1 cm. (From Anderson and Moore, 2004, figs 1b and 3.)

1989; Bull and Loydell, 1995), and it has yielded a diverse asteroid fauna (Peach and Horne, 1899; Spencer 1914–1940; Mykura and Smith, 1962). The oldest beds exposed are graded siltsones whose sandy bases contain abundant fragments of material referred to the enigmatic arthropod *Dictyocaris*. Brachiopods, orthoconic nautiloids and trace fossils are found near the base of the Gutterford Burn mudstones. The graptolites, both dendroids and graptoloids, the latter mainly monoclimacids, are mostly recorded from the Gutterford Burn Flagstones and the lower 20 m of the overlying flaggy sandstones.

The eurypterids are concentrated within the Eurypterid Bed, which occurs near the top of the Gutterford Burn Flagstones, some 25 m higher in the sequence than the shell bed mentioned above. The thickness of the Eurypterid Bed has historically been recorded as 30 cm, but more recently it has been reported as 0.5–1 m thick (Anderson, 2003; Anderson and Moore, 2004). Eurypterid skeletons and exuviae are commonly found articulated as carbonized cuticle compressions, and they occur here together with other non-trilobite arthropods, calcareous algae, graptolites, corals, crinoid ossicles, tentaculitids, brachiopods, gastropods, conulariids and orthocones. The eurypterids recorded are the stylonuroids *Parastylonurus ornatus* (Laurie, 1892) (see Figure 2.16), *Parastylonurus hendersoni* Waterston, 1979, *Hardieopterus macrophthalmus* (Laurie, 1892), *Laurieopterus elegans* (Laurie, 1899), *Drepanopterus lobatus* Laurie, 1899, *Drepanopterus pentlandicus* Laurie, 1892, *Drepanopterus bembycoides* Laurie, 1899, and *Kiaeropterus cyclophthalmus* (Laurie, 1892); and the non-stylonuroids *Carcinosoma scotica* (Laurie, 1899), *Nanahughmilleria conica* (Laurie, 1892), *Eurypterus minor* Laurie, 1899, and *Slimonia dubia* Laurie, 1899 (see Waterston 1962, 1979; Tollerton, 1989; Tetlie, 2006b; Tetlie *et al.*, 2007). The xiphosuran *Bembicosoma pomphicus* Laurie, 1899 (Figure 2.17), the scorpion

Dolichophonus loudonensis (Laurie, 1899) (Figure 2.18), the phyllocarid *Ceratiocaris* sp. and the putative phyllocarid *Dictyocaris ramseyi* Salter, 1860 make up the non-trilobite arthropod fauna. Nearly all of these species have Gutterford Burn as their type – and in many cases only known – locality.

The asteroid fauna occurs in two horizons in transitional strata between the Gutterford Burn flagstones and the overlying, mainly argillaceous beds. Trilobites, brachiopods and graptolites are also known from these transitional beds.

Interpretation

Palaeoenvironmental analysis initially indicated that the Reservoir through to Cock Rig formations were essentially deposited as part of a submarine fan system (Robertson, 1989), though this interpretation is now thought to be at best equivocal, and that more probably this part of the sequence represents in general basin-fill or distal storm deposits of shallow-water origin, with the Cock Rig Formation representing the establishment of an offshore bar (Bull and Loydell, 1975; Clarkson *et al.*, 2001). Sedimentation, whatever, appears to have been rapid. The 2000 m of sediment of the Reservoir and the lower part of the overlying Wether Law Linn formations was all deposited within the *crenulata* Biozone. The recent detailed logging of the Gutterford Burn section has additionally indicated that volcanic activity in the form of volcaniclastic and individual ash-fall bands played a considerable role in the formation of the Eurypterid Bed (Anderson, 2003). The whole of the North Esk and Pentlands early Silurian succession, from Reservoir to Henshaw formations, represents a regressive sequence that changes from a marine to a terrestrial, semi-arid desert setting, with all the sediments accumulating near the southern margin of the Midland Valley rift.

Within the context of chelicerate studies Scottish Siluro-Devonian localities have become renowned for yielding a diversity of stylonuroid eurypterids, and foremost among these sites is Gutterford Burn. Stylonuroids are characterized by their long fifth and sixth prosomal appendages, narrow abdomen, and long and styliform telson (Waterston, 1979), the form of their prosomal legs being considered a diagnostic character uniting the group in one overview of eurypterid classification (Tollerton, 1989).

Figure 2.18 *Dolichophonus loudonesis* (Laurie, 1899); holotype, National Museums of Scotland, NMSG.1897.32.196; Gutterford Burn Flagstones, Reservoir Formation, Llandovery Series, Silurian, North Esk Inlier, Pentland Hills. Almost complete specimen. (Lithograph from Laurie, 1899, plate 1, fig. 1.)

They are claimed to have been able to walk on their long, stilt-like legs, and some species have even been suggested as capable of doing so on the shore, though undoubtedly most were aquatic (see Størmer, 1934; Waterston, 1979; Selden, 1984).

With the re-assignment of *Eurypterus cyclophthalmus* to *Kiaeropterus*, *E. minor* is now the earliest known species of *Eurypterus* and is almost certainly ancestral to all other *Eurypterus* species, which collectively span the Wenlock to Přídolí (Silurian) time interval (Tetlie, 2006b; Tetlie *et al.*, 2007). The eurypterid fauna of the Pentlands was placed by Kjellesvig-Waering (1961) in his Hughmilleridae–Stylonuridae biofacies phase, purportedly the least marine of the three biofacies identified by him. However this does not appear to be consistent with the interpretation of the environment of deposition, as indicated above, for the Gutterford Burn sediments.

Bembicosoma pomphicus was recently shown to be a xiphosuran (Anderson and Moore, 2004), as Laurie (1899) originally suspected, even though he described it together with other species from the Pentland Hills that were undoubtedly eurypterids. It is now believed to be a 'synziphosurine', thus making it one of the earliest of this loose grouping of xiphosurans, and has been placed in the same family as *Bunodes*, *Limuloides* and *Pasternakevia*. *P. loudonensis*, similarly, is one of the earliest known scorpions. The phyllocarid assignment of *Ceratiocaris* is accepted, but *Dictyocaris* has, historically, only questionably been considered a phyllocarid and it remains essentially of unknown affinity.

In general the invertebrate fauna of the Reservoir and Deerhope formations appears to be biogeographically discrete, as it is largely distinct from that found in the Girvan area to the west, and from elsewhere in Britain. The younger Wether Law Linn Formation has faunal connections with the Baltic region to the east, suggesting an open marine connection between there and eastern Scotland during latest Llandovery times.

Gutterford Burn has particularly close arthropod network links with the other eurypterid rich Siluro-Devonian Midland Valley sites of Slot Burn, Dunside, and Turin Hill. It contains, however, an especially rich stylonuroid fauna unmatched elsewhere. Ties are also present with the Ludlow through to Přídolí series Anglo-Welsh arthropod sites of Church Hill, the Whitcliffe, Ludford Lane and Ludford Corner, Tin Mill Race, Perton Lane, and Bradnor Hill. All of these have important eurypterid faunas but stylonuroids are almost entirely absent from them.

Conclusions

The Llandovery Series rocks of the Gutterford Burn site are extremely important for non-trilobite arthropod research in several respects. The site is a key historical locality with respect to such investigations, made famous through the late 19th century collecting of John Hardie and the scientific work of John Laurie. It has a diverse eurypterid fauna – there are some twelve species known from here and for all of these it represents the type locality, and among them it also boasts a particularly rich stylonuroid fauna. The site is also the type and only known locality for one of the earliest synziphosurine chelicerates and one of the earliest scorpions.

SLOT BURN, AYRSHIRE (NS 681 321–NS 680 321)

Derek J. Siveter

Introduction

Slot Burn lies about 4.5 km north of Muirkirk in the Lesmahagow Inlier. This is one of four inliers of Silurian age in the central part of the Midland Valley of Scotland, along with the smaller inliers of the Hagshaw Hills, Charmichael and Eastfield (see Figures 2.5 and 2.11). Structurally the Lesmahagow Silurian is folded into an asymmetrical anticline, and in terms of age it includes Llandovery and Wenlock series sediments, at least, with those of the Slot Burn site belonging to the Wenlock Series, some 426 million years old. Enveloping the inlier are Devonian and Carboniferous strata.

Murchison (1856) was an early commentator on the geology of the Lesmahagow area. He was followed in the late 19th century by Peach and Horne (1899; see Figure 2.19), who provided in their classic memoir on the Scottish Silurian a much more in-depth account, including a description of the rocks in Slot Burn. The mapping of Jennings (1961) provided the basis for our current understanding of the geology of the inlier. In particular it led to the establishment of stratigraphical units for the Silurian succession there, and these have been used without qualification by nearly all authors subsequently. Rolfe (1973b, 1992b), Ritchie (1968, 1985), Walton and Oliver (1991), and Dineley (1999a), for example, all employed the stratigraphical

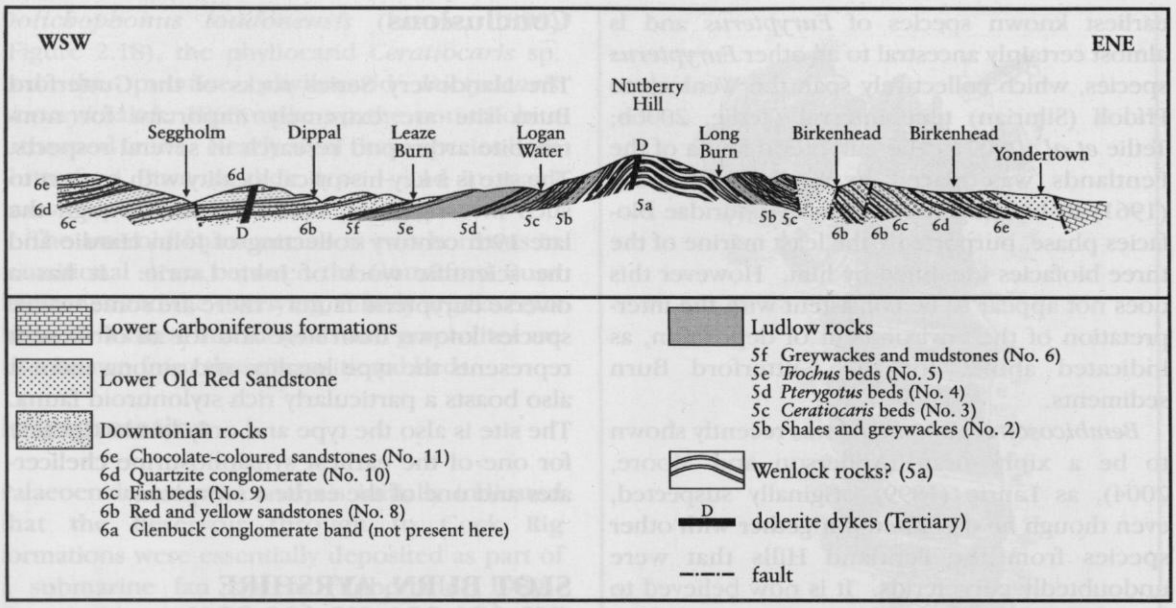


Figure 2.19 Cross-section of the geology between Seggholm and Yondertown, Lesmahagow Inlier. (After Peach and Horne, 1899, fig. 117.)

terminology of Jennings in their various geological and palaeontological works relating to the inlier. Most recently, however, investigations by Paterson *et al.* (1998) have produced a slightly modified lithostratigraphy for a few of the units. Lovelock (1998) carried out a biofacies and environmental analysis of the Lesmahagow Silurian strata.

Historically, the Silurian rocks of the Lesmahagow, Hagshaw and Carmichael inliers have been notable for yielding a variety of non-trilobite arthropods (see, for example, Currie, 1927; Rolfe, 1960, 1962a, 1962b, 1973, 1992b; Ritchie, 1968; Selden and White, 1983; Siveter, 2000a; Palmer, 2000; Tetlie and Braddy, 2004). Peach and Horne were among the earliest authors to note arthropods from Slot Burn, recording two eurypterids, a phyllocarid crustacean and a myriapod from here. Størmer (1934, 1936), Lamont (1955), Ritchie (1968) and Waterston (1979) (see Figure 2.20) all studied the eurypterids from Slot Burn. Plotnick (1999) then used a eurypterid species database from here in his analysis of the habitats of Siluro-Devonian members of the group. Rolfe (1980) and Almond (1985) commented on supposed myriapods from the locality.

Thus in terms of its arthropod fauna, Slot Burn came to prominence essentially because of its eurypterids. It is, however, probably an even more famous locality for fossil fish and it has been included in the JNCC volume covering that topic (Dineley and Metcalf, 1999). The site is otherwise known in the literature as 'Segholm', 'Seggholm', or 'Seggieholm', after the house of the same name that lay about 180 m downstream from the locality, and which even at the time of Peach and Horne was in ruin. In addition to the fossil arthropod importance of this site, the area is also independently selected for the GCR for the Silurian–Devonian Chordata selection category.

Description

Jennings (1961) divided the Silurian of the Lesmahagow Inlier into Priesthill succeeded by Waterhead and then Dungavel groups, with each containing several formations. Above the Dungavel Group there are Old Red Sandstone conglomerates and sandstones of the Devonian. Paterson *et al.* (1998) recognized a Ponesk Burn Formation for those strata originally forming the lower part of the Patrick Burn Formation, Priesthill Group, of Jennings. Other modifications that Paterson and his co-workers introduced were to alter slightly the boundaries of the Castle, Kip Burn and Blaeberry formations within the Priesthill Group. Also, they did not recognize the Passage Formation of Jennings at the base of the Waterhead Group, and they reassigned the argillaceous strata in the lower part of this formation to the underlying Dunside Formation at the top of the Priesthill Group. The incoming of red beds into the sequence was arbitrarily taken by Paterson and his colleagues to mark the base of the Waterhead Group.

The Priesthill Group is generally thought to be of late Llandovery age, though on palynological grounds beds as old as those within the Patrick Burn Formation of this group, and so all younger formations of the group, may be Wenlock in age (Wellman, 1995; Anderson and Moore, 2004). The Waterhead Group has been assigned to the Wenlock Series, and some part of the Dungavel Group may belong to the Ludlow Series (Wellman and Richardson, 1993; Cocks *et al.*, 1992; Palmer, 2000; Paterson *et al.*, 1998)

The stream in Slot Burn flows ENE into the head of Greenock Water, and on the sides of the burn are sediments of the Slot Burn Formation of the Waterhead Group. In the vicinity of Slot Burn and its tributary from Spindle Burn the formation is about 85 m thick. It is composed of similar sediments to those of the slightly older Dippal Burn Formation of the same group. They comprise thin beds of alternating greenish-grey mudstone, siltstone and silty sandstone. Planar bedding or sometimes ripple- or cross-bedding is present in the sandstones. Basal erosion surfaces and loading features are typical of some of the beds.

Grey and red variegated mudstones occur near the base of the formation, these being transitional from the red sandstones, siltstones and mudstones of the underlying Monument Formation. The variegated units are succeeded by the grey mudstones and laminated siltstones that make up the 5 m thick Slot Burn Fish Bed, which itself includes two main productive horizons, a lower one 1–1.3 m thick and an upper one 1 m thick that occurs some 15–20 m upstream (Paterson *et al.*, 1998; Dineley, 1999a). This same mudstone-siltstone lithology occurs several times within the lower part of the Slot Burn Formation, and is also reflected in the dark grey fissile mudstones that form the Dippal Burn Fish Bed which crops out about 1.5 km to the east. The Slot Burn Fish Bed contains, as well as important early vertebrates, arthropods that form the basis for listing the site in the present volume. In addition to Slot Burn, the eponymous formation is also exposed in the tributaries that lead into Dippal Burn from the north and also in the adjacent Auchingilloch Glen. Peach and Horne (1899) described the Slot Burn and Dippal Burn fish beds as part of their stratigraphical group number nine, horizon 6c (Figure 2.19).

The stylonuroids *Stylonurella spinipes* (Page, 1859), *Parastylonurus ornatus* (Laurie, 1892), and *Brachyopterella ritchiei* Waterston, 1979, together with the non-stylonuroids *Lanarkopterus dolichoschelus* (Størmer, 1936) and *Nanahughmilleria* sp. make up the eurypterid fauna recorded from Slot Burn (see Peach and Horne, 1899; Størmer, 1934, 1936; Lamont, 1955; Ritchie, 1968; Waterston, 1979; Plotnick, 1999; Figures 2.20 and 2.21). The site stands as the type locality for the *Lanarkopterus* and *Brachyopterella* species.

The phyllocarid *Ceratiocaris laxa* (Etheridge, Jones and Woodward; see Rolfe and Burnaby, 1961) and a myriapod have also been listed from Slot Burn (Peach and Horne, 1899). However the presence of *Ceratiocaris*, at least, has been dismissed (Ritchie, 1968) and the myriapod record remains unsubstantiated. Nevertheless, the type species of the enigmatic *Dictyocaris*, *D. slimoni* Salter, 1860, a genus considered by some to possibly be a phyllocarid, has also been found in association with *L. dolichoschelus*. The enigmatic arthropod *Pseudarthron whittingtoni* Selden and White, 1983 has recently been listed (Paterson *et al.*, 1998) from Slot Burn, though when the species was established just a single specimen was available, from the Slot Burn Formation of South Hill quarries in the Lesmahagow Inlier, some 10 km to the NNW. Associated, non-arthropod elements in the Slot Burn site include the agnathans *Birkenia*, *Lasanius*, *Lanarkia*, *Sheilia* and *Ateleaspis*, together with *Pachytheca*, *Taitia* and *Parka* plant material (Ritchie, 1968; Dineley, 1999a)

Interpretation

The Priesthill group is fully marine in its lower part (Ponesk Burn Formation) and in its upper part (Patrick Burn Formation) it changes to restricted marine influenced by turbidite flows (Paterson *et al.*, 1998). The Waterhead Group, which consists of red and purple siltsones and sandstones, is continental in origin. These latter sediments were fluvially derived, except for some within the Dippal Burn and Slot Burn formations, including the fish bed horizons, which are probably of lacustrine origin. The

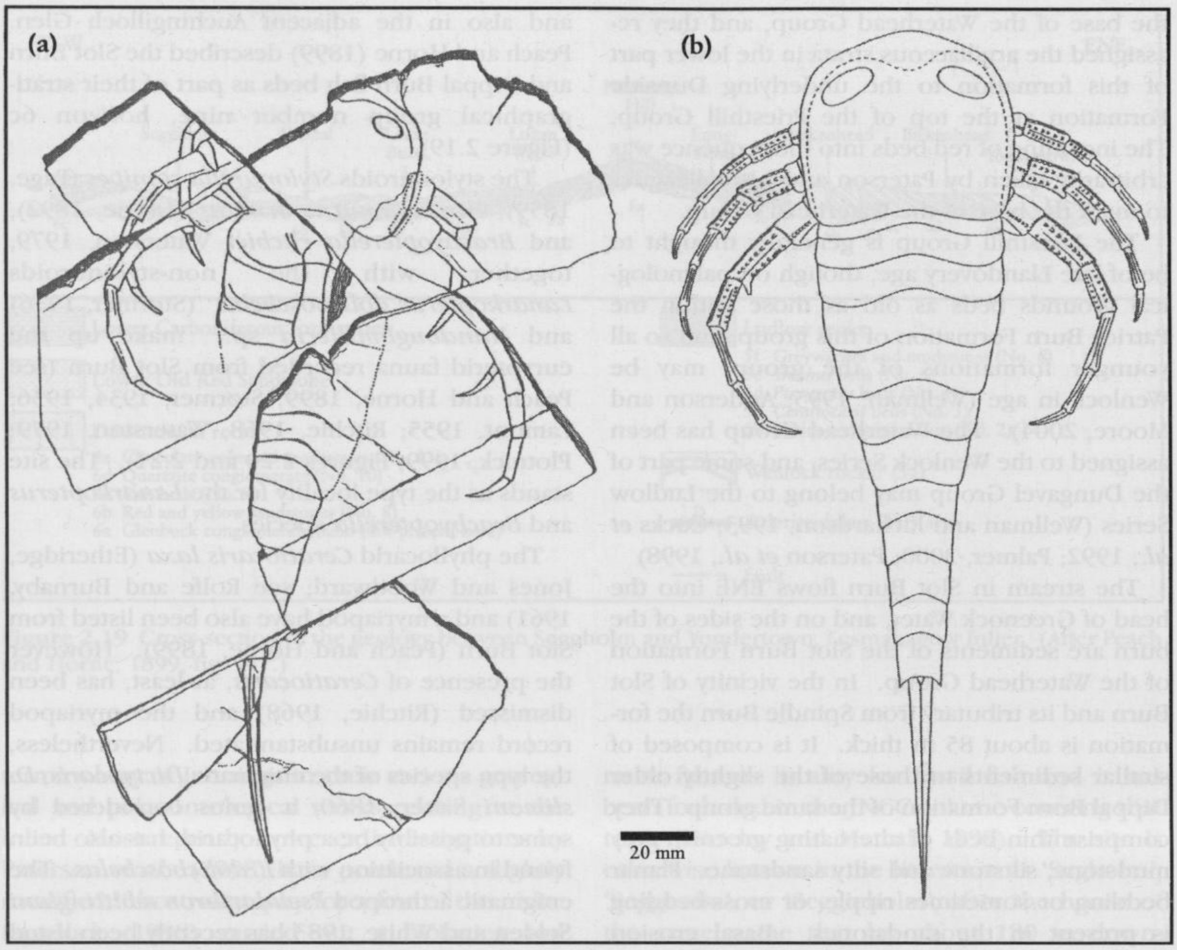


Figure 2.20 ***Brachyopterella ritchiei*** **Waterston, 1979; holotype, National Museums of Scotland, NMS G.1968.14; Slot Burn Formation, Waterhead Group, Wenlock Series, Silurian, Slot Burn, Lesmahagow Inlier. (a) Line drawing of the holotype specimen; (b) reconstruction, dorsal view. (From Waterston, 1979, text-fig. 11.)**

fluviatile sedimentation that existed throughout most of the Waterhead Group times was apparently interrupted twice through blockage to the drainage system, which led to the formation of lakes and the deposition, when waters were at their highest, of the sediments comprising the fish beds. The Dungavel Group sediments indicate stable terrestrial conditions. The Silurian succession of Lesmahagow, as with almost all other Silurian successions in the Midland Valley, charts a regression from the marine turbidites of the Llandovery through into the fluviatile and lacustrine non-marine facies of Wenlock and later times. In the Girvan area, however, marine conditions continued into the early Wenlock.

Størmer (1936) and Lamont (1955) both described material of *Lanarkopterus dolichoschelus*, originally a manuscript species of Laurie (see Peach and Horne, 1899), before Ritchie assembled much more material, both from his own field collections and also from that identified by him from museums. This enabled the morphology of the species to be known almost completely and a new genus to be established for it. *Lanarkopterus* is known only from the Lesmahagow area. Similarly, prior to the establishment of *B. ritchiei*, *Brachyopterella* was known from just one species based on three specimens. The description of the Scottish material showed for the first time the nature of the opisthosoma and abdominal appendages in a species of this genus. The material of *Stylonurella spinipes* from Slot Burn, a single

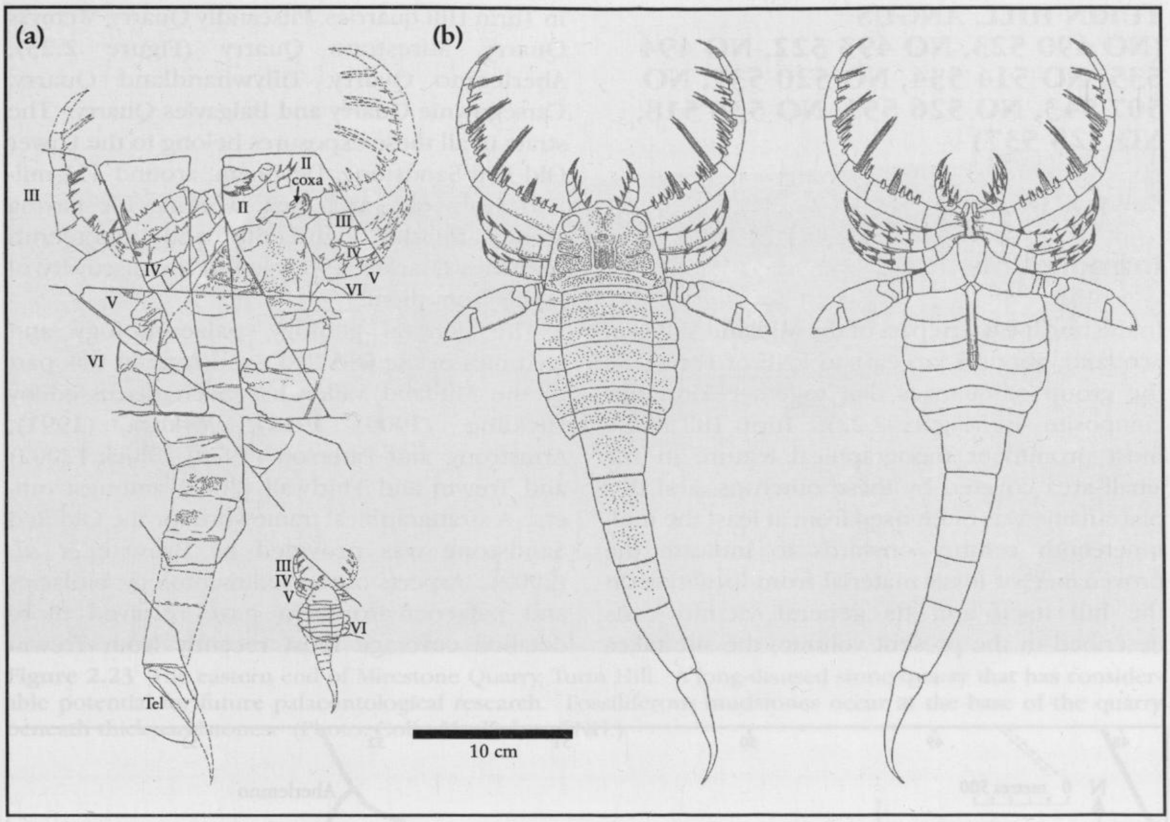


Figure 2.21 *Lanarkopterus dolichoschelus* (Størmer, 1936); Slot Burn Formation, Waterhead Group, Wenlock Series, Silurian, Slot Burn, Lesmahagow Inlier. (a) Drawing of largest and smallest individuals, National Museums of Scotland, NMS G.1967.65.1 and 2 respectively. II–IV, first to fourth 'walking' legs; VI, swimming leg; Tel, telson. (b) Reconstruction, dorsal and ventral views. (From Ritchie, 1968, figs 3–5.)

specimen, was only the second specimen of this species to have been found and added to our knowledge the morphology of the species. The affinities of *Pseudarthron whittingtoni* are unknown.

Slot Burn has close network links with the other Scottish Siluro-Devonian arthropod sites at Gutterford Burn, Dunside and Turin Hill. These other sites are also rich in eurypterids, and in both Slot Burn and especially Gutterford Burn stylonuroid species are well represented. Slot Burn also has links with the younger, Ludlow through to Přídolí Series Anglo-Welsh arthropod sites of Church Hill, The Whitcliffe, Ludford Lane and Ludford Corner, Tin Mill Race, Perton Lane, and Bradnor Hill, all of which have eurypterid faunas, though of a different composition. The fish-eurypterid biofacies of the Slot Burn site has been compared, at least in broad compositional terms, with that of penecontemporaneous sites in the nearby Hagshaw Hills and ones from Wenlock and Ludlow age rocks of the Ringerike area of Norway (Rolfe, 1961; Ritchie, 1968).

Conclusion

This Lesmahagow site is best known for its eurypterid fauna, totalling five species, two of which have it as their type locality. The eurypterid specimens from here have added significantly to our knowledge of rare species. The fauna is of Wenlock Series (Silurian) age, unlike those of other eurypterid-based sites described in this volume from Scotland, which occur in Llandovery Series or Devonian strata, or those from the Anglo-Welsh area, which are from Ludlow and Přídolí series rocks. Analogues of the Slot Burn biofacies are present in Silurian strata of the adjacent Hagshaw Hills and the Ringerike area, Norway.

TURIN HILL, ANGUS (NO 490 523, NO 493 522, NO 494 535, NO 514 534, NO 520 537, NO 507 543, NO 526 551, NO 538 518, NO 528 537)

Derek J. Siveter

Introduction

In the north-eastern part of the Midland Valley of Scotland, about 5 km east to ENE of Forfar, lie the group of quarries that together form this composite site (Figure 2.22). Turin Hill is the most prominent topographical feature in the small area covered by these outcrops, and this place-name was often used from at least the mid-nineteenth century onwards to indicate the provenance of fossil material from localities on the hill itself and its general vicinity. As described in the present volume, the site takes in Turin Hill quarries, Pitscandly Quarry, Wemyss Quarry, Mirestone Quarry (Figure 2.23), Aberlemno Quarry, Tillywhandland Quarry, Carsegownie Quarry and Balgavies Quarry. The strata in all these exposures belong to the Lower Old Red Sandstone, Devonian, around 411 million years old, and their working for paving stones in the eighteenth and nineteenth centuries (Mackie, 1980) led to the discovery of fossils from them.

The general geology, palaeontology and tectonics of the Old Red Sandstone in this part of the Midland Valley has been discussed by Hickling (1908, 1912), Mykura (1991), Armstrong and Paterson (1970), Bluck (2002) and Trewin and Thirlwall (2002) amongst others. A stratigraphical framework for the Old Red Sandstone was provided by Browne *et al.* (2002). Aspects of the sedimentology, biofacies and palaeoenvironment have received more detailed coverage most recently from Trewin

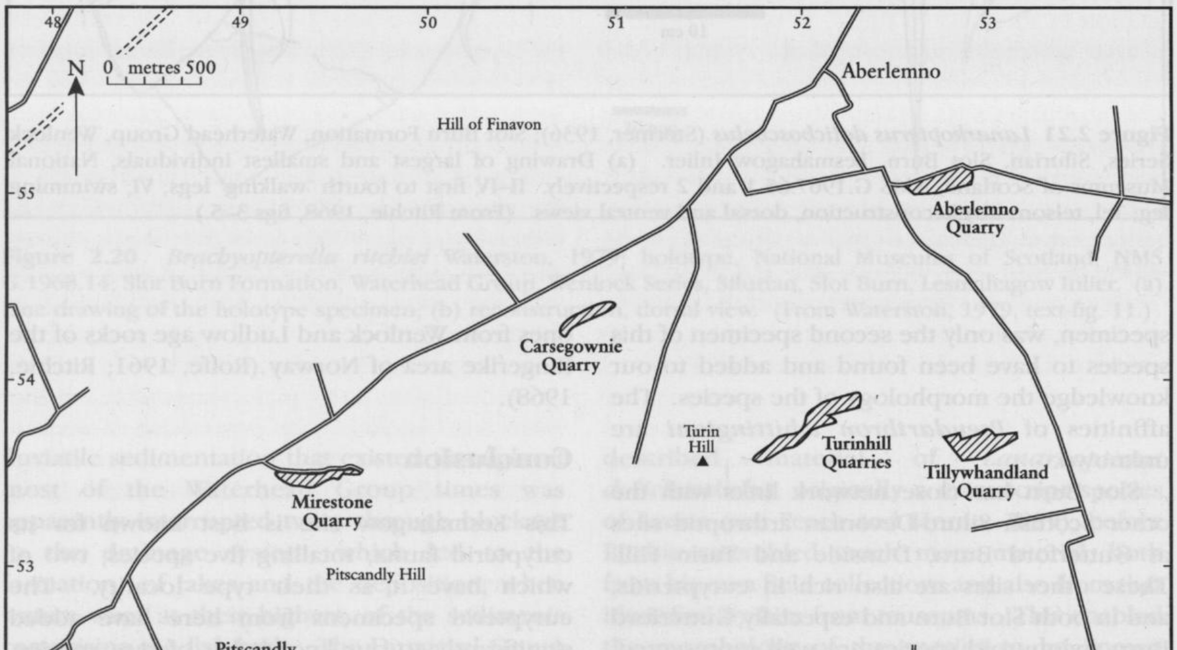


Figure 2.22 Location of quarries comprising the Turin Hill GCR site.

Figure 2.23 The eastern end of Mirestone Quarry, Turin Hill. A long-disused stone quarry that has considerable potential for future palaeontological research. Fossiliferous mudstones occur at the base of the quarry beneath thick sandstones. (Photo: Colin MacFadyen/SNH.)

and Davidson (1996), Bluck (2000), Browne and Barclay (2005a) and Browne (2005a,b). Also, various localities that are included in this composite Turin Hill site were described in the field guide to accompany the 1978 international symposium on the Devonian System (Armstrong *et al*., 1978).

Several authors have documented the arthropods from Turin Hill and associated Midland Valley localities. Page (1856a,b, 1859), Agassiz (1844), Salter (1859a), Woodward (1864b, 1865a, 1866, 1872), Waterston (1962, 1964, 1975) and Braddy (2000) have discussed the eurypterids, much of the finest material of which was recovered in the nineteenth century by James Powrie. Page (1856b, 1859), Peach (1882, 1899), Rolfe (1980), Almond (1985, 1986) and Wilson and Anderson (2004) have documented millipede and kampecarid myriapods. The arthropods from here are associated with fluvial and lacustrine settings and, significantly, some are implicated with the terrestrialization of the group.

Sites on and around Turin Hill that have been included in other GCR volumes include Aberlemno Quarry, in the volumes for fossil plants, fossil fish and the Old Red Sandstone (Cleal and Thomas, 1995; Dineley and Metcalf, 1999; Barclay *et al*., 2005); Tillywhandland Quarry, in those for fossil fish and the Old Red Sandstone; and Clocksbriggs (also known as 'Wemyss') Quarry, which was described with Aberlemno Quarry under the site name 'Turin Hill' in that for fossil plants.

Description

The quarries comprising this site belong to the Arbuthnott-Garvock Group of Lower Devonian, Lochkovian and Pragian age (Browne and Barclay, 2005a). Only some of them have been logged in modern times and most have been abandoned for decades, if not a century, or more.

Undifferentiated quarries and exposures under the name 'Turin Hill' (NO 514 534 and NO 520 537) have produced numerous fine specimens of *Pterygotus anglicus* Agassiz, 1844 (Figures 2.24 and 2.25), a eurypterid much celebrated in 19th century works, and estimated (Kjellesvig-Waering, 1964) to reach up to 1.75 metres in length from the anterior of the carapace to the end of the telson. 'Turin Hill quarries' also represent the type locality for *Stylonurus ensiformis* Woodward, 1864, which has recently been regarded as a junior synonym of *Stylonurus powriensis* Page, 1856 (Agassiz,

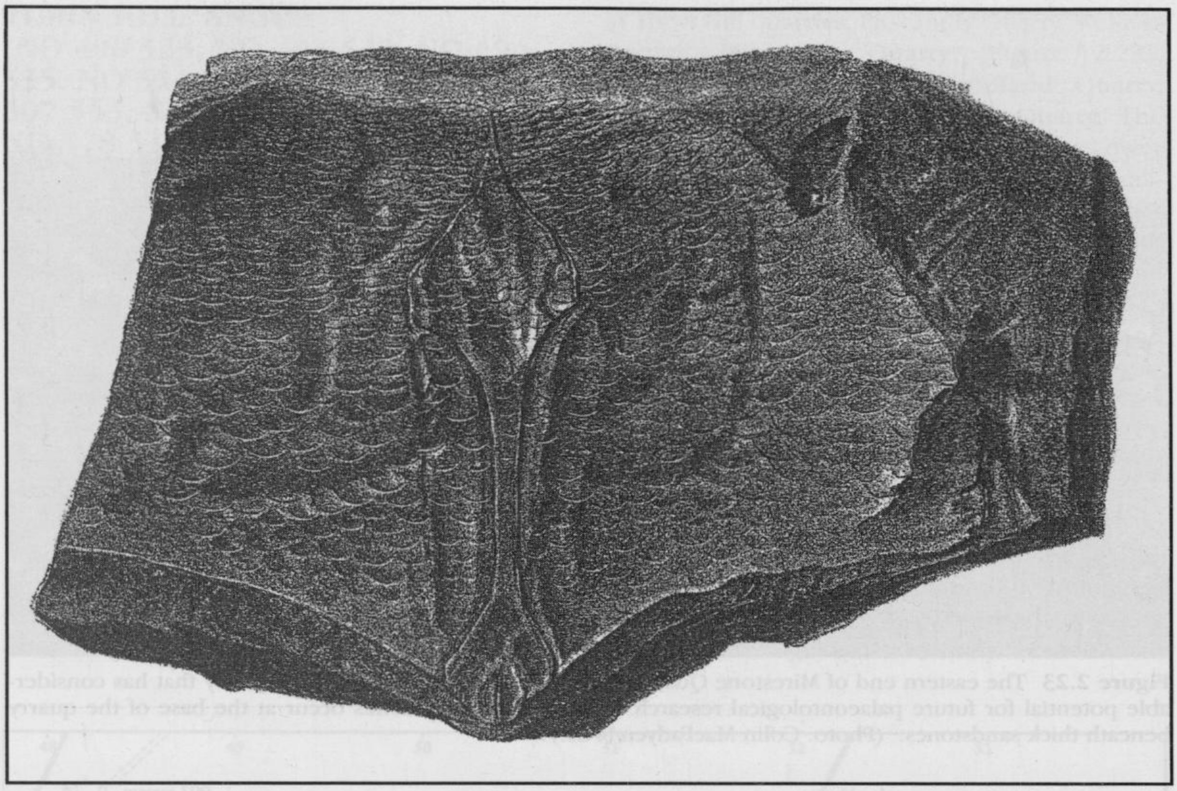


Figure 2.24 *Pterygotus anglicus* Agassiz, 1844; National Museums of Scotland, Kinnaird Collection 49, Lower Devonian, Balruddery. Opercular plates with the median appendage attached. (Lithograph, from Agassiz, 1844.)

1844; Hickling, 1912; Woodward, 1864b, 1866; Salter, 1859a; Kjellesvig-Waering, 1964; Waterston, 1964; Braddy, 2000). In addition the kampecarid *Kampecaris forfarensis* Page, 1856 has been recorded from here (Peach, 1882; Hickling, 1912).

Tillywhandland Quarry (NO 528 537) exposes beds of the Dundee Flagstone Formation of early early Lochkovian age (Richardson and MacGregor, 1986). According to Trewin and Davidson (1996) it was the main source in the nineteenth century of fossil specimens in laminite lithologies labelled 'Turin Hill'. The sequence here includes a fish bed, one of eight recognized in the Strathmore region and between which correlation is uncertain (Armstrong and Paterson, 1970; Armstrong *et al.*, 1978; Trewin and Davidson, 1996; Dineley, 1999c; Browne, 2005b). About 3 m of medium to coarse-grained sandstones, in part trough cross-bedded and in part parallel-laminated, and with two pebble-lined erosion surfaces, form the base of the section. Above this is the fish-bearing laminite, which is about 1.3 m thick, with sandstone dykes penetrating upwards into its basal 0.5 m, and with a 6 cm thick bentonite 1 m above its base. Succeeding the fish bed there is an 11 m coarsening upwards sequence of siltsones and fine sandstones with minor laminites. The sandstones below the fish bed indicate high-energy fluvial channel deposits, the fish bed laminites represent phytoplankton-based lacustrine deposits, and the overlying siltstones and sandstones indicate the infilling and shallowing of the lake. The fish bed has yielded plant and eurypterid material in addition to early vertebrates, and it shows evidence of burrowing. The eurypterids recorded from the quarry are *Pterygotus anglicus* and *Parahughmilleria* sp. (Hickling, 1912; Armstrong *et al.*, 1978; Braddy, 2000). *Archidesmus macnicoli* Peach, 1882, a very rare millipede, has been recovered from the fish bed and from laminites in the overlying siltsones (Wilson and Anderson, 2004; Figure 2.26).

Pitscandly Quarry (NO 490 523) showed some 40 m of strata when it was logged in the late 1970s (Armstrong *et al.*, 1978). The lower 20 m comprises indifferently exposed conglomerates

Figure 2.25 *Pterygotus anglicus* Agassiz, 1844; From Indurated shale overlying the 'Arbroath Paving-stone', Turin Hill Range, near Forfar. One of the most entire specimens obtained. From the Museum of James Powrie, Esq., F.G.S., Reswallie, Forfar. 1–5, appendages; C, antennae; i, small triangular plate; O, oval marginal eyes; P, metastoma or post-oral plate.' (Lithograph, × 0.5, from Woodward, 1866, plate 2, fig. 1.)

and arkosic sandstones. Above these are about 10 m of grey, horizontally laminated, fine-grained sandstones interbedded with grey, green and red mudstones. The genesis of these beds has been interpreted as fluvial/lacustrine, and the mudstones have yielded *Kampecaris forfarensis*. Up-section, overlying the essentially

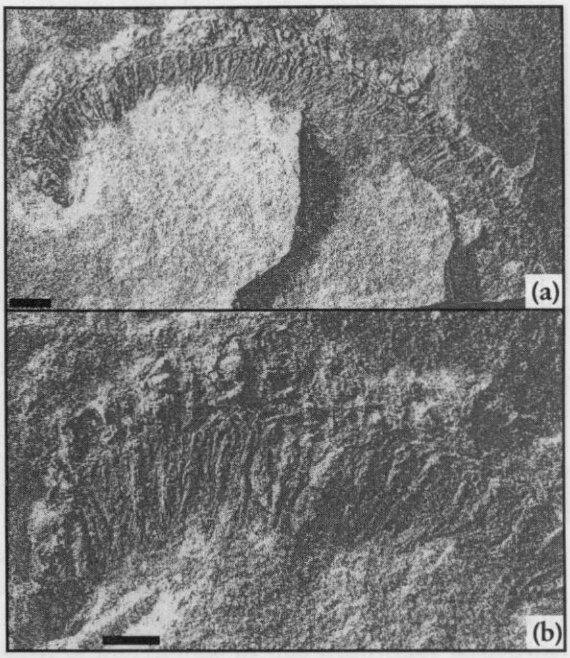


Figure 2.26 *Archidesmus macnicoli* Peach, 1892; University of Aberdeen, Department of Geology, AUGD 12302b; Fish bed, Dundee Formation, Arbuthnott–Garvock Group, Lower Devonian, Tillywhandland Quarry, 8 km ENE of Forfar, Midland Valley of Scotland. Scale bar in (a) = 2mm, (b) = 1mm. (Photographs from Wilson and Anderson, 2004, figs 4.1 and 4.2.)

lacustrine deposits, there are about 10 m of braided fluvial conglomeratic deposits that have an erosion surface or channelling at their base. Pitscandly is the type locality for *Stylonurus powriensis* (Page, 1856; see also, for example, Woodward, 1865a, 1872b; Hickling, 1912; Kjellesvig-Waering, 1966; Braddy, 2000).

Wemyss Quarry (NO 493 522), adjacent to Pitscandly Quarry, and Mirestone Quarry (NO 494 535), on the north side of Pitscandly Hill, are possible sources of some 19th century arthropod material.

Aberlemno Quarry (NO 526 551) exposes some 9.5 m of strata along a 300 m face (Armstrong *et al.*, 1978; Dineley, 1999c; Browne, 2005a). The lowest 2 m of sediments are largely fine sandstones and laminated siltstones and mudstones of the Dundee Flagstone Formation, interpreted as those of a shallow lake (Figure 2.27 and see Figure 2.29). They have yielded a fauna of fish, plants, and arthropods, the latter including (Armstrong *et al.*, 1978) the eurypterids *Pterygotus* and *Erieopterus* (though note that Braddy, 2000, has dismissed British

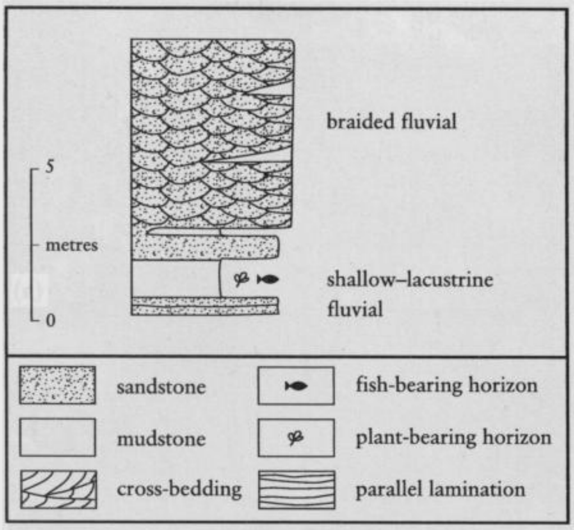


Figure 2.27 Section of Aberlemno Quarry. (From Browne, 2005a, after Armstrong *et al.*, 1978 and Dineley, 1999c.)

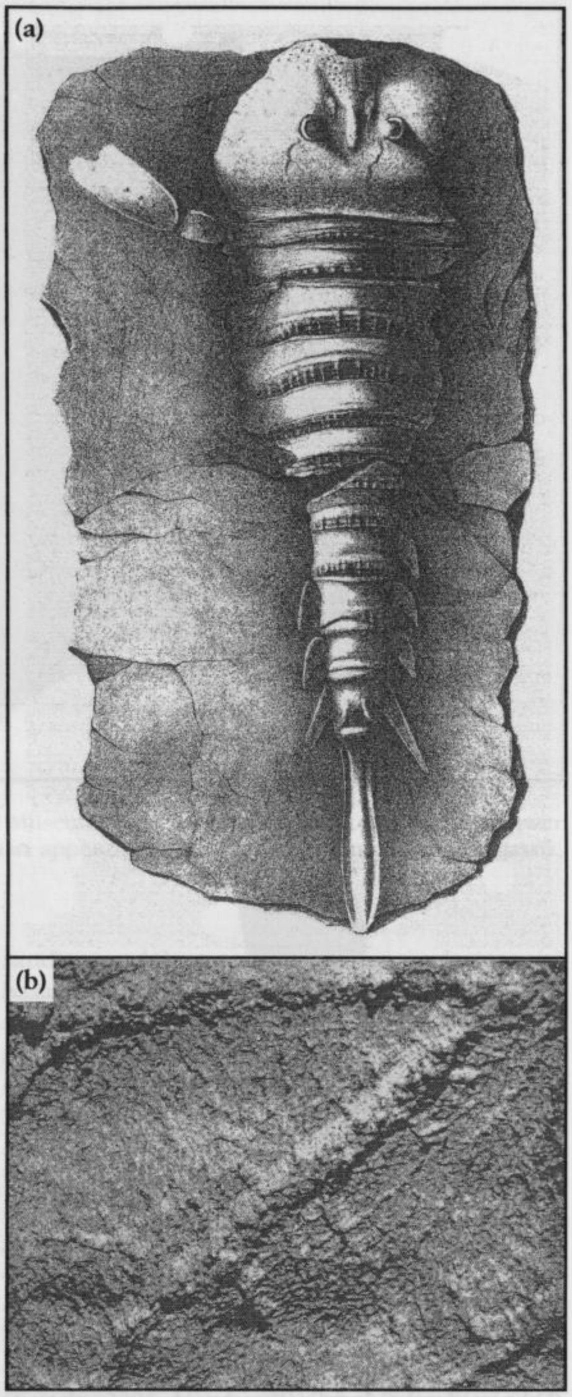


Figure 2.28 *Tarsopterella scottica* Woodward, 1865; lectotype, National Museums of Scotland, NMS G.1891.92.103; Arbuthnott–Garvock Group, Lower Devonian, probably from Balgavies Quarry, 7 km east of Forfar. Found in 1863 by James Powrie. This specimen is just over one metre long. (a) Entire specimen. (Lithograph, from Woodward, 1872b, plate 23.) (b) Photograph, latex cast of gill tract of the second mesosomal segment, × 6. (From Waterston, 1975, plate 2, fig. 5.)

records of the latter genus), and the enigmatic *Dictyocaris*. The highest 7.5 m comprises trough-bedded sandstones belonging to the Scone Sandstone Formation, which are thought to have formed in a braided stream complex. The Aberlemno fish bed within the Dundee Flagstone Formation here has been correlated on palynological grounds with a lower Lochkovian horizon in the Anglo-Welsh Basin (Richardson *et al.*, 1984).

Carsegownie (or Carsgownie) Quarry (NO 507 543) has yielded *Pterygotus anglicus* (see Hickling, 1912; Armstrong and Paterson, 1970).

Balgavies Quarry (NO 538 518) is probably the type locality for the stylonurid eurypterid *Tarsopterella scotica* Woodward, 1865 (see Woodward, 1865a, 1872b; Hickling, 1912: his 'Montreathmont'; Waterston, 1975; Braddy, 2000; Figure 2.28).

Other Arbuthnott–Garvock Group, Midland Valley fossil localities that have also yielded arthropods (see Armstrong and Paterson, 1970, fig. 1; Braddy, 2000, fig. 1) include the following:

Montreathmont Muir, 12 km ENE of Forfar, for eurypterids (Armstrong and Paterson, 1970; Braddy, 2000).

Canterland Den, 30 km NE of Forfar, from where *P. anglicus* and *Kampecaris forfarensis* have been listed (Peach, 1882; Hickling, 1912).

Carmyllie quarry complex, 12 km ESE of Forfar, is probably the type locality for the stylonuroid *Pagea sturrocki* Waterston (1962) and *Pterygotus anglicus* is also recorded from here (Hickling, 1912; Waterston, 1962). One of these quarries also yielded a syntype specimen of *Archidesmus macnicoli* (Peach, 1882; Wilson and Anderson, 2004).

Kelly Den, 18 km south-east of Forfar is the type locality of the monotypic *Erieopterus brewsteri* Woodward, 1864, a species recently considered to be based on a juvenile specimen of *Tarsopterella scotica*, but which, note, has priority over the latter species (see Woodward, 1865a; Kjellesvig-Waering, 1958; Braddy, 2000). The stream section here is also possibly the type locality of the chasmataspid chelicerate *Forfarella mitchelli* Dunlop, Anderson and Braddy (1999; see also Braddy, 2000). Chasmataspids are known from just five species globally, one from Ordovician rocks of the USA, two from the Devonian strata of Scotland (the other is *Achanarraspis reedi* Anderson, Dunlop and Trewin, 2000 from the Middle Devonian of Caithness), and two from the Lower Devonian of Germany.

Farnell is a locality 16 km ENE of Forfar from where *Pterygotus anglicus* and *Pterygotus minor* Woodward, 1864 have been recorded. The latter species, however, based on a small juvenile specimen with more dorsally placed eyes than the former, has recently been re-interpreted as a junior synonym of *P. anglicus* (Woodward, 1864b; Hickling, 1912; Braddy, 2000).

Whitehouse Den, 11 km SSW of Forfar, has yielded the hughmillerid eurypterid *Nanahughmilleria pygmaea* Salter (1859b; see Braddy, 2000).

Balmashanner Quarry, 1 km south of Forfar, has yielded eurypterid material that probably belongs to *N. pygmaea* (Salter, 1859b; see Braddy, 2000).

Balruddery, 22 km south-west of Forfar, has yielded *P. anglicus* (Agassiz, 1844; Hickling, 1912; Salter, 1859a; Kjellesvig-Waering, 1964; Braddy, 2000) and *Kampecaris forfarensis* (Peach, 1892; Hickling, 1912).

Interpretation

The laminite deposits and associated fish/arthropod fauna of the Dundee Formation, Arbuthnott-Garvock Group, represent those of 'Lake Forfar', which is speculated to have formed as a result of drainage impediments to the south-west caused by local volcanic activity, together with progradation of synsedimentary fault-controlled alluvial fans in the north-west (Trewin and Davidson, 1996). Annual, varve-type deposits of the Tillywhandland fish bed laminites are reckoned to have formed over about 2000 years.

The eurypterid fauna of the Lower Old Red Sandstone, Devonian, of the Midland Valley numbers about seven species, and comprises two main facies assemblages: a clastic fluvial sequence and a finer-laminated lacustrine sequence (Braddy, 2000; Figure 2.29). The benthic stylonuroids (*Pagea*, *Stylonurus*, *Tarsopterella*) are thought to have inhabited river channel systems surrounding Lake Forfar. The pterygotids (*Pterygotus*) and hughmillerids (*Hughmilleria*, *Parahughmilleria*, *Nanahughmilleria*), together with the chasmataspid *Forfarella*, are believed to have lived primarily in the lake shallows. The occurrence, incidentally, of pterygotids in this freshwater lacustrine setting suggests that the tripartite eurypterid biofacies model of Kjellesvig-Waering (1961), in which the Carcinosomatidae–Pterygotidae phase was interpreted as the most open marine of the three, is open to question (Braddy, 2000). Myriapods occurred with plants on the lake margins. The kampecarids perhaps favoured freshwater aquatic habitats (Almond, 1985). Marine faunas are absent. Various faunal elements, including eurypterids and millipedes, were washed into the deeper parts of the lake (Trewin and Davidson, 1996; Wilson and Anderson, 2004). The pterygotids, the most common of the arthropods, are preserved as near complete exuviae or as fragments, ranging in size from about 15 cm to 1.8 m.

The morphology of *Pterygotus* and *Hughmilleria* in general indicates that they were active, nektonic predators, whereas that of the stylonuroids suggests that they were part of the benthos (Størmer, 1934). Various aspects of the morphology of the 'Turin Hill' stylonuroids were related by Waterston (1979) to maintaining stability in a relatively high-energy environment. Additionally, the excellent preservation of the Balgaves Quarry type material of *Tarsopterella scotica* has been used to interpret the nature of its gill tracts as essentially extensions of the body wall, thus confirming that the eurypterid gill is more comparable with the respiratory structures in scorpions rather than those of xiphosurans (Waterston, 1975).

This Turin Hill site has close arthropod

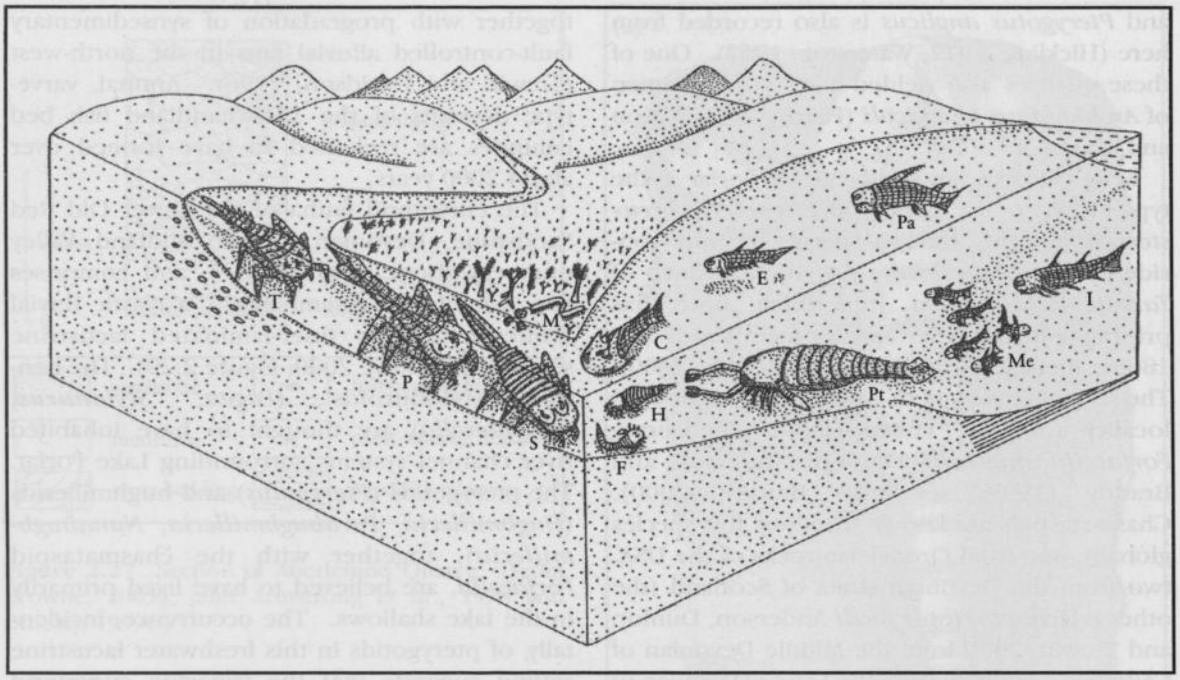


Figure 2.29 Palaeoecological reconstruction of Turin Hill arthropod assemblage, including elements of the associated vertebrate fauna. A myriapod (M) is within the terrestrial flora (largely hypothetical) on the lake margins. Pterygpotids (Pt), hughmillerids (H) and the chasmataspid *Forfarella* (F) inhabit the shallow lake margins. The stylonurids *Pagea* (P), *Stylonurus* (S) and *Tarsopterella* (T) inhabit the river channels surrounding the lake. The cephalaspids (C) live in the shallow lake margins. The acanthodians inhabit open water – *Ishnacanthus* (I) chases a shoal of *Mesocanthus* (M), *Euthacanthus* (E) searches the substrate, and *Parexus* (Pa) patrols for prey. (From Braddy, 2000.)

network links with the other Scottish Siluro-Devonian arthropod sites of Gutterford Burn, Dunside, Slot Burn, and Rhynie, especially the first three, which are also essentially eurypterid-based. It also has links with the Ludlow through to Přídolí Series Anglo-Welsh arthropod sites of Church Hill, The Whitcliffe, Ludford Lane and Ludford Corner, Tin Mill Race, Perton Lane, and Bradnor Hill, all of which also have important eurypterid faunas, but ones that contrast in composition with those from Turin Hill. Stonehaven (upper Wenlock–?lowermost Ludlow series), Ludford Lane and Ludford Corner (upper Silurian) and Rhynie (Lower Devonian) are other arthropod networked GCR sites yielding myriapods.

In terms of palaeogeography, between early and late Devonian times Scotland moved north from around 30° south to 20° south. The Iapetus Ocean had perhaps finally closed and Scotland had become part of the Old Red Sandstone continent of Euramerica, sandwiched between Greenland and Scandinavia. However, the presence of extensive volcanism in the Lower Old Red Sandstone from the Lorne Province, north-west of the Highland Boundary Fault through the Midland Valley and across the Southern Uplands Fault to the Cheviot Hills, might indicate continuing subduction in this region (Thirlwall, 1981).

Conclusion

This composite Lower Devonian site has yielded excellent fossil material of *Pterygotus anglicus* and other eurypterids, notably stylonuroids, most of which was collected and first investigated during the course of classic 19th century studies of this major, extinct arthropod group. Some of the quarries comprising the site represent the type localities for some of the eurypterid species found there. Very rare millepede and kampecarid myriapods also occur, the aforementioned, at least, being potentially important in helping to assess the nature of arthropod terrestrialization.

STONEHAVEN, ABERDEENSHIRE (NO 881 866)

Derek J. Siveter and D. Palmer

Introduction

This site is located in the north-easternmost part of the Midland Valley of Scotland, immediately south of where the Highland Boundary Fault intersects the coastline (see Figure 2.5). The most important part of the site concerning the present volume centres on Cowie Harbour, a kilometre north of Stonehaven town (Figure 2.30). However, strata that put the site into geological, tectonic and palaeoenvironmental context are exposed over about 2.0 km, from Stonehaven Harbour in the south to Craigeven Bay in the north (see MacGregor, 1968; Dineley, 1999a). The rocks along this stretch of coast are referred largely to the Stonehaven Group, which forms the lowest part of the Old Red Sandstone, with the whole of the latter in the Midland Valley reaching its greatest thickness, some 8 km, in this region. The Old Red Sandstone is largely of Devonian age, but the deposits of the Stonehaven Group were laid down in mid-Silurian times, around 422 million years ago.

The geology of this area has been described in detail or put into context by Hickling (1908), Campbell (1911, 1912a, 1912b, 1913), Carroll (1995), Trewin and Thirlwall (2002), Browne *et al.* (2002) and Browne and Barclay (2005a, 2005b). The site was also included in the field

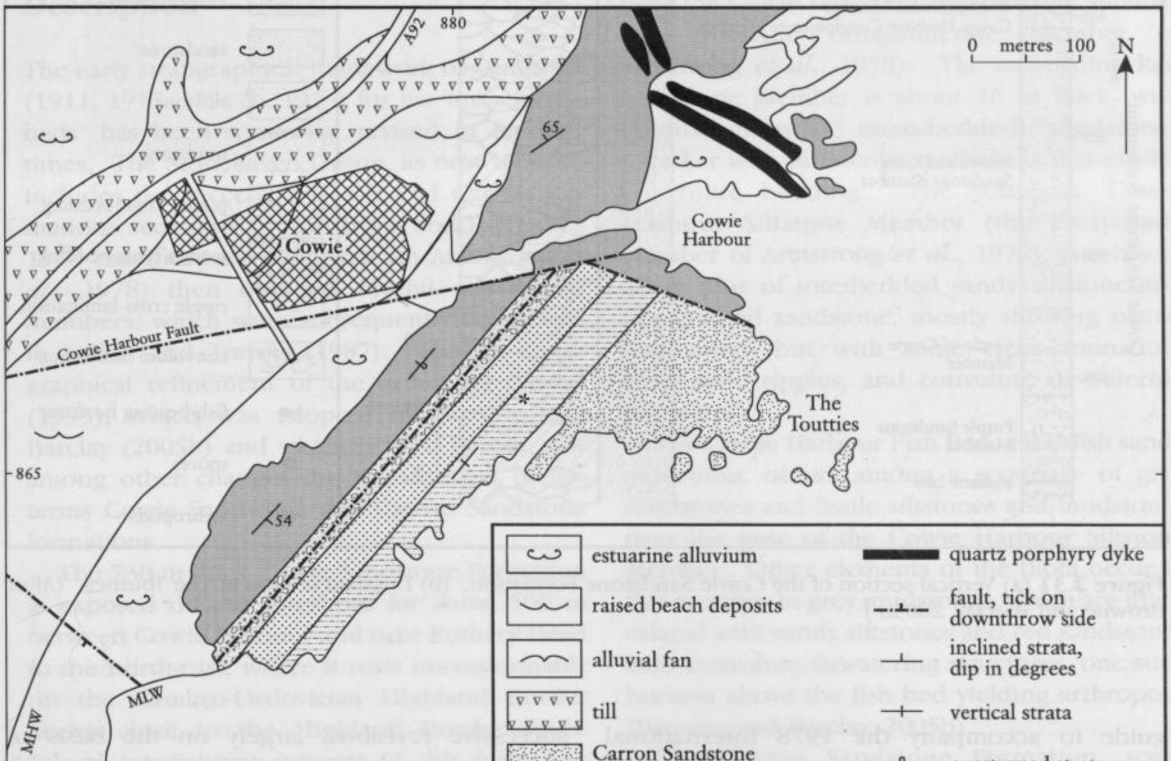


Figure 2.30 Geological sketch map of The Toutties area. (After Browne and Barclay, 2005b.)

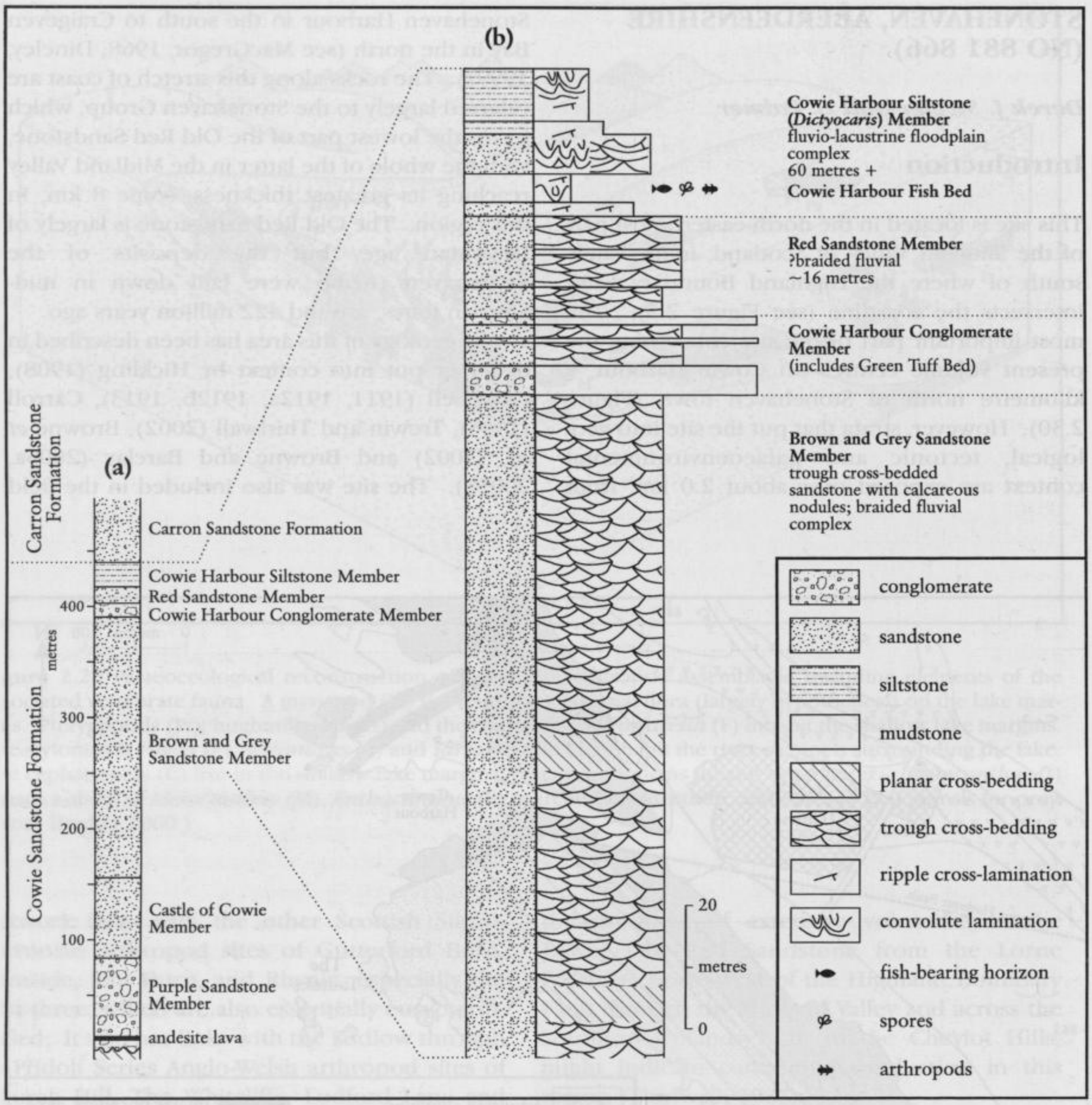


Figure 2.31 (a) Vertical section of the Cowie Sandstone Formation. (b) Detailed section at The Toutties. (After Browne and Barclay, 2005b.)

guide to accompany the 1978 International Symposium on the Devonian System by Armstrong *et al.* (1978), and the guides covering Fife and Angus by MacGregor (1968), and the Aberdeen area by Gillen and Trewin (1987). Discussion of the sedimentology has been presented in modern times by Armstrong *et al.* (1978), Gillen and Trewin (1987), Phillips and Carroll (1995), Robinson *et al.* (1998) and Browne and Barclay (2005b). The relative age of the Stonehaven Group has been the subject of successive revisions, largely on the basis of arthropods and then palynomorphs, through the work of Campbell (1912a, 1912b), Lamont (1952), Hanken and Størmer (1975), Marshall (1991) and Wellman (1993).

The palaeobiota associated with the Old Red Sandstone of the Midland Valley of Scotland has had world renown since the pioneering researches of Hugh Miller (1841) and the Swiss palaeontologist and glaciologist Louis Agassiz (1844). They focussed particularly upon the remarkable agnathan fish fauna but also included notices of the accompanying arthropods and plants. The arthropods from the Stonehaven area – eurypterids, myriapods and a species of uncertain affinity – have been the subject of comment since the time of Campbell (1912a). Recent research by Almond (1985, 1986) and by Anderson and Wilson (2002) has assessed the most important components of this fauna, the fossil myriapods. These include the earliest known millepedes, one species of which represents a fully terrestrialized example and the earliest known land animal.

Other aspects of the strata exposed at Stonehaven are also significant and have been included, under the site name 'The Toutties', in the GCR volumes on Devonian stratigraphy (Barclay *et al.*, 2005) and fossil fishes (Dineley and Metcalf, 1999).

Description

The early stratigraphical framework of Campbell (1911, 1912a, 1912b, 1913) for his 'Stonehaven beds' has been somewhat revised in modern times. The Stonehaven Group, as now termed, includes the successive Cowie and Carron formations according to Armstrong and Paterson's 1970 classification. Donovan (in Armstrong *et al.*, 1978) then outlined several constituent members, which were subsequently formalized in Gillen and Trewin (1987). Further stratigraphical refinement of the group by Carroll (1995), which was adopted by Browne and Barclay (2005b) and which is used herein, saw among other changes the introduction of the terms Cowie Sandstone and Carron Sandstone formations.

The 730 m thick Cowie Sandstone Formation is exposed on the foreshore for some 500 m between Cowie Harbour and near Ruthery Head in the north-east, where it rests unconformably on the Cambro-Ordovician Highland Border Series close to the Highland Border Fault. Inland intermittent outcrop of this formation has been mapped over 13 km to the west, on the north-west limb of the Strathmore Syncline. The formation, which is represented by about 450 metres of beds at The Toutties, is subdivided into six members (Armstrong *et al.*, 1978; Carroll, 1995; Browne and Barclay, 2005b; Figures 2.30 and 2.31).

The unconformity at the base of the Cowie Sandstone Formation is exposed in steeply dipping (70–80°) and structurally disturbed strata. A thin and locally derived basal breccia of the lowest, Purple Sandstone Member, containing clasts of spilite, black shale and jasper, can be seen resting on weathered and reddened slaty rocks of the Highland Border Series. In total this member comprises about 93 m of medium-grained sandstones, the basal 60 m of which (the Basal Breccia Member of Armstrong *et al.*, 1978) are pebbly and conglomeratic, and low in the unit there is an andesitic lava horizon.

The succeeding Castle of Cowie Member is made up of 75 metres of medium-grained sandstones, red siltstones and sandy siltstones. Soft brown, grey and green sandstones, which contain calcareous nodules, volcaniclastic material and, locally, pebbles, form the next, Brown and Grey Sandstone Member. Overlying the latter are 12.5 m of conglomerates that are interbedded with tuffaceous sandstone, and which comprise the Cowie Harbour Conglomerate Member (the Volcanic Conglomerate Member of Armstrong *et al.*, 1978). The succeeding Red Sandstone Member is about 16 m thick, with medium-grained, cross-bedded sandstones together with tuffaceous sandstones that exhibit convolute bedding. The youngest, Cowie Harbour Siltstone Member (the Dictyocaris Member of Armstrong *et al.*, 1978), consists of 60 m plus of interbedded sandy siltstone and fine-grained sandstone, mostly showing planar lamination, but with some cross-lamination, small-scale ripples, and convolute de-watering structures.

The Cowie Harbour Fish Bed, a reddish sandy mudstone, occurs among a sequence of grey sandstones and fissile siltstones and mudstones near the base of the Cowie Harbour Siltstone Member. Other elements of the biota occur in this member in grey mudstones, which are intercalated with sandy siltstones and red sandstones with convolute dewatering structures, one such horizon above the fish bed yielding arthropods (Browne and Barclay, 2005b).

The Carron Sandstone Formation, some 820 m thick and unfossiliferous, comprises mainly brown, reddish-brown and grey, medium-grained sandstones that locally are pebbly and have a considerable volcanic component. They are thinly bedded in the lower part of the formation, and trough cross-bedded in the upper part. The formation is seen overlying the Cowie Harbour Siltstone Member at low tide at The Toutties (Carroll, 1995). The succeeding

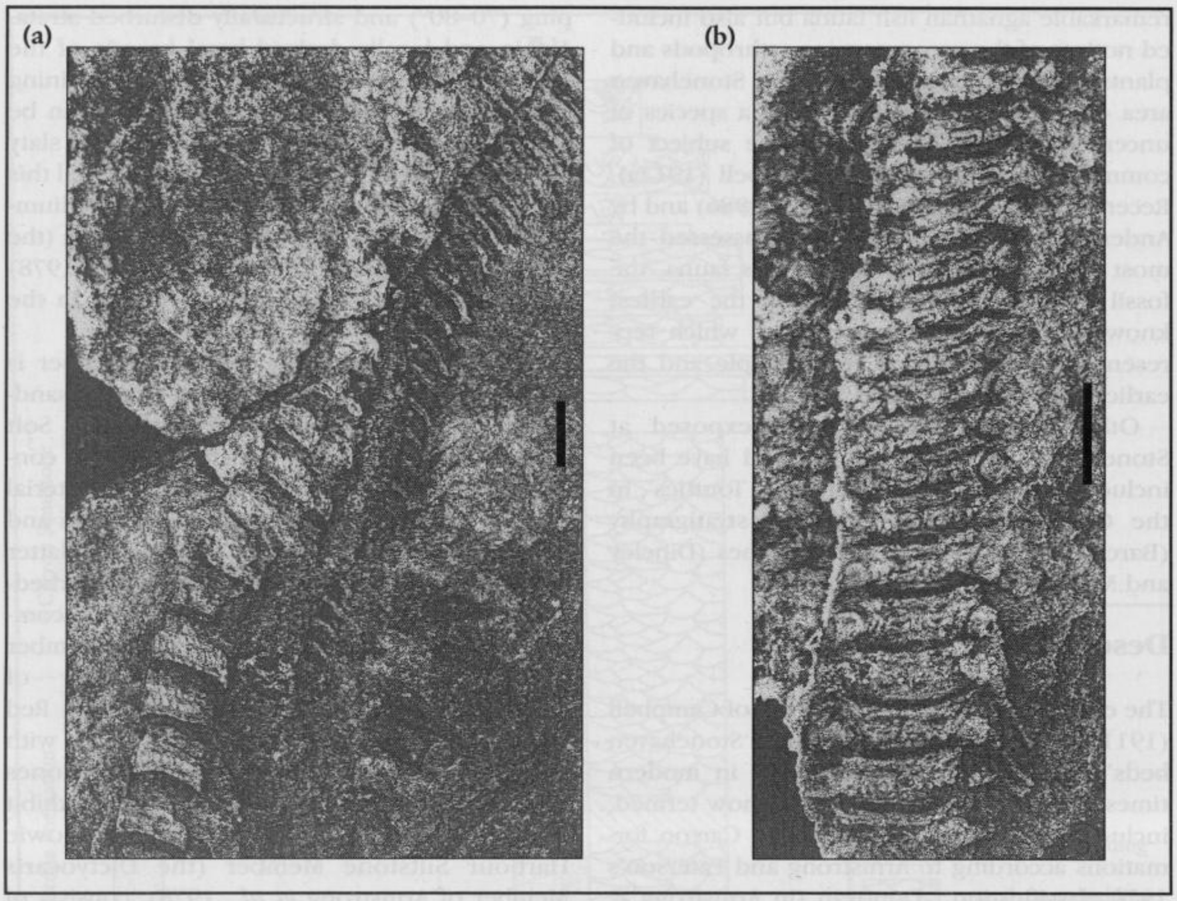


Figure 2.32 *Albadesmus almondi* Wilson and Anderson, 2004; holotype, Australian Museum, Sydney, F.64847a; Cowie Harbour Siltstone (Dictyocaris) Member, upper Wenlock or lower Ludlow Series, Silurian, Cowie Harbour, Stonehaven. (a) Photograph, dorsal view of entire specimen with tergites and sternites slid apart, anterior towards the top. (b) Latex mould of sternites with paramedian pores and lateral coxae. Scale bars are 2 mm. (From Wilson and Anderson, 2004, figs 8.1 and 8.3.)

Dunnottar–Crawton Group lies with slight unconformity on the Carron Sandstone Formation. It is some 1600 m in thickness and in its basal part comprises the 60 m thick Downie Point Conglomerate.

From a palaeontological standpoint the main interest lies in the Cowie Harbour Fish Bed and adjacent strata, which were first described in 1911 by Campbell. Macconochie had previously collected fossils from this part of the sequence for the Geological Survey in 1881, but the first agnathan fish were not found until 1912 (Campbell, 1912a,b). The fish, *Hemiteleaspis heintzi*, *Traquairaspis campbelli* and *Birkenia* sp., are uncommon. They are complemented by rare plant fragments, and a diverse fauna of arthropods which historically have been recorded as the phyllocarid *Ceratiocaris* sp., the eurypterids *Nanahughmilleria norvegica* (Kiaer, 1911) and *Pterygotus* sp., the enigmatic *Dictyocaris slimoni* Salter, 1860, the myriapods *Archidesmus* sp. and a species that possibly belongs to *Kampecaris* (Campbell, 1913; Størmer, 1935; Westoll, 1951, 1977; Armstrong and Paterson, 1970; Hanken and Størmer, 1975; Almond, 1985; Dineley, 1999a; Browne and Barclay, 2005b). Recently, millipedes from the Palaeozoic of Scotland have been re-assessed on the basis of existing and new material, and the new species *Albadesmus almondi*, *Cowiedesmus eroticopodus* and *Pneumodesmus newmani* established, all of them from the Cowie Sandstone Formation of Cowie Harbour (Wilson and Anderson, 2004; Figures 2.32–2.34).

For many years the fossiliferous deposits of

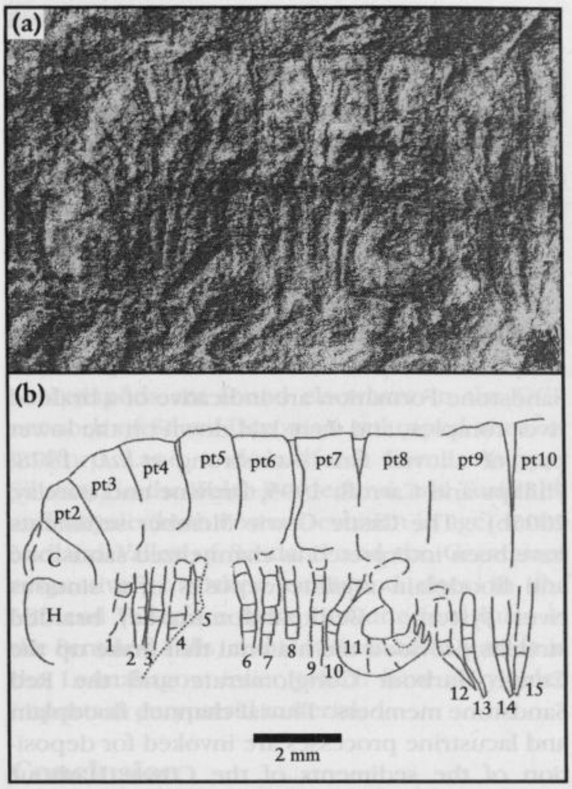


Figure 2.33 *Cowiedesmus eroticopodus* Wilson and Anderson, 2004; holotype, Australian Museum, Sydney, F.64845a; Cowie Harbour Siltstone (Dictyocaris) Member, upper Wenlock or lower Ludlow Series, Silurian, Cowie Harbour, Stonehaven. (a) Photograph, lateral view of anterior part of specimen. (b) Interpretive drawing (modified). C, collum; H, head; pt2–pt10, pleurotergites, with a modified leg associated with pt8. (From Wilson and Anderson, 2005, figs 7.2 and 7.3.)

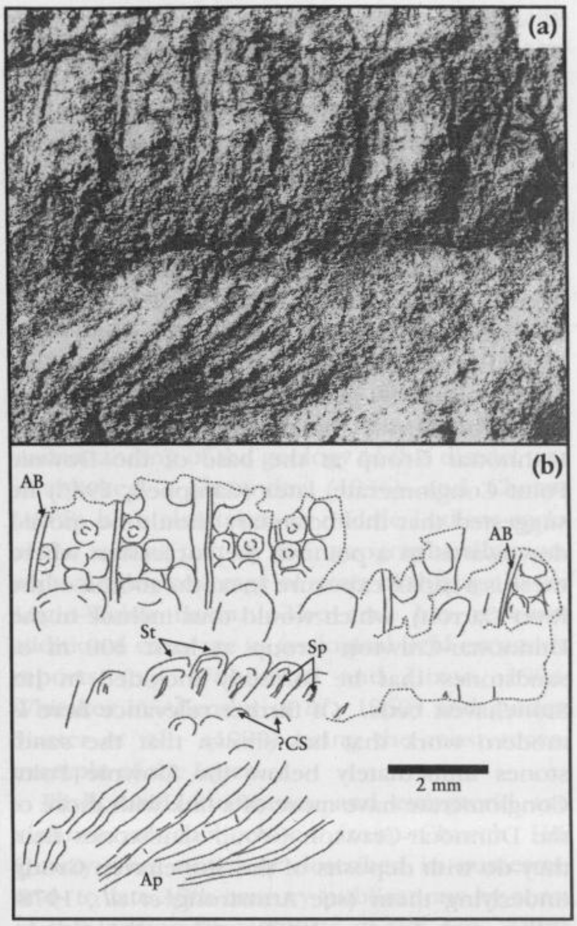


Figure 2.34 *Pneumodesmus newmani* Wilson and Anderson, 2004; holotype, National Museums of Scotland, Edinburgh, NMS G. 2001.109.1; Cowie Harbour Siltstone (Dictyocaris) Member, upper Wenlock or lower Ludlow Series, Silurian, Cowie Harbour, Stonehaven. (a) Photograph, dorsolateral view, anterior to the right. (b) Interpretive drawing (modified). AB, Anterior Bar; Ap, appendages; CS, coxal socket; Sp, Spiracle; St, Sternite. (From Wilson and Anderson, 2004, figs 9.2 and 9.3.)

the Cowie Formation were thought to be 'Downtonian' in age, that is approximating to the Přídolí Series (upper Silurian) of current usage, on the basis of a comparison of the fish and arthropods with those from Old Red Sandstone successions elsewhere, especially the Welsh Borderland. Lamont (1952) was one of the first to question this correlation and to suggest that the deposits and their fauna, along with similar fossils from the southern part of the Midland Valley of Scotland, might be of an older, late Llandovery to early Wenlock age. Work by Hanken and Størmer (1975) on eurypterids of the Ringerike region, Norway, where *N. norvegica* also occurs, and comparison of the eurypterid-vertebrate fauna from there with that from Estonia, suggested that that part of the Ringerike sequence was early Ludlow in age, and thus by implication that the 'Stonehaven beds' were also. The relatively recent recovery from the Cowie Sandstone Formation of a palynomorph assemblage consisting of cryptospores, trilete spores and dispersed plant fragments has provided new age constraints for this unit (Marshall, 1991; Wellman, 1993). This assemblage can be assigned to the *Artemopyra brevicostata* (?*E.* cf. *protophanus*)–*Hispanaediscus verrucatus* (cf. *S. verrucatus*) Assemblage Biozone of Richardson and MacGregor (1968). Such an assignment, involving in part a comparison of the

Stonehaven spore assemblage with those from Welsh Borderland type Silurian sections, indicates the Cowie Sandstone Formation to be of late Wenlock (early Homerian) or possibly earliest Ludlow (earliest Gorstian) age.

The Carron Sandstone Formation may be significantly younger than the Cowie Sandstone Formation, Marshall *et al.* (1994) claiming that there is a break in sedimentation between them, based on differences in mineralogical composition, palaeomagnetism and burial history. It should also be noted that although Campbell (1911) originally placed the boundary between his Stonehaven beds and the overlying Dunnottar Group at the base of the Downie Point Conglomerate, later (Campbell, 1913) he suggested that this boundary should be moved downwards to a point in the succession where there is a gap in exposure (near the mouth of the River Carron), which would thus include in the Dunnottar-Crawton Group at least 100 m of sandstones that he formerly included in his Stonehaven beds. Of further relevance here is modern work that has shown that the sandstones immediately below the Downie Point Conglomerate have more of a link with those of the Dunnotar-Crawton Group sandstones than they do with deposits of the Stonehaven Group underlying them (see Armstrong *et al.*, 1978; Gillen and Trewin, 1987). Thus the Carron Sandstone Formation might be best considered with the overlying Dunnottar-Crawton Group, though on mapping grounds the base of the Dunnottar Conglomerate is a key horizon (Trewin and Thirlwall, 2002).

Interpretation

The Stonehaven Group represents the fill of the Stonehaven Basin, which was controlled by strike-slip faulting (Bluck, 2000, 2001). One interpretation of the relationship between the Cowie Sandstone and Carron Sandstone formations argues for the Cowie Sandstone Formation to be the fill of a separate sub-basin and not to be, like the Carron Sandstone Formation, a part of the major fining upward sequence of the Lower Old Red Sandstone. The junction between these two formations would thus be a major stratigraphical and structural discontinuity. Others record a transitional boundary between the two formations (see Carroll, 1995; Phillips and Carroll, 1995; Trewin and Thirlwall, 2002; Browne and Barclay, 2005b).

The dominant palaeocurrent direction in both the Cowie and Carron formations has been given in one study as trending to the north-west with a metamorphic source terrane lying to the south-east (Robinson *et al.*, 1998), whereas other work indicates transport to the ESE at the base of the Cowie Sandstone Formation, and to the south-west at other times during the deposition of this unit (Gillen and Trewin, 1987).

The sediments of the Purple Sandstone and Grey Sandstone members of the Cowie Sandstone Formation are indicative of a braided river complex, and were laid down on the lower part of alluvial fans (Armstrong *et al.*, 1978; Phillips and Carroll, 1995; Browne and Barclay, 2005b). The Castle Cowie Member sediments have been interpreted as channelized sandstone and floodplain argillite deposits of a sinuous river system. Bedload-dominated, braided streams provided the material that make up the Cowie Harbour Conglomerate and the Red Sandstone members. Fluvial channel, floodplain and lacustrine processes are invoked for deposition of the sediments of the Cowie Harbour Siltstone Member. The horizontally laminated and cross-bedded sandstones that comprise the major part of this unit have been interpreted as the distal deposits of turbidity currents brought into the lake from a fluvial source. Periodically, the lake appears to have been deep and stratified, with anoxic bottom conditions, as evidenced by the finer-grained carbonaceous siltstones that are devoid of wave ripples or trace fossils.

With reference to the arthropods from the Stonehaven area, the *Kampecaris* (?) sp. described by Størmer (1935) was suggested by Almond (1985) to be a new genus though he did not allocate it to any major group. The kampecarids as a whole were considered by Almond (1985) to be a discrete group possibly most closely related to the millipedes (Diplopoda); they occur in a number of Old Red Sandstone facies rocks of Přídolí to Pragian age in Scotland and the Welsh Borderland. The record of *Archidesmus* sp. from Stonehaven was not commented on by Almond (1985), nor by Wilson and Anderson (2004), though the latter authors considered the genus to be a millipede containing only *Archidesmus macnicoli* from the Lower Devonian of the Midland Valley (see Turin Hill site report herein). *Cowiedesmus eroticopodus*, *Albadesmus almondi*, and

Pneumodesmus newmani were all regarded as archipolypodan millipedes and each assigned to their own new monotypic genus (Wilson and Anderson, 2004). The presence of spiracles in ***P. newmani*** represents the earliest evidence globally for a tracheal respiratory system, and thus air breathing and land dwelling, in any animal. Trace fossil – as opposed to body fossil – evidence suggests that arthropod terrestrialization had begun even earlier, by Ordovician times at least (Johnson *et al.*, 1994; MacNaughton *et al.*, 2002).

Myriapods are found elsewhere in the GCR network of Siluro-Devonian arthropod sites, at Ludford Lane and Ludford Corner (upper Silurian) in the Welsh Borderland, and Turin Hill and Rhynie (both Lower Devonian in age) in the Midland Valley of Scotland and the Grampians respectively. Other arthropod sites in the Midland Valley are those of Gutterford Burn in the Pentland Hills, and Slot Burn and Dunside in the Lesmahagow inlier, which have all yielded important eurypterid material.

Conclusion

This site contains rocks that form the base of the Old Red Sandstone in the Midland Valley of Scotland and are of late Wenlock or earliest Ludlow age. The millipede species from here represent the earliest in the geological column. Also material of one of them preserves spiracles, indicating a tracheal respiratory system and making it the earliest known fully terrestrialized animal. Other arthropod elements include eurypterids, which have been used to help give a relative age to the host sediments, and the enigmatic *Dictyocaris*. All of these factors make the site of international importance.

CHURCH HILL, HEREFORDSHIRE (SO 4120 7380)

Derek J. Siveter

Introduction

This Welsh Borderland site is located about 9 km to the west of Ludlow and 0.75 km to the east of the village of Leintwardine. The sediments that crop out hereabouts belong mostly to the Ludlow Series, of late Silurian age, around 420 million years old. The ground here forms part of the northern limb of the Downton Syncline, close to its axial trace. The southern limb of the syncline also represents the northern limb of the Ludlow Anticline that plunges to the ENE.

The geology of this general area has been discussed from at least the time of Murchison (1839, 1854) in the mid-nineteenth century, with Lightbody (1869) and Marston (1865) being other commentators at about this time on the local rocks and fossils. The site was afterwards included in the ground around Ludlow investigated by Elles and Slater (1906). However it was half a century later, through the detailed mapping of Whitaker (1962) of the Ludlow strata of the Leintwardine area, that our modern understanding of the geology of this district was established. Alexander (1936) and Cherns (1988) have also taken in middle Ludlow rocks of the area as part of their geographically more wide-ranging coverage of strata of this age in the Anglo-Welsh Basin. The area has received additional coverage in geological field excursion reports (e.g. Woodward and Dixon, 1904; Whitaker in Allender *et al.*, 1960) and guides, Siveter *et al.* (1989) being the most recent example of the latter.

Phyllocarid crustaceans and eurypterid and xiphosuran chelicerates from Church Hill Quarry were noted or described in numerous mid- to late 19th century publications by some of the leading protagonists of the day. These works included those of Salter (1857, 1859a, 1873), Woodward (for example 1865b, 1870, 1871c, 1872b, 1872), Jones (1886), Jones and Woodward (1888), La Touche (1884) and Peach (1899). In the last century, Church Hill chelicerates were covered most notably in Kjellesvig-Waering's (1961) comprehensive study on Welsh Borderland eurypterids, and they also variously featured in the publications of Størmer (1952, 1955), Hessler (1969), Eldredge (1974), Bergström (1975), Morris (1980), Rolfe (1980), Almond (1985), Selden (1986), Anderson and Selden (1997), Anderson *et al.* (1998) and Plotnick (1999). The crustaceans from Church Hill await modern study.

In the context of this arthropod volume Church Hill Quarry is important for having yielded a variety of non-trilobite arthropods in an unusual palaeoenvironmental setting. Eurypterids belonging to five species and at least four genera have been collected from here. The site is also one of just a few globally that have produced xiphosurans of Silurian age, and it has also yielded several phyllocarid species.

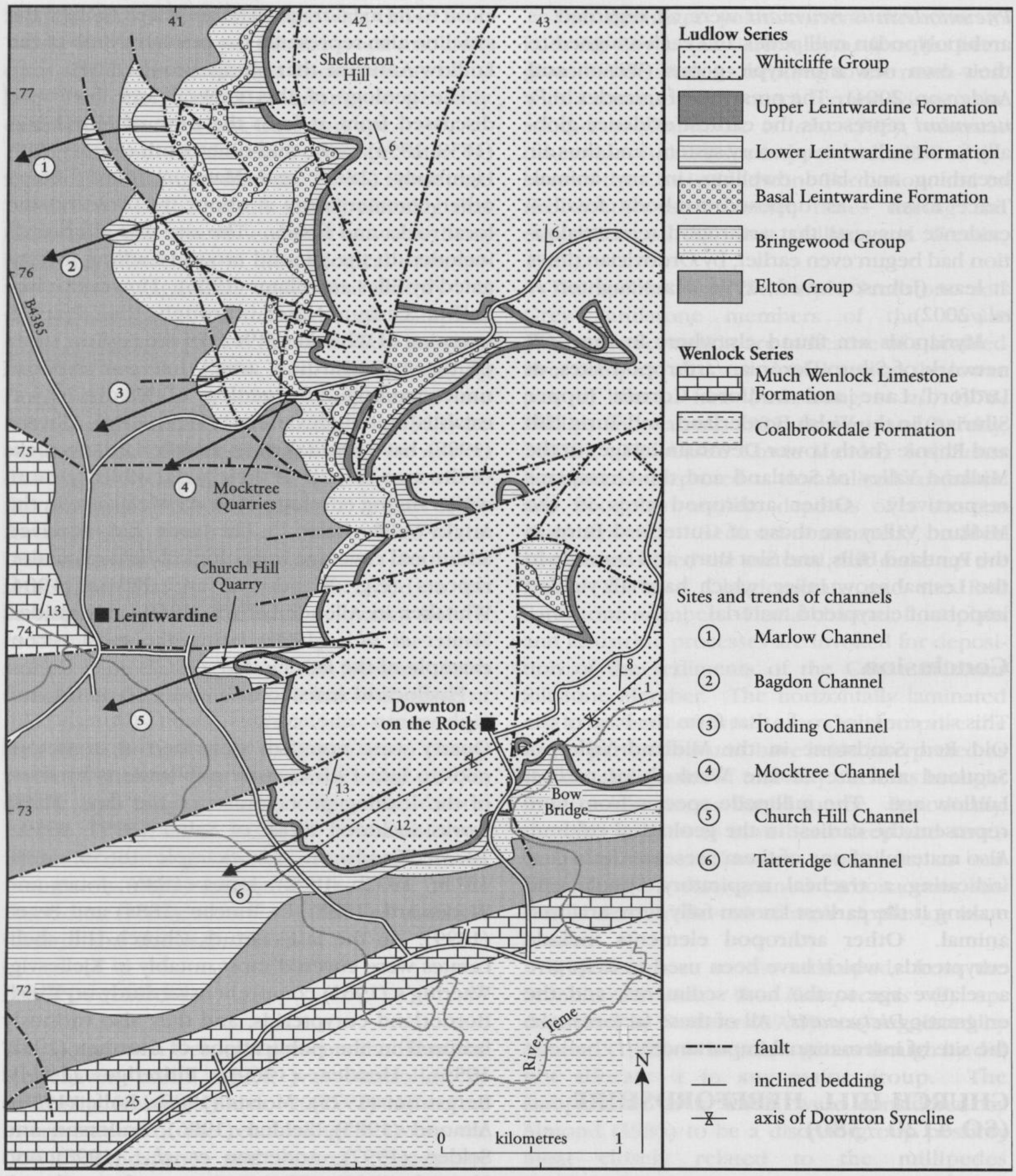


Figure 2.35 The Silurian geology of the Leintwardine area, Herefordshire, showing six submarine channels trending from the shelf edge towards the basin, including that at the Church Hill Quarry site. (After Siveter, 2000d and Whitaker, 1962.)

Church Hill Quarry has also recently featured in the companion GCR volumes to the present one that have identified important sites in Britain for the Silurian stratigraphy (Aldridge *et al.*, 2000), and for fossil fishes (Dineley and Metcalf, 1999); in addition to the fossil arthropod importance of this site, the area is also independently selected for the GCR for the Silurian-Devonian Chordata and Ludlow selection categories.

Description

The Church Hill Quarry site is bounded to the north and south by, respectively, the local Church Hill and Trippleton faults (Figure 2.35), and the strata here have a shallow regional dip to the ESE of around 10° or less. The general succession, up-sequence and uphill from west to east, comprises the Middle Elton, Lower Leintwardine, Upper Leintwardine and Lower Whitcliffe formations of the Ludlow Series. The Lower Leintwardine Formation, the unit that is the main focus of palaeontological interest at the site, consists of thin-bedded calcareous siltstones within which are fossiliferous bands. These siltstones are the Mocktree Shales or the Dayia Beds of earlier authors (e.g. Elles and Slater, 1906; Alexander, 1936); they are separated from the underlying Middle Elton sediments by an erosion surface (Whitaker, 1962). A variety of sedimentary features occur in them, for example slump structures, prod, skip and groove marks, and reworked boulders of the Upper Bringewood Formation (Aymestry Limestone). The quarry exposures that form the basis of the site have been abandoned for over a hundred years (see Hawkins and Hampton, 1927), and are now reduced to a series of overgrown scars. However during the course of a recent PhD investigation by David Gladwell (University of Leicester, 2005), a new exposure and new collections have been made.

The Lower Leintwardine Formation here boasts an especially interesting fauna (see Siveter 2000d). In addition to non-trilobite arthropods, and early fishes, it includes in particular complete starfish specimens. Other notable faunal elements include current aligned graptolite specimens, annelid material, and beautifully preserved crinoids. Trilobites, brachiopods and bryozoa form part of the associated, more standard invertebrate fauna.

Xiphosura is represented by *Limuloides limuloides* (Woodward, 1865, Figure 2.36), *Cyamocephalus loganensis* Currie, 1927 and *Pseudoniscus* sp. (see Eldredge, 1974), and, according to a recent study (Anderson, 1999), *Limuloides sperratus* (Woodward, 1872) and *Bunodes salweyi* (Woodward, 1872). The eurypterids present are *Pterygotus arcuatus* Salter, 1859, *Erettopterus marstoni* Kjellesvig-Waering, 1961, *Necrogammarus salweyi* Woodward, 1870 (note: publication date is probably 1871), *Carcinosoma punctatum* (Salter, 1859), and *Salteropterus? longilabium* Kjellesvig-Waering, 1961. The phyllocarids have been assigned to *Ceratiocaris* and include *C. attenuata*, *C. cassioides*, *C. gigas*, and *C. halliana* (all established in 1886 by Jones; see Morris, 1980), *C. ludensis* Woodward, 1871, *C. murchisoni* (Agassiz, 1839), and *C. pardoeana* La Touche, 1884 (Figures 2.37 and 2.38). The site stands as the type locality for nearly all of these species.

Interpretation

Alexander (1936) was the first to suggest that there is an erosional discontinuity marking the bottom of the Lower Leintwardine Formation, the sediments of which infill a channel, at Church Hill. The subsequent investigation of Whitaker (1962; see also 1994) demonstrated that the Church Hill channel was one of six in the area, all of which he interpreted as submarine canyon heads (Figure 2.35). They trend in an ENE–WSW direction, from the shelf edge at the western margin of the Midland Platform, towards the deeper water areas of the Welsh Basin. The Church Hill Channel has a gradient of 10°, cutting out to the west successively older Ludlow strata. The channel margin, showing Lower Leintwardine Formation channel fill resting unconformably on Middle Elton Formation sediments below the channel base, is present at Trippleton Lane.

The fauna of Church Hill channel as a whole is very distinctive and is mirrored closely or identically in the other five channels, with the combination of faunal composition and palaeoenvironmental setting being unknown outside rocks of this age and this part of the Welsh Borderland. Both Whitaker (1962) and Hawkins and Hampton (1927) thought that the fauna was indigenous to the channels, though the latter authors mistakenly placed them in a shallow lagoonal, rather than truly marine, situation. Goldring and Stevenson (1972), however, believed that the fauna was transported into the channels. Publication of Gladwell's research into the special nature of the channel fauna offers the possibility of addressing this and related questions. Kjellesvig-Waering (1961) assigned the eurypterid fauna of Church Hill to his Carcinosomatidae–Pterygotidae biofacies, the most open marine of the three phases that he identified for Siluro-Devonian eurypterid faunas.

(a) (b)

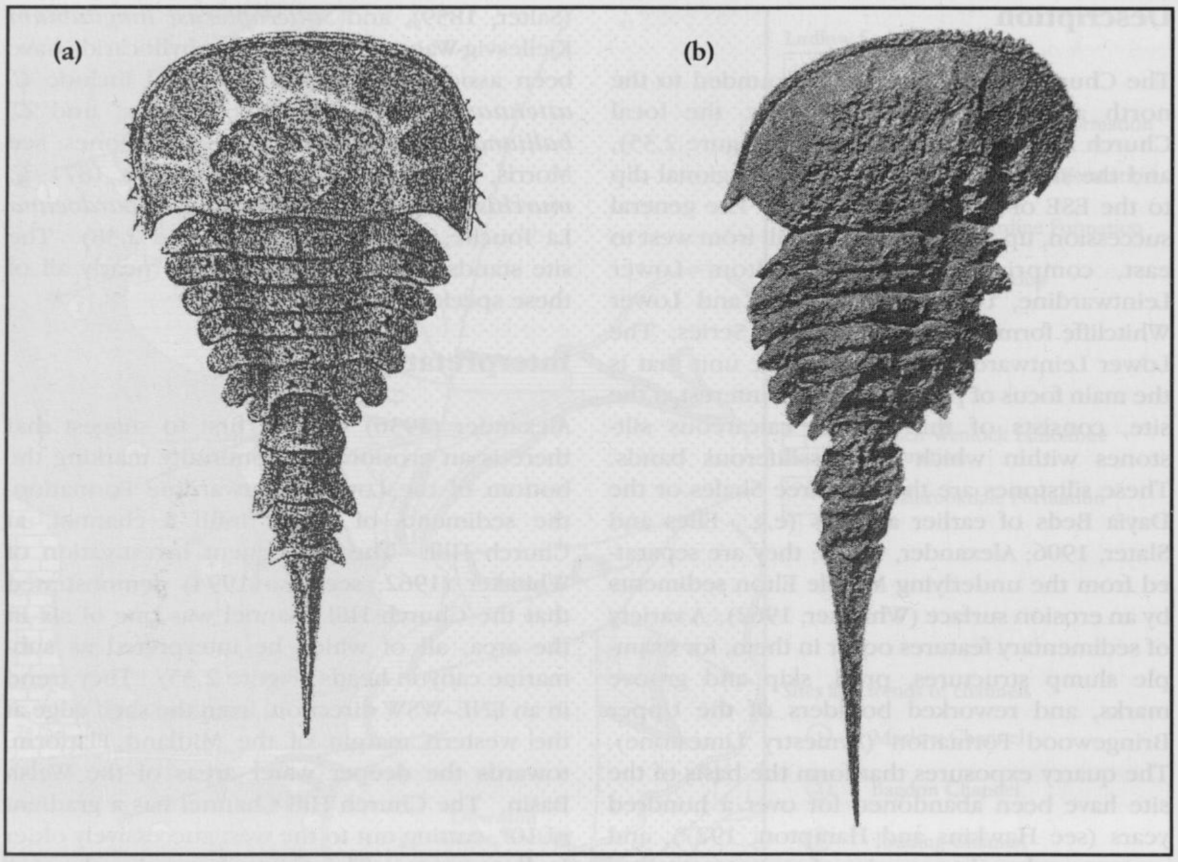


Figure 2.36 *Limuloides limuloides* Woodward, 1865; holotype, British Geological Survey, GSM 32393; Lower Leintwardine Formation, Ludlow Series, Silurian, Church Hill, Leintwardine area, Herefordshire. (a) Reconstruction (from Woodward, 1865b, plate 14, fig. 7a). (b) Photograph, × 1.95 (from Bergström, 1975, plate 1, fig. 7).

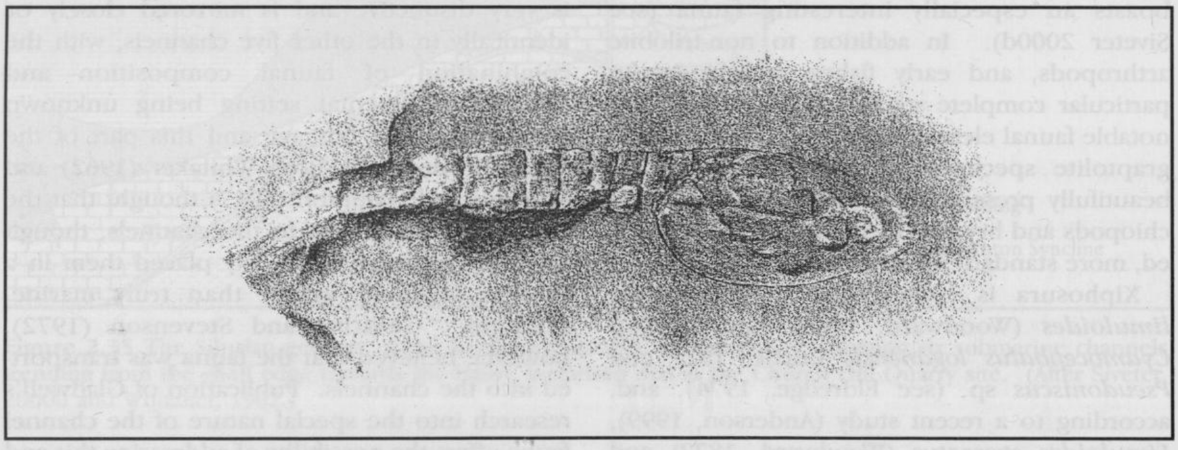


Figure 2.37 *Ceratiocaris halliana* Jones, 1886; syntype, Natural History Museum, London, In.43891, × 1.5; Lower Leintwardine Formation, Ludlow Series, Silurian, Leintwardine area, Herefordshire. (Lithograph, from Jones and Woodward, 1888, plate 5, fig. 6a.)

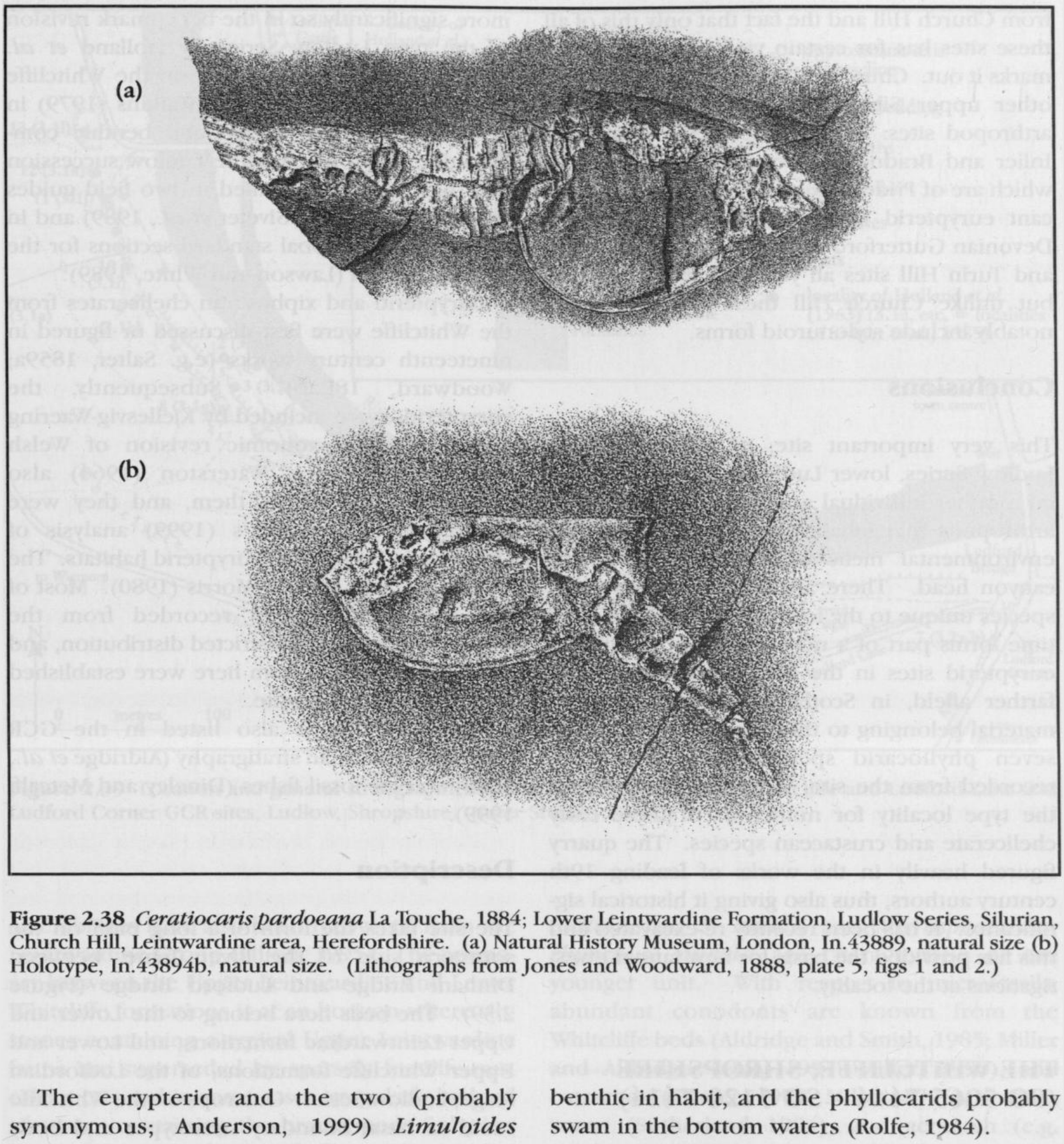


Figure 2.38 *Ceratiocaris pardoeana* La Touche, 1884; Lower Leintwardine Formation, Ludlow Series, Silurian, Church Hill, Leintwardine area, Herefordshire. (a) Natural History Museum, London, In.43889, natural size (b) Holotype, In.43894b, natural size. (Lithographs from Jones and Woodward, 1888, plate 5, figs 1 and 2.)

The eurypterid and the two (probably synonymous; Anderson, 1999) *Limuloides* species from Church Hill are unknown elsewhere. *Pseudoniscus* records globally are very rare, the genus being known from just a few specimens of Silurian age from the Baltic, the USA, and Scotland. *C. loganensis* is known from just three specimens. *N. salweyi* was determined as a pterygotid eurypterid only relatively recently (Selden, 1986); previous authors suggested either a crustacean (Salter, 1959a; Woodward, 1870, Hessler 1969) or myriapod affinity (Peach, 1899; Rolfe, 1980; Almond, 1985). The phyllocarids from Church Hill need revision before their distribution can be assessed. The xiphosurids and eurypterids were benthic in habit, and the phyllocarids probably swam in the bottom waters (Rolfe, 1984).

Church Hill Quarry is one of four closely related GCR Silurian arthropod sites in the compact Ludlow–Downton–Leintwardine area, the others being those of the Whitcliffe, Ludford Lane and Ludford Corner, and Tin Mill Race. The strata at Church Hill, early Ludfordian in age, are slightly older than the late Ludfordian to early Přídolí sediments that variously occur at these other sites. They are also fully marine, whereas the sediments at Ludford and Tin Mill Race are at least in part quasi-marine, this succession reflecting the late stage infilling of the Anglo-Welsh Basin. All of these sites have important eurypterid faunas, but the uniqueness of that from Church Hill and the fact that only this of all these sites has for certain yielded phyllocarids, marks it out. Church Hill also has links with two other upper Silurian Anglo-Welsh Basin GCR arthropod sites: Perton Lane in the Woolhope Inlier and Bradnor Hill near Kington, both of which are of Přídolí age and have yielded significant eurypterid faunas. The Scottish Siluro-Devonian Gutterford Burn, Slot Burn, Dunside, and Turin Hill sites all yield eurypterid faunas, but unlike Church Hill these other localities notably include stylonuroid forms.

Conclusions

This very important site, of upper Silurian, Ludlow Series, lower Ludfordian age, has yielded a rather individual and varied suite of fossil arthropods that inhabited a distinctive palaeoenvironmental niche – that of a submarine canyon head. There are least four eurypterid species unique to the locality, which at the same time forms part of a network of upper Silurian eurypterid sites in the Welsh Borderland and, farther afield, in Scotland. Rare xiphosuran material belonging to three genera, and at least seven phyllocarid species, have also been recorded from the site. Church Hill stands as the type locality for numerous of these early chelicerate and crustacean species. The quarry figured heavily in the works of leading 19th century authors, thus also giving it historical significance. It has been recently re-excavated and this has provided the basis for new faunal investigations at the locality.

THE WHITCLIFFE, SHROPSHIRE (SO 5065 7444 – SO 5120 7414)

Derek J. Siveter

Introduction

This site lies within the confines of Ludlow in the central Welsh Borderland, and it encompasses many outcrops of late Ludlow age, around 419 million years old, that form part of the northern limb of the Ludlow Anticline.

Murchison referred to exposures on the Whitcliffe when he established the Silurian System (1835, 1839). This locality was also included in the stratigraphical study of the Ludlow district of Elles and Slater (1906), and more significantly so in the benchmark revision of the type Ludlow Series by Holland *et al.* (1963). Certain key sections on the Whitcliffe were, in addition, logged by Watkins (1979) in his study of Welsh Borderland benthic communities. Most recently the Ludlow succession here has been documented in two field guides (Bassett *et al.*, 1979; Siveter *et al.*, 1989) and in a review of the global standard sections for the Silurian System (Lawson and White, 1989).

Eurypterid and xiphosuran chelicerates from the Whitcliffe were first discussed or figured in nineteenth century works (e.g. Salter, 1859a; Woodward, 1872b). Subsequently, the eurypterids were included by Kjellesvig-Waering (1961) in his taxonomic revision of Welsh Borderland species, Waterston (1964) also commented on one of them, and they were referred to in Plotnick's (1999) analysis of Llandovery–Lochkovian eurypterid habitats. The xiphosuran was cited in Morris (1980). Most of the eurypterid species recorded from the Whitcliffe have a very restricted distribution, and most of the species from here were established on material from the site.

The Whitcliffe is also listed in the GCR volumes for Silurian stratigraphy (Aldridge *et al.*, 2000) and for fossil fishes (Dineley and Metcalf, 1999).

Description

The site takes the form of a long bluff on the southern side of the River Teme, between Dinham Bridge and Ludford Bridge (Figure 2.39). The beds here belong to the Lower and Upper Leintwardine formations, and Lower and Upper Whitcliffe formations, of the Ludfordian Stage, Ludlow Series. Outcrops on the Whitcliffe stand as basal boundary stratotypes and body stratotypes for the Upper Leintwardine and the Lower and Upper Whitcliffe formations (Holland *et al.*, 1963; Lawson and White, 1989).

Both Lower and Upper Leintwardine formations comprise calcareous siltstones, and in the latter formation they show honeycomb weathering. The boundary between the two Leintwardine formations is drawn just below a thin shale layer and coincides with the introduction of the trilobites *Alcymene puellaris* and *Encrinurus*, and the brachiopod *Aegiria grayi*. The Upper Leintwardine Formation has yielded abundant conodont microfossils (Aldridge and Smith, 1985), and well-preserved palynomorph

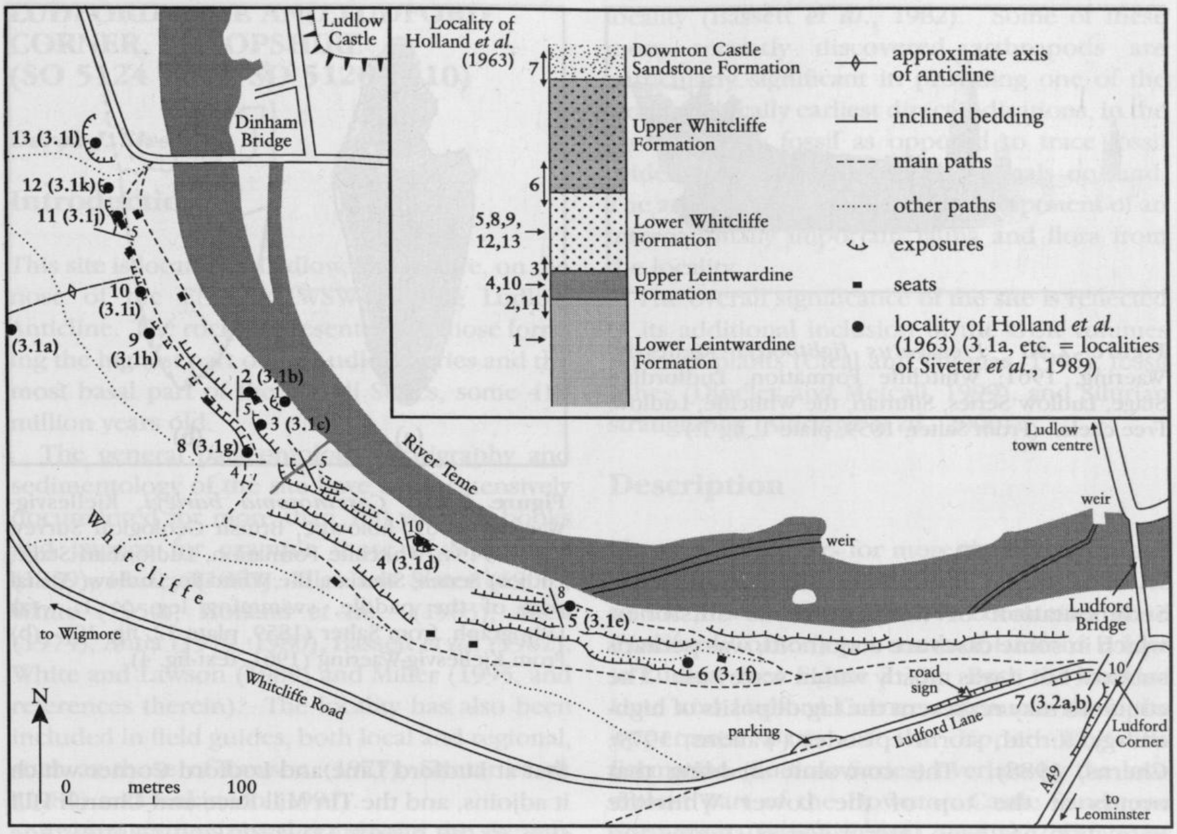


Figure 2.39 Location and general stratigraphical position of localities at the Whitcliffe and Ludford Lane and Ludford Corner GCR sites, Ludlow, Shropshire. (After Siveter, 2000c.)

assemblages have also been recovered from the Leintwardine Group (Elliott, 1995). The boundary between the Upper Leintwardine and Lower Whitcliffe formations is at an horizon where siltstones containing a typical Upper Leintwardine fauna are superseded by sparsely fossiliferous, calcareous and in some cases irregularly bedded siltstones containing the brachiopods *Salopina lunata* and *Protochonetes ludloviensis*.

The disused Whitcliffe Quarry (Holland *et al.*, 1963, locality 6) displays beds of the Lower Whitcliffe Formation, above which are the typically less thickly bedded olive calcareous siltstones of the Upper Whitcliffe Formation. The boundary between the two is defined at the top of a laterally persistent, 18 cm-thick horizon characterized by convolute bedding. The macrofauna of the Whitcliffe beds includes brachiopods, bivalves, orthoconic nautiloids and gastropods. Macrofossils are generally more abundant in Upper Whitcliffe than in Lower Whitcliffe strata, and shell bands rich in *P. ludloviensis*, *S. lunata* and *Microsphaeridiorhynchus*? *nucula* are characteristic of the younger unit. With respect to microfossils, abundant conodonts are known from the Whitcliffe beds (Aldridge and Smith, 1985; Miller and Aldridge, 1993, 1997; Miller, 1995), and ostracods (Siveter, 1978; Miller, 1995), chitinozoans (Sutherland 1994), and acritarch (e.g. Lister, 1970) and spore (e.g. Richardson and Lister, 1969) assemblages have also been recovered.

The Ludfordian rocks of the Whitcliffe represent the type horizon and locality for the eurypterid species *Pterygotus lightbodyi*, *Pterygotus denticulatus*, and *Carcinosoma harleyi*, all established by Kjellesvig-Waering (1961) (Figures 2.40 and 2.41). The eurypterid *Erettopterus spatulatus* Kjellesvig-Waering, 1961 and the xiphosuran *Bunodes* sp. have also been recorded from here (Woodward, 1872b; Kjellesvig-Waering, 1961; Morris, 1980).

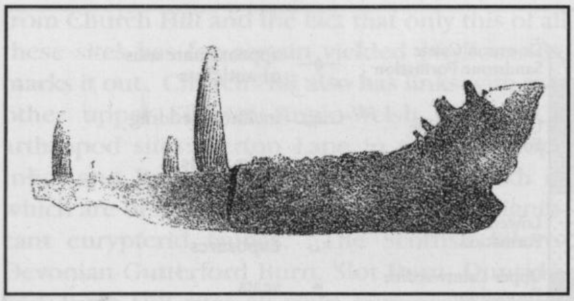


Figure 2.40 *Pterygotus lightbodyi* Kjellesvig-Waering, 1961; Whitcliffe Formation, Ludfordian Stage, Ludlow Series, Silurian, the Whitcliffe, Ludlow. Free chela. (From Salter, 1859, plate 1, fig 7.)

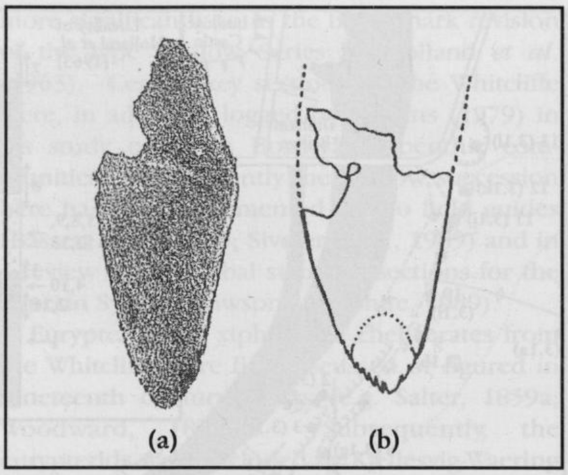


Figure 2.41 *Carcinosoma harleyi*, Kjellesvig-Waering, 1961; holotype, British Geological Survey, GSM 89434; Whitcliffe Formation, Ludfordian Stage, Ludlow Series, Silurian, the Whitcliffe, Ludlow. Distal part of the paddle, swimming leg, × 1. (a) Lithograph, from Salter (1859, plate 12, fig. 19). (b) From Kjellesvig-Waering (1961, text-fig. 4).

Interpretation

Sedimentation of the calcareous siltstones, which in some cases are coquinoid, was perhaps subtidal but it was mostly within wave base. The coquinas may represent the lag deposits of high-energy, turbid, storm episodes (Watkins, 1979; Cherns, 1988). The convolute bedding that occurs at the top of the Lower Whitcliffe Formation has been interpreted as slumps and other wet sediment deformation features that perhaps indicate occasional periods of instability on the platform.

These shallow marine Ludfordian sediments accumulated on the shelf area of the Midland Platform, on the eastern margin of the Welsh Basin (see Siveter *et al.*, 1989; Bassett *et al.*, 1992). They represent late-stage infilling of the Anglo-Welsh Basin, and preface the quasi-marine and fluviatile deposits of the Přídolí Series in the Ludlow area and elsewhere in the Welsh Borderland.

Carcinosoma harleyi from the Whitcliffe has not been recorded elsewhere. *Pterygotus lightbodyi* is also unique to the site, except for one specimen from the upper Ludlow of Batch Common, a nearby locality in the Ludlow Anticline. *P. denticulatus* has, subsequent to the investigations of Kjellesvig-Waering (1961), also been recorded from the Přídolí of the adjacent locality of Ludford Lane (Manning and Dunlop, 1995). *Erettopterus spatulatus* is known from several localities of upper Ludlow or basal Přídolí age in the Ludlow area and at Kington in Herefordshire.

The Whitcliffe site is particularly closely linked geographically with three others in this volume: that at Ludford Lane and Ludford Corner which it adjoins, and the Tin Mill Race and Church Hill sites in the nearby Downton and Leintwardine areas respectively. It overlaps in terms of stratigraphy with Ludford Lane and Ludford Corner, as both have latest Ludfordian (Upper Whitcliffe Formation) rocks, whereas Church Hill has slightly older, lower Ludfordian sediments, and Tin Mill Race slightly younger, lower Přídolí Series strata. The Whitcliffe is also linked with two other, more southerly Welsh Borderland GCR arthropod sites: Bradnor Hill near Kington, and Perton Lane in the Woolhope Inlier, both of which have, like Tin Mill Race and Ludford Lane and Ludford Corner, important eurypterid faunas of basal Přídolí age. All the Scottish Siluro-Devonian sites with eurypterids – Gutterford Burn, Slot Burn, Dunside, and Turin Hill – differ from the Whitcliffe in having stylonuroids as part of their fauna.

Conclusions

The Whitcliffe forms one of a series of closely-knit, mainly eurypterid-based arthropod sites in the upper Silurian of the Welsh Borderland. It stands as the type locality for three out of the four species of eurypterid recorded from here, and for one of the species it represents the only known locality.

LUDFORD LANE AND LUDFORD CORNER, SHROPSHIRE (SO 5124 7414–SO 5120 7410)

Derek J. Siveter

Introduction

This site is located in Ludlow, Shropshire, on the nose of the ENE- to WSW-trending Ludlow Anticline. The rocks represented are those forming the highest part of the Ludlow Series and the most basal part of the Přídolí Series, some 418 million years old.

The general palaeontology, stratigraphy and sedimentology of the site have been extensively documented for more than 150 years in books and papers, for example those of Murchison (1839), Harley (1861), Elles and Slater (1906), White (1950), Holland *et al.* (1963), Allen (1974), Antia (1979, 1980), Bassett *et al.* (1982), White and Lawson (1989) and Miller (1995, and references therein). The locality has also been included in field guides, both local and regional, such as those of Lawson (1977), Siveter *et al.* (1989) and Jenkinson (1991).

From a stratigraphical standpoint the site represents the reference section for the Siluro-Devonian boundary in Britain. This was prior to the base of the Devonian being defined in Czechoslovakia and also before the recognition and international adoption of the Přídolí Series as the fourth series of the Silurian System, the base of which is taken in the Anglo-Welsh area as approximating to the base of the Downton Group. The site remains however one of several key sites in this part of the Welsh Borderland that define the Ludlow Series, and the Downton Group (Přídolí Series) in their type areas.

Eurypterids from the site were first discussed in nineteenth century texts, for example those of Salter (in Sedgwick and M'Coy, 1855; Salter, 1859a) and Woodward (1872b), before being taxonomically revised by Kjellesvig-Waering (1958, 1961). They have been subsequently investigated by Manning (1993); assessed in terms of habitat by Plotnick (1999); and referred to by Tetlie (2006a). In relatively recent years acid digestion extraction techniques have yielded arachnid and myriapod fossils from here (Jeram *et al.*, 1990; Manning, 1993; Manning and Dunlop, 1995; Dunlop, 1996, 1999; Shear and Selden, 1995). A ceratiocarid crustacean has also been questionably recorded from the locality (Bassett *et al.*, 1982). Some of these more recently discovered arthropods are particularly significant in providing one of the stratigraphically earliest direct indications, in the form of body fossil as opposed to trace fossil evidence, of the presence of animals on land. The arthropods form a notable component of an internationally important fauna and flora from the locality.

The overall significance of the site is reflected in its additional inclusion in the GCR volumes on fossil plants (Cleal and Thomas, 1995), fossil fishes (Dineley and Metcalf, 1999), and Silurian stratigraphy (Aldridge *et al.*, 2000).

Description

The outcrop occurs for more than 100 m along Whitcliffe Road ('Ludford Lane') and continues to the junction with the A49 Leominster Road ('Ludford Corner') just south of Ludford Bridge in Ludlow (see Figure 2.39). Both the Ludford Lane and Ludford Corner exposures show the uppermost parts of the Upper Whitcliffe Formation (Ludlow Series) overlain by the lowermost part of the Downton Castle Sandstone Formation (Přídolí Series) (Figure 2.42). The site displays a body stratotype for the Upper Whitcliffe Formation, the type sections for the Ludlow Bone Bed and Platyschisma Shale members of the Downton Castle Sandstone Formation, and a reference section for the succeeding Sandstone Member of this formation (Bassett *et al.*, 1982; Lawson and White, 1989; White and Lawson, 1989).

The Ludlow Bone Bed Member, discovered in 1835 by Dr J. Lloyd and the Reverend T.T. Lewis, is marked at Ludford Lane and Ludford Corner by a distinct recess in the section. It comprises 0.2 m of lenticular and ripple-laminated siltstones containing several thin layers of discontinuous vertebrate-rich sands. The bone comprises mostly fish remains, such as acanthodian scales and agnathan denticles (e.g. Agassiz, 1839; Harley, 1861; White, 1950; Turner, 1973; Dineley, 1999b). The succeeding Platyschisma Shale Member is up to 2 m thick and consists of parallel and cross-laminated and unlaminated mudstones and shales, with some siltstones. The overlying Sandstone Member, comprising mostly sandstones and siltstones alternating with thin mudstones, is present in Ludford Lane, but is seen best by the A49 road at Ludford Corner.

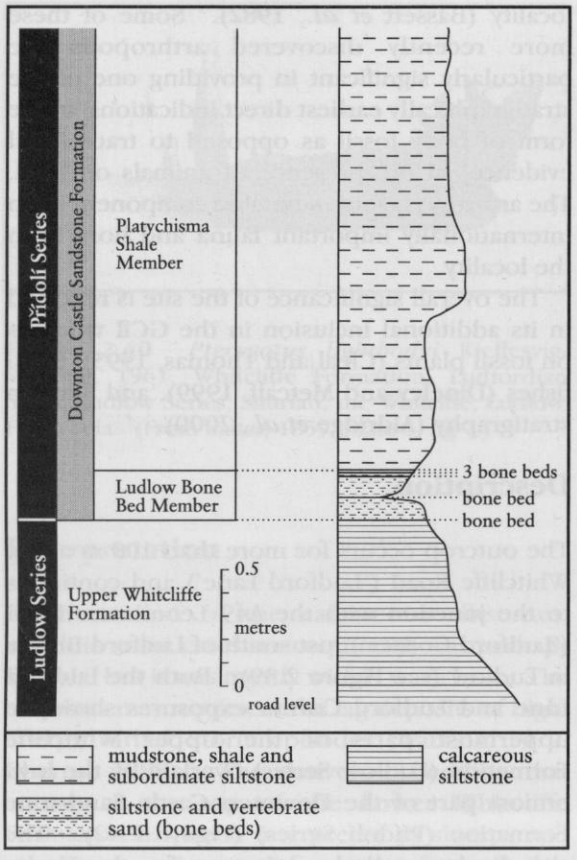
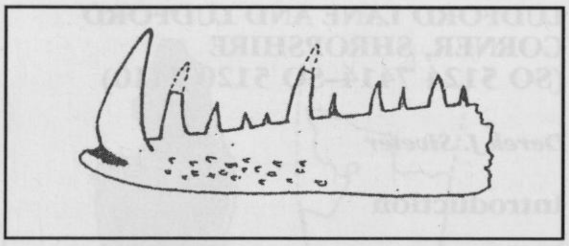


Figure 2.42 Stratigraphy of the Ludlow Series (Whitcliffe Group)/ Přídolí Series (Downton Group) boundary section, Ludford Lane and Ludford Corner site, Ludlow. (After Siveter, 2000f.)

The olive calcareous siltstones of the Upper Whitcliffe Formation, of which about 0.5 m or more can be seen at the site, have a fully marine fauna that includes articulate and inarticulate brachiopods, bivalves, bryozoans and also the ostracod *Calcaribeyrichia torosa*. Some of these faunal elements occur in the overlying Ludlow Bone Bed Member but in general the Downton Castle Sandstone Formation is characterized by a somewhat different, reduced diversity assemblage. At the base of this formation several brachiopods disappear and *Modiolopsis* bivalves, the inarticulate brachiopod *Lingula minima* and the biostratigraphically significant ostracods *Frostiella groenvalliana, Londinia arisaigensis* and *Nodibeyrichia verrucosa* enter the sequence. Early land plants such as *Cooksonia* (see for example Lang, 1937; Bassett *et al.*, 1982; Edwards *et al.*, 1996), together with a diverse fish fauna (Turner, 1973; Dineley, 1999b), also occur in the Downton Castle Sandstone Formation. Of the microfossil groups, conodonts are rare, but species of *Ozarkodina* have been recovered from just below the top of the Whitcliffe Formation and from the Ludlow Bone Bed Member (Aldridge and Smith, 1985; Miller and Aldridge, 1993, 1997; Miller, 1995). Land-derived spores substantially increase in numbers in the basal part of the Downton Castle Sandstone Formation, and marine phytoplankton (mainly acritarchs), show a corresponding decrease (Richardson and Lister, 1969; Richardson and Rasul, 1990).



Figuure 2.43 *Erettopterus brodiei* Kjellesvig-Waering, 1961; holotype, British Geological Survey, GSM 89411, ramus, possibly the free one, of the chela, ×2; Downton Castle Sandstone Formation, Přídolí Series, Silurian, Ludford Lane, Ludlow. (From Kjellesvig-Waering, 1961, text-fig. 2.21.)

Of significance for the present volume, the Downton Castle Sandstone Formation here has yielded the following eurypterids: *Erettopterus brodiei* Kjellesvig-Waering, 1961 (Figure 2.43); *Erettopterus spatulatus* Kjellesvig-Waering, 1961; *Erettopterus gigas* Salter, 1859; *Eurypterus cephalaspis* Salter, 1855; *Hughmilleria*? *acuminata* (Salter, 1859); *Herefordopterus banksii* (Salter, 1856); *Parahughmilleria salteri* Kjellesvig-Waering, 1961; *Nanahughmilleria* sp.; *Pterygotus denticulatus* Kjellesvig-Waering, 1961; and *Stylonurus* sp. (see Kjellesvig-Waering, 1961; Manning and Dunlop, 1995; Tetlie, 2006a). *Palaeophonus lightbodyi* Kjellesvig-Waering, 1954, also from this site, was originally described as a scorpion, but later it was listed (Kjellesvig-Waering, 1961) as a eurypterid. The Ludlow Bone Member, specifically, has yielded the trigonotarbid arachnid *Palaeotarbus jerami* (Dunlop, 1996; Figure 2.44), aquatic scorpions (Jeram *et al.*, 1990), probable terrestrial scorpions (Manning, 1993; Dunlop, 1996), the arthropleurid myriapod *Eoarthropleura ludfor-*

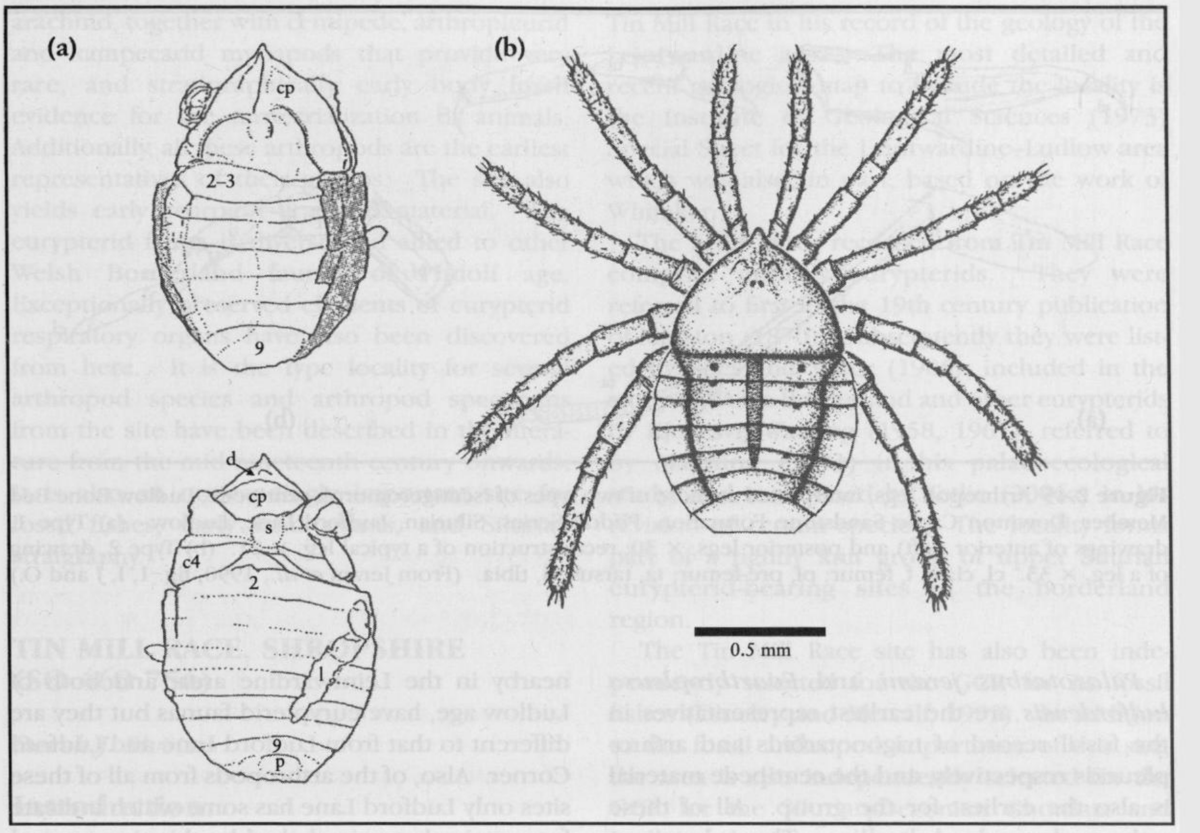


Figure 2.44 *Palaeotarbus jerami* (Dunlop, 1996); holotype, Ulster Museum, Belfast, K25850; Ludlow Bone Bed Member, Downton Castle Sandstone Formation, Přídolí Series, Silurian, Ludford Lane, Ludlow. (a) Interpretive drawings of specimen, dorsal (left) and ventral views, × 31 (from Jeram *et al*., 1990, fig. 1, B and D). cp, carapace; c4, coxa of fourth leg; d, doublure; l, leg; p, pygidium; s, sternum; 2, 2-3, etc. indicate either tergite (dorsal) or sternite (ventral) number. (b) Reconstruction. (From Dunlop, 1996, text-fig. 3.)

densis Shear and Selden, 1995, and unnamed kampecarid myriapods and at least two types of centipede (Jeram *et al*., 1990; Figure 2.45). The site represents the type locality for several of the above species.

Interpretation

This overall regressive sequence was deposited on the eastern margin of the remnant Anglo-Welsh Basin (Siveter *et al*., 1989; Bassett *et al*., 1992). The sediments indicate a fairly quick and fluctuating change from a relatively shallow, mainly clear though sometimes turbid, proximal shelf environment (conquinoid siltstones of the Whitcliffe Group) to near-shore, perhaps coastal plain conditions (Sandstone Member, Downton Castle Sandstone Formation) (see Watkins, 1979; Allen and Tarlo, 1963; Allen, 1974, 1985; Bassett *et al*., 1982; Miller, 1995).

The faunal and sedimentological change at the base of the Ludlow Bone Bed Member is ascribed by most authors to a sudden regression and transgression (see Miller, 1995), and the sediments may reflect shallow subtidal to low intertidal conditions, recurrent storm reworking, and the accumulation of vertebrate-rich lags (Smith and Ainsworth, 1989). The presence of land animals and plants certainly indicates close proximity to shore. The Platyschisma Shale Member probably represents intertidal environments. The occurrence of hummocky cross-stratification sequences in the succeeding Sandstone Member indicates shallow marine, subtidal to intertidal, storm-generated conditions (Siveter *et al*., 1989; Smith and Ainsworth, 1989). Overall, the sedimentary and restricted faunal characteristics of the Sandstone Member suggest the formation of sand bodies in a marine influenced environment near land.

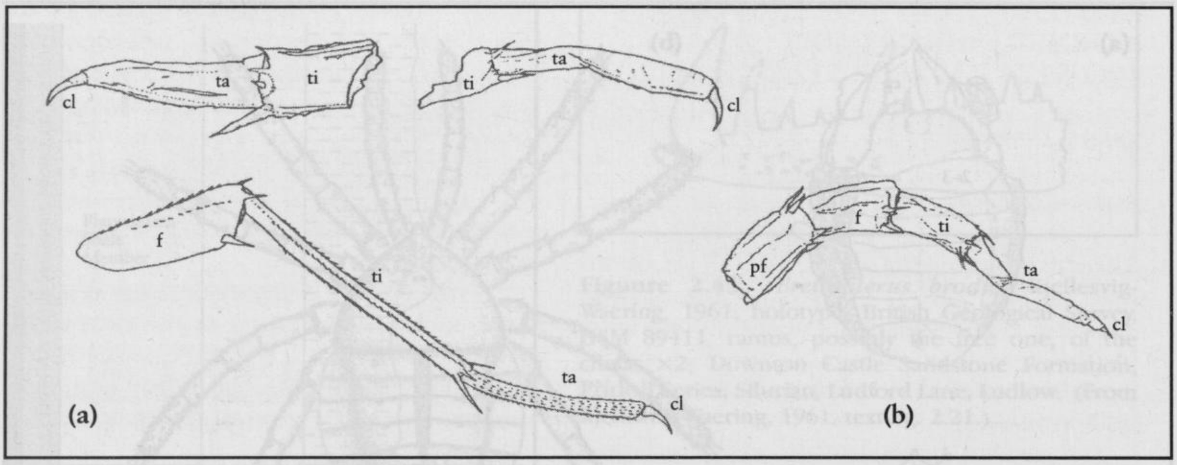


Figure 2.45 Arthropod legs, interpreted as those of two types of ?scutigeromorph centipede; Ludlow Bone Bed Member, Downton Castle Sandstone Formation, Přídolí Series, Silurian, Ludford Lane, Ludlow. (a) Type 1, drawings of anterior (left) and posterior legs, × 30; reconstruction of a typical leg, × 21. (b) Type 2, drawing of a leg, × 33. cl, claw; f, femur; pf, pre-femur; ta, tarsus; ti, tibia. (From Jeram *et al*., 1990, fig. 1, I, J and O.)

Palaeotarbus jerami and *Eoarthropleura ludfordensis* are the earliest representatives in the fossil record of trigonotarbids and arthropleurids respectively, and the centipede material is also the earliest for the group. All of these arthropods are land dwelling. The only terrestrial body fossils worldwide to pre-date these, by just a few million years, are millipedes from the late Wenlock–early Ludlow of the Stonehaven site in the Midland valley of Scotland (Wilson and Anderson, 2004). The scorpions from the Ludford Lane site await formal description.

The eurypterid species from this locality are diverse. Also, eurypterid respiratory organs have been recovered from here that suggest that these chelicerates had a dual respiratory system: lamellate book gills, which are homologous with those of modern xiphosurans and arachnid book lungs, together with a Kiemenplatten on the roof of the branchial chamber. The Kiemenplatten is interpreted as an accessory aerial respiratory organ, and thus these eurypterids may have been partially terrestrial (Manning and Dunlop, 1995).

This site is closely linked with respect to its eurypterid fauna to several others in the Welsh Borderland: Tin Mill Race in the nearby Downton Gorge area and, to the south, Bradnor Hill near Kington and Perton Lane in the Woolhope Inlier. All of these sites are Přídolí in age and share several species in common. The Church Hill and Whitcliffe arthropod sites, the latter adjacent to the present site and the former nearby in the Leintwardine area, and both of Ludlow age, have eurypterid faunas but they are different to that from Ludford Lane and Ludford Corner. Also, of the arthropods from all of these sites only Ludford Lane has some which indicate for certain that animals had by this time moved onto land, and hence it is arguably the most important of this group. In addition to Ludford Lane and Ludford Corner, other Siluro-Devonian sites described in the present volume that include arthropod elements indicative of terrestrialization are all from Scotland: Stonehaven, Turin Hill and Rhynie. The eurypterid faunas found at the Scottish Siluro-Devonian arthropod sites of Gutterford Burn, Dunside, Slot Burn and Turin Hill all include a greater representation of stylonuroids than the single record (*Stylonurus* sp.; Manning and Dunlop, 1995) from Ludford Lane and Ludford Corner. In addition to the latter record, however, three specimens of *Stylonurus megalops* (Salter, 1859) are known from the Downton Group of the nearby Ludlow Railway Cutting (Kjellesvig-Waering, 1961), and the monotypic *Parastylonurus sigmoidalis* Kjellesvig-Waering (1971) from the same stratigraphical unit some 6 km to the north-west in Corve Dale.

Conclusions

This upper Silurian locality is a front rank site within the context of the present volume. The Downton Group here contains a trigonotarbid arachnid, together with centipede, arthropleurid and kampecarid myriapods that provide very rare, and stratigraphically early body fossil evidence for the terrestrialization of animals. Additionally, all these arthropods are the earliest representatives of their groups. The site also yields early scorpion arachnid material. The eurypterid fauna is diverse and allied to other Welsh Borderland faunas of Přídolí age. Exceptionally preserved elements of eurypterid respiratory organs have also been discovered from here. It is the type locality for several arthropod species and arthropod specimens from the site have been described in the literature from the mid-nineteenth century onwards. It is also an outstandingly important site for fossil fishes, early land plants, and Silurian straigraphy.

TIN MILL RACE, SHROPSHIRE (SO 460 754)

Derek J. Siveter

Introduction

Tin Mill Race is situated on the River Teme some 5.5 km west of Ludlow, and 10 km ENE of Leintwardine in the central Welsh Borderland. The locality lies within the Downton Syncline, just 0.5 km to the NNE of the synclinal axis, and thus comprises some of the youngest Silurian strata in the Ludlow–Leintwardine area, which are about 417 million years old.

The general geology of this area has been described in many publications from the time of Murchison (1839), most recently those of Bassett *et al.* (1982) and White and Lawson (1989), both of which covered the stratigraphy, facies and fauna of the Přídolí Series of the region. Historically, rocks of this age in the Anglo-Welsh area were referred to the Downton Series, the name being derived from the Downton area of the River Teme, of which the Tin Mill Race site forms a part. An early reference to the beds exposed at this site is that of Lightbody (1873). Elles and Slater (1906) included the locality and several others nearby in their account of the highest Silurian rocks of the Ludlow district, and they gave a detailed log of the section at Tin Mill race which has provided the basis for subsequent studies. Whitaker (1962), for example, commented on fossils from Tin Mill Race in his record of the geology of the Leintwardine area. The most detailed and recent geological map to include the locality is the Institute of Geological Sciences (1973) Special Sheet for the Leintwardine–Ludlow area which was also, in part, based on the work of Whitaker.

The arthropods recorded from Tin Mill Race comprise entirely eurypterids. They were referred to first in the 19th century publication of Marston (1870). Subsequently they were listed by Elles and Slater (1906); included in the study of Welsh Borderland and other eurypterids by Kjellesvig-Waering (1958, 1961); referred to by Manning (1993) in his palaeoecological study; and mentioned by Tetlie (2006a) in his revision of certain species. The locality forms part of a tightly knit group of upper Silurian eurypterid-bearing sites in the borderland region.

The Tin Mill Race site has also been independently selected for the GCR for its fossil fishes (Dineley and Metcalf, 1999). In addition to the fossil arthropod importance of this site, the area is also independently selected for the GCR for the Silurian-Devonian Chordata and Ludlow selection categories.

Description

The sediments exposed at Tin Mill Race belong to the Temeside Shales Formation of the Přídolí Series, the type section for which is on the Teme at Ludlow, though an additional reference section is that at the old quarry in Tin Mill Wood near Tin Mill Race (White and Lawson, 1989). The strata at the mill race site were originally named the 'Tin Mill Shales' by Lightbody (1863). Elles and Slater (1906) later referred to these beds as the 'Temeside Shales' or 'Eurypterus Shales', and in current usage they are the Temeside Shales Formation.

For the most part the mill race section (Figure 2.46) comprises some 8.5 m of shales and marls, intercalated with a few sandy/gritty horizons. In the lower half of the section the shales are rubbly, and a local bone bed occurs some 1.5 m above a thin red shale horizon. In their upper part the shales are olive coloured, and here the Temeside Bone Bed occurs, this purportedly being a correlative of the one of the same name at Ludlow. The olive shales are capped by a grey micaceous grit – the so-called 'Fragment Bed' – which is crowded with carbonaceous remains

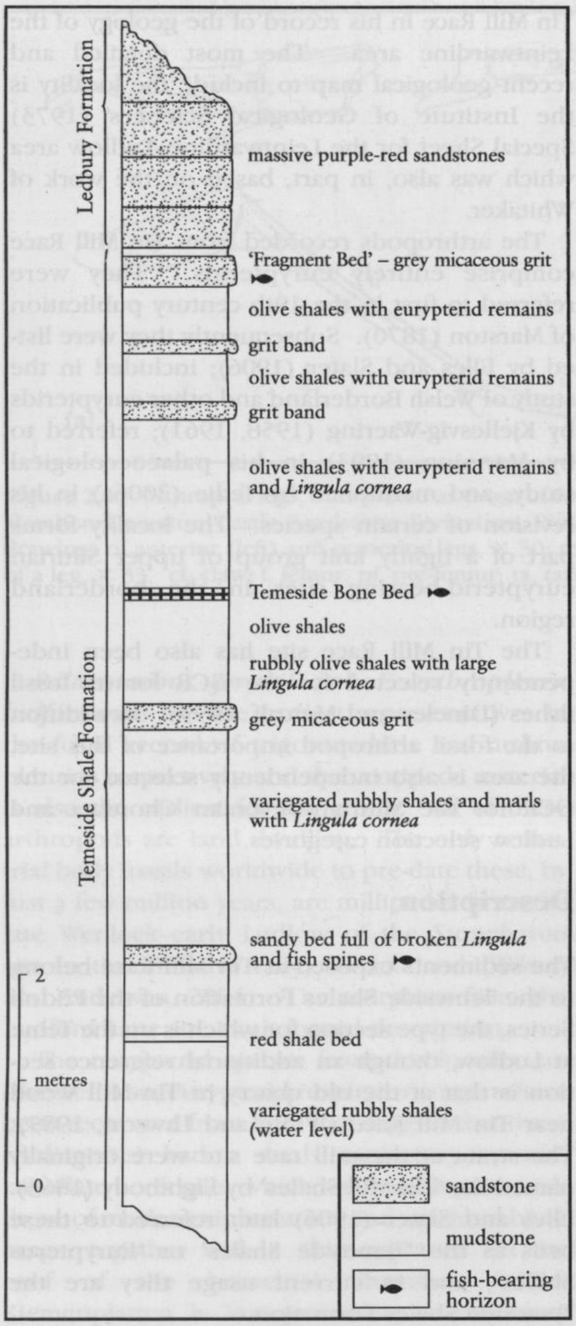


Figure 2.46 The section at Tin Mill Race, Downton area, Shropshire, comprising the Temeside Shales Formation and the Ledbury Formation, Downton Group, Přídolí Series. (After Dineley, 1999b and Elles and Slater, 1906.)

and forms the top of the Temeside Shales Formation. Above the Fragment Bed there are about two metres of massive purple-red sandstones that form the lowest part of the Ledbury Formation (Přídolí Series).

Eurypterids were recorded from the Temeside Bone Bed of Tin Mill Race by Marston (1870), and from the same horizon and from throughout the upper part of olive shales at the site by Elles and Slater (1906). Kjellesvig-Waering (1961) recorded the following species from here: *Eurypterus cephalaspis* Salter, 1855; *Erettopterus gigas* (Salter, 1859); *Erettopterus spatulatus* Kjellesvig-Waering, 1961 (Figure 2.47); *Hughmilleria banksii* (Salter, 1856) and *Parahughmilleria salteri* Kjellesvig-Waering, 1961. Many of Kjellesvig-Waering's records were based on specimens collected in the late 1950s by Robert H. Denison, whose material was deposited in the Chicago Natural History Museum. Also, the species Kjellesvig-Waering referred to as *Hughmilleria banksii* has subsequently been placed in *Herefordopterus*, following the revision of Tetlie (2006a).

Interpretation

By Přídolí times the Anglo-Welsh Basin, which had existed as a marine basin since Cambrian times, had essentially filled up, and quasi-marine environments prevailed. The sediments of the Temeside Shales Formation are considered to have accumulated largely in intertidal mud flats subject to prolonged exposure, and with sand shoals marginal to large rivers (Allen and Tarlo, 1963; Allen, 1974, 1985; Antia, 1981, 1983; Bassett *et al.*, 1982; White and Lawson, 1989).

The eurypterid fauna from Tin Mill Race is most closely associated with those from the Ludford Lane and Ludford Corner site in the Ludlow Anticline, Bradnor Hill some 30 km to the south-west near Kington in the south central Welsh Borderland, and Perton Lane in the Woolhope Inlier. All these Přídolí age sites have yielded several species in common. Tin Mill Race is also closely linked to the nearby arthropod sites of Church Hill in the Leintwardine area, and the Whitcliffe site in Ludlow. Eurypterids also occur in these other two sites, but the species composition in all three sites is mutually exclusive and, unlike at Tin Mill Race, other arthropods are also known from them. All of the Scottish Siluro-Devonian sites in this volume that include eurypterid faunas, namely Gutterford Burn, Dunside, Slot Burn and Turin Hill, differ immediately from Tin Mill Race in having yielded stylonuroid species. The stylonuroid *Marsupipterus sculpturatus* Caster and Kjellesvig-Waering, 1955 is, however, known from the Přídolí (Downton Castle Sandstone) of

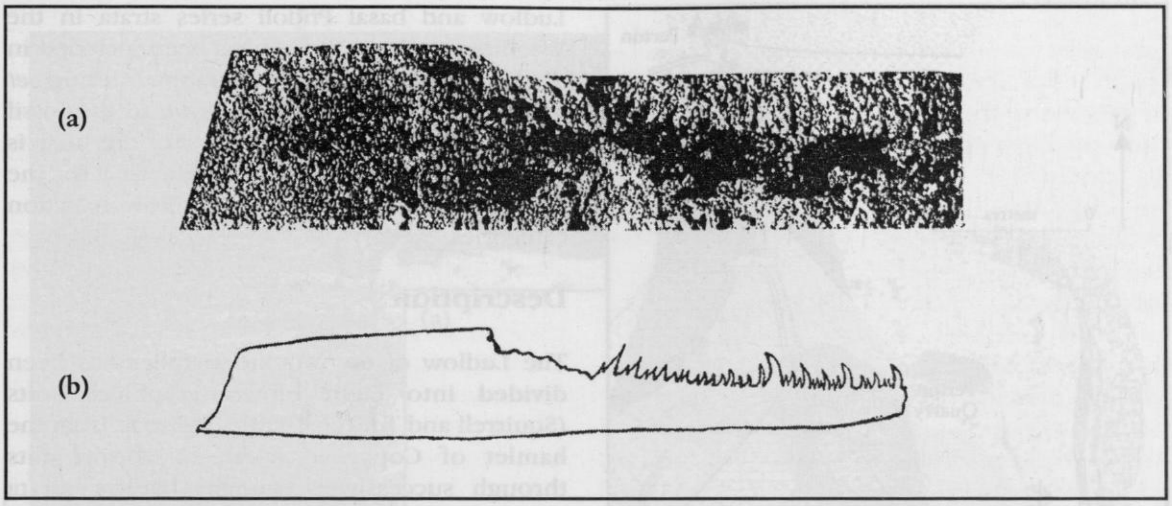


Figure 2.47 *Erettopterus spatulatus* Kjellesvig-Waering, 1961; Chicago Natural History Museum, PE 1524, fixed ramus of chela, collected by Robert H. Denison, 1950s; Temeside Shales Formation, Downton Group, Přídolí Series, Tin Mill Race, Downton area, Shropshire. (a) Photograph, × 3. (b) Interpretive drawing. (From Kjellesvig-Waering, 1961, plate 94, fig. 7 and text-fig. 3.34.)

nearby Forge Bridge, Downton (Kjellesvig-Waering, 1961).

Conclusion

Tin Mill Race, a locality of Přídolí age, forms part of a network of Welsh Borderland upper Silurian arthropod sites that have produced significant eurypterid faunas. Many of the specimens from this site were collected in the 1950s, that is, relatively recently by comparison with the recovery of material from other, classic 19th century Welsh Borderland eurypterid sites.

PERTON LANE, HEREFORDSHIRE (SO 596 406)

Derek J. Siveter

Introduction

The Perton Lane site consists of a very small roadside quarry immediately south of the hamlet of Perton in the southern Welsh Borderland Silurian inlier of Woolhope. The inlier is periclinal in structure and Perton Lane is situated in its northernmost part where late Ludlow and earliest Přídolí age rocks, some 417 million years old, are exposed.

The most recent study of the geology and faunas of the Woolhope area is that of Squirrell and Tucker (1960; see also 1967, 1982). Earlier commentators on the Silurian geology of the district include Murchison (1839), Phillips (1848), Strickland (1853), Brodie (1871), Gardiner (1927) and Pocock (1930). Correlation of the Woolhope sequence with the Silurian of other areas in the UK has been given in Cocks *et al.* (1971, 1992), and Butler *et al.* (1997) have mapped out the extent of the Woolhope Basin on the basis of subsurface analysis.

The site is important in arthropod terms for its eurypterid fauna. The first to discover eurypterids from Perton Lane was the Reverend P. B. Brodie (1869, 1871) in the late 19th century, and Henry Woodward (1871a,b) described some of this material at the same time. In the 20th century the eurypterid fauna from this site has been documented by Kjellesvig-Waering. He firstly produced a paper dealing specifically with Perton material, and then published broader taxonomic revisions of the group, one of which covered Welsh Borderland species that included material from here (1951, 1958, 1961). Plotnick (1999) included the Perton eurypterids in his assessment of Siluro-Devonian habitats of the group, and Tetlie (2006a) has recently undertaken a taxonomic revision of certain species from the site.

The Perton Lane site has also yielded an internationally important collection of early land plants in the form of both micro- and macrofloras, and thus has been selected for the GCR

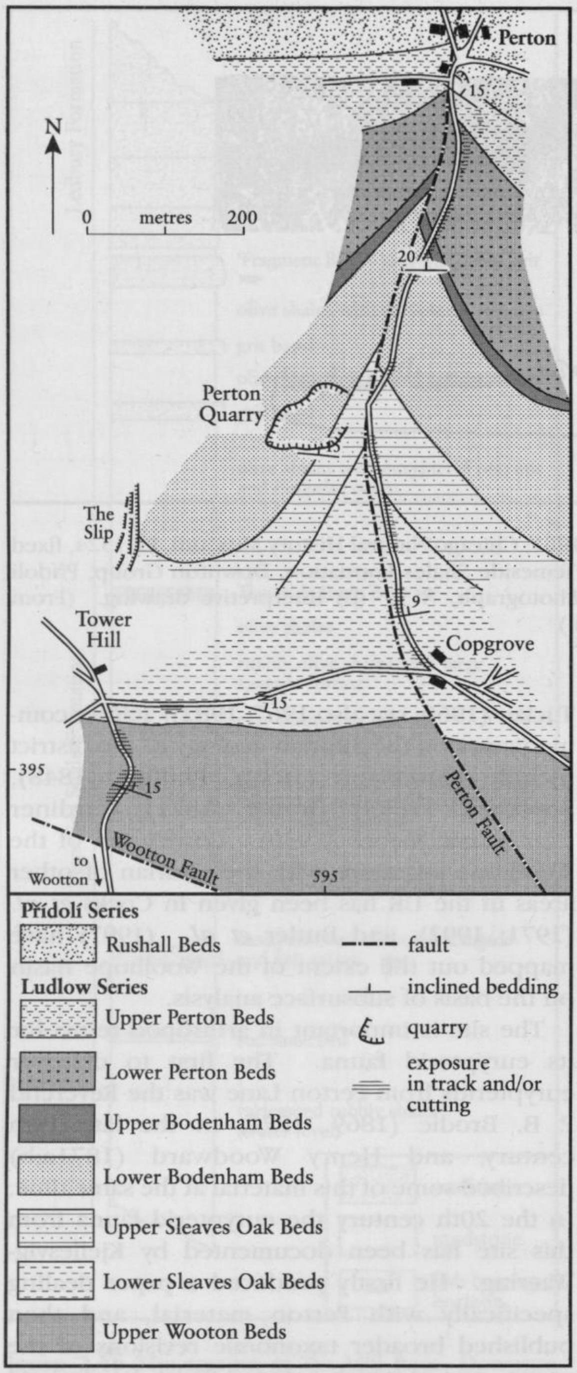


Figure 2.48 The geology of the area south of Perton, Woolhope Inlier, Herefordshire. (After Siveter, 2000e, and Squirrell and Tucker, 1960.)

and described in a companion GCR volume to the present one, on Palaeozoic Palaeobotany (Cleal and Thomas, 1995). The site also forms the northernmost extent of the Perton Road and Quarry site, which takes in the best section of Ludlow and basal Přídolí series strata in the Woolhope Inlier, and so it has been included in the GCR for its Silurian stratigraphy (Aldridge *et al.*, 2000). Therefore, in addition to the fossil arthropod importance of this site, the area is also independently selected for the GCR for the Palaeozoic Palaeobotany and Ludlow selection categories.

Description

The Ludlow of the Woolhope Inlier has been divided into eight biostratigraphical units (Squirrell and Tucker, 1960). The road from the hamlet of Copgrove north to Perton cuts through successively younger Ludlow strata (Figure 2.48), including excellent exposures in the large, disused Perton Quarry where the uppermost Upper Sleaves Oak Beds below the lower part of the Lower Bodenham Beds have been made available. The Perton Lane site, some 400 m north of Perton Quarry, exposes in total a few metres of the Upper Perton Beds (uppermost Ludlow Series) together with the overlying Rushall Beds (basal Přídolí Series).

The Upper Perton Beds consist of fairly well-bedded, calcareous and argillaceous siltstones. In the inlier as a whole they have a fauna that consists largely of brachiopods, bivalves, gastropods, and orthoconic nautiloids, together with numerically minor faunal elements such as trilobites, cornulitids and hyolithids (Squirrel and Tucker, 1960). Conodonts also occur in the uppermost Perton Beds (Squirrell and Tucker, 1960; Aldridge, 1985; Miller and Aldridge, 1993, 1997; Miller, 1995).

The Rushall Beds comprise fine-grained siltstones and mudstones together with some sandstone horizons. Compared to the underlying Ludlow Series strata, these beds have a fauna that is much reduced, and is dominated by inarticulate brachiopods and fish remains – a bone bed having been recorded at the base of the Rushall unit. Conodonts and ostracods (Siveter, 1989; Miller, 1995) also occur. The Rushall Beds also contain early vascular land plants and their spores, most famously *Cooksonia pertoni* (see Cleal and Thomas, 1995 and references therein).

Of significance for the present volume, Kjellesvig-Waering (1951,1961) identified the following eurypterids from the 'Downtonian' (= Přídolí) of Perton Lane: *Eurypterus cephalaspis* Salter, 1855; *Hughmilleria banksii* (Salter, 1856); *Salteropterus abbreviatus* (Salter, 1859);

Figure 2.49 *Eurypterus cephalaspis* Salter, 1855; Natural History Museum, London, I.3033, largely complete specimen, collected by Reverend R.B. Brodie, 1870, basal Downton Group, Perton, Přídolí Series, Woolhope Inlier. Holotype of *Eurypterus brodiei* Woodward, 1871. (a) Photograph, × 2 (from Kjellesvig-Waering , 1951, plate 3, fig. 1) (b) from Woodward (1871b).

Erettopterus gigas (Salter, 1859); *Mixopterus* sp.; *Carsinosoma*? sp.; and *Tarsopterella*? sp. (Figures 2.49 and 2.50). Tetlie (2006a) has now referred *Hughmilleria banksii* to his new monotypic genus *Herefordopterus*, and confirmed the occurrence of this species and *S. abbreviatus* at Perton; both of these have Bradnor Hill near Kington as their type locality. He also commented on pterygotid and mixopterid specimens from Perton, the latter probably confirming the presence here of *Mixopterus*. In addition to the fossil arthropod importance of this site, the area is also independently selected for the GCR for the Silurian–Devonian Chordata selection category (Dineley and Metcalf, 1999).

Interpretation

In the late Silurian this locality was sited on the western margin of the Midland Platform, which formed the eastern flank of the Welsh Basin (Siveter *et al.*, 1989; Bassett *et al.*, 1992). Overall, the sediments and biota along the road north from Perton Quarry indicate a regressive sequence, from the relatively shallow, open marine shelf deposits of the Ludlow to the more restricted and ultimately terrestrially influenced, alluvial plain environment of the Přídolí (Bassett *et al.*, 1982; Allen, 1985). The eurypterid-bearing Rushall Beds probably represent littoral deposits.

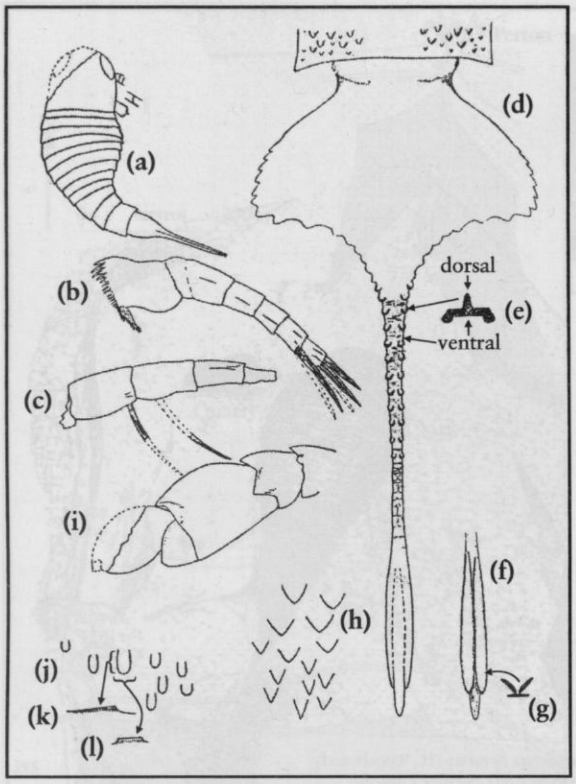


Figure 2.50 Eurypterids from the basel Downton Group, Přídolí Series, Perton, Woolhope Inlier. (a, b) *Hughmilleria banksii* (Salter, 1856). (a) GSM Zf-2871 and GSM Zf-2871, juvenile specimen, length is 18.5 mm. (b) Walking leg. (c) *Mixopterus* sp., GSM 88910, part of (probably the third) walking leg. (d–h), *Salteropterus abbreviatus* (Salter, 1859). (d) Reconstruction of ventral side of telson. (e) Cross-section through proximal part of telson. (f) Reconstruction of dorsal side of trilobed part of telson. (h) Sculpture of the cuticle, largest triangular scale is 4 mm wide. (i) *Eurypterus cephalaspis* Salter, 1855, reconstruction of the distal joints of the swimming leg, based on GSM Zf-2868, GSM Zf-2868a, and GSM Zi-3932. (j–l) *Carcinosoma*? sp., reconstruction of sculpture, based on GSM Zi-3955. All specimens are from the British Geological Survey. (From Kjellesvig-Waering, 1951, text-fig. 2 and 1961.)

The Perton Lane site is closely linked to the other Welsh Borderland arthropod sites that are also recognized for their eurypterid faunas. These are Bradnor Hill some 35 km to the north-west near Kington, and the Church Hill, The Whitcliffe, Ludford Lane and Ludford corner, and Tin Mill Race sites the same distance to the north in the Ludlow–Leintwardine–Downton area. In terms of its eurypterid fauna, that of Perton Lane is similar to those from Ludford Corner and Ludford Lane, Tin Mill Race, and Bradnor Hill. All these Přídolí age sites share several species in common, whereas the eurypterids from the Church Hill and The Whitcliffe, both Ludlow Series sites, are distinct from the others and from each other. The composition of the eurypterids in the Scottish Siluro-Devonian sites of Gutterford Burn, Dunside, Slot Burn and Turin Hill is also different to that of Perton Lane, most notably in that they have a rich stylonuroid fauna, as opposed to the solitary specimen of *Tarsopterella*? sp. from the Woolhope Inlier site (Kjellesvig-Waering, 1961).

Conclusions

This site is one of a network of Ludlow and early Přídolí age in the Welsh Borderland that have yielded important eurypterid faunas. It also has historical significance in that eurypterid material from here was described from the late 19th century onwards.

BRADNOR HILL, HEREFORDSHIRE (SO 291 577)

Derek J. Siveter

Introduction

Bradnor Hill is situated about 0.75 km north of Kington, Herefordshire. This area lies on the main strike of Silurian rocks as they trend south-west from the Ludlow Anticline in the central part of the Welsh Borderland towards the Builth and Llandovery districts in central Wales.

The Silurian geology of the country around Kington was originally mapped on the 1:63 000 scale by the Geological Survey (Ramsey *et al.*, 1850). Subsequently this general area was included in the stratigraphical and facies reviews of upper Silurian strata of Stamp (1923), King (1934), Kirk (1951), Holland and Lawson (1963), and Bassett *et al.* (1982). Upper Silurian rocks from ground topographically and stratigraphically immediately below the Bradnor Hill site were described and logged in detail by Holland and Williams (1985). Most recently, the British Geological Survey compiled a new map of the area on the 1:50 000 scale, incorporating new data based on aerial photograph interpretation, limited field reconnaissance, and published papers (Wilby, 2004). There is no Geological Survey memoir of the area.

This site is of considerable significance for the present arthropod volume because it yielded in the mid-19th century a rich eurypterid fauna of late Silurian, early Přídolí Series age, the study of which involved some of the leading geological figures of the day. Salter (1856, 1859a,b) was pre-eminent in researching this material. R.W. Banks (1856), who lived locally and was a banker by profession but who enthusiastically embraced the fledgling science of geology, was involved in bringing the eurypterid discoveries at Bradnor Hill to light and in studying them. Huxley, also, interpreted some of the specimens, and material from Kington featured in one of Woodward's (1872b) monographs of British 'Crustacea'. Further indication of the importance of the Bradnor Hill finds was the involvement of Murchison. He briefly referred to the geology of the area in his benchmark 1839 work, was in discussion with Banks in considering the nature of the Silurian strata and the eurypterid and other fossils of the Kington area (see Banks, 1893 and, for example, Murchison, 1872), and in 1855 he communicated the contents of Banks' 1856 paper to the Geological Society of London.

In the last century Størmer (1934, 1973) commented on Kington eurypterid species; Kjellesvig-Waering (1950, 1958, 1961, 1986) discussed members of the group from here as part of his wide-ranging studies of eurypterids and fossil scorpionids; one of the species received brief mention by Waterston (1964); and all species from the locality were referred to by Plotnick (1999). Very recently, two species from here have received modern systematic interpretation by Tetlie (2006a).

The agnathan and gnathostome fish from Bradnor Hill have merited inclusion of the site in the GCR for its fossil fishes (Dineley and Metcalf, 1999).

Description

The Bradnor Hill site, comprising the old quarry at Bradnor Green, is now on the edge of a golf course. The hill is underlain by Ludlow Series rocks and is capped by Old Red Sandstone type sediments of Přídolí age, some 417 million years old.

In the lane leading from Newton to Bradnor Hill, Banks (1856) described a fossiliferous upper Ludlow horizon, 5–7.5 cm thick, which contained a variety of invertebrates and fish remains and which he regarded as the equivalent of the Ludlow Bone Bed. Above this he recorded layers with the bivalves '*Orthonota amygdalina*' and '*Trochus helicites*', these being succeeded by thin tilestone beds containing a small *Lingula* species and traces of *Pterygotus*. This sequence occurs in the lower part of Newton Lane, one of the sections investigated by Holland and Williams (1985), who recognized it in modern stratigraphical terms as straddling the Ludlow–Přídolí series boundary. They described from there about 0.35 m of Upper Whitcliffe Formation (Ludlow Series) and 0.6 m of Downton Castle Sandstone Formation (Přídolí Series) strata. In the nearby section on the Kington bypass, they recorded some 0.8 m of Upper Whitcliffe Formation, overlain by 2.22 m of Downton Castle Sandstone Formation, the latter comprising, in ascending order, the Ludlow Bone Bed, the Platyschisma Shale and the Sandstone members. Eurypterid fragments were registered by them occurring near the base and the top of the Platyschisma Shale Member, this unit also yielding *Turbocheilus helicites*.

There are no descriptions in modern lithostratigraphical terms of the full succession in the old quarry complex on Bradnor Hill, though it must comprise strata of Přídolí age that belong wholly to the Downton Castle Sandstone Formation. A summary of Banks' (1856) description of the section in the quarry is as follows:

- A few tilestones below soil level.
- Three beds of hard, unfossiliferous, bluish-white stone, in total about 2.75 m thick.
- A grey to blackish-grey layer, 7–15 cm thick, with small iron-stained nodules. On the western side of the quarry contains *Pterygotus*, fish and 'vegetable' remains.
- A yellowish-white, close-grained sandstone, 1–1.25 m thick. Contains *Pterygotus*, fish and *Trochus* material. Passes on the eastern side of the quarry into a blue and even harder stone with *Lingula cornea* and *Pterygotus* remains. Probably represents the equivalent of the Downton Sandstone (of the Ludlow area).
- A grey layer with *Pterygotus* and fish remains, and 'vegetable' matter.
- A yellow sandstone, about 1.25 m thick. Represents the main bed at the base of the quarry, and in its lower portion comprising flagstones. Contains *Pterygotus* and fish remains down to its base, where there are

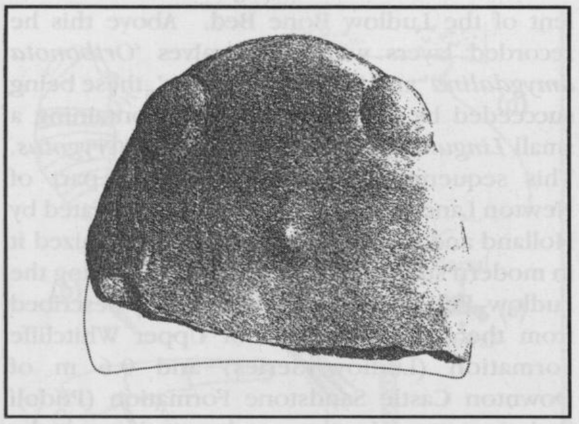


Figure 2.51 *Erettopterus gigas* Salter, 1859; lectotype, carapace, collection of Richard Banks; Downton Sandstone Formation, Přídolí Series, Kington, Herefordshire. (From Salter (1859a, plate 8, fig. 1.)

also horizons with *Trochus helicites* and *Lingula*.

Ludlow rock. A hard, unmanageable, 'greenstone'.

In the mid-1990s the exposure at Bradnor Hill Quarry was recorded as comprising 1.5 m of flaggy sandstones overlying 5 m of cross-bedded yellow sandstone (Dineley, 1999b), though correlation of these beds with those described by Banks (1856) was considered uncertain. The beds low in the original quarry section that produced the eurypterids are now, according to the most recent report, covered by metres of scree (Tetlie, 2006a).

In addition to the main quarry at Bradnor Hill, Banks (1856) also mentioned other quarries in the Bradnor Hill/Kington area that produced eurypterids. These were those near the iron foundry, reportedly lower down Bradnor Hill (see Dineley, 1999b); at Lodge farm in the adjoining parish of Huntington; at New Barn Farm on the southern side of the River Arrow, Kington; and high on the Radnor Forest, approached by the road from New Radnor to Harley. Most, if not all of these additional exposures are no longer effectively available (see, also, Dineley 1999b).

Kjellesvig-Waering (1961) recorded the following species from 'Bradnor Hill' and 'Kington' (Figures 2.51–2.53): *Erettopterus gigas* Salter, 1859; *Erettopterus spatulatus* Kjellesvig-Waering, 1961; *Eurypterus cephalaspis* Salter, 1855; *Hughmilleria banksii* (Salter, 1856); *Nanahughmilleria pygmaea* (Salter, 1859); *Parahughmilleria salteri* Kjellesvig-Waering, 1961; *Pterygotus ludensis* Salter, 1859; *Salteropterus abbreviatus* (Salter, 1859); and *Slimonia*? *stylops* (Salter, 1859). Tetlie (2006a) revised *Hughmilleria banksii* and *S. abbreviatus* from here; in the process he referred the former to its own monotypic genus, *Herefordopterus*, which was inferred to lie between the *Hughmilleria* and *Slimonia*/*Salteropterus* clades, and he regarded the latter as a possible senior synonym of *S.*? *stylops*, another Kington-based species. In total, Bradnor Hill/Kington represents the type locality for about half of the above species. The fish fauna from Bradnor Hill, which includes heterostracans, thelodonts, osteostracans and acanthodians, has been described by Banks (1856) Huxley and Salter (1856), Symonds (1859), Denison (1964) and Turner (1973).

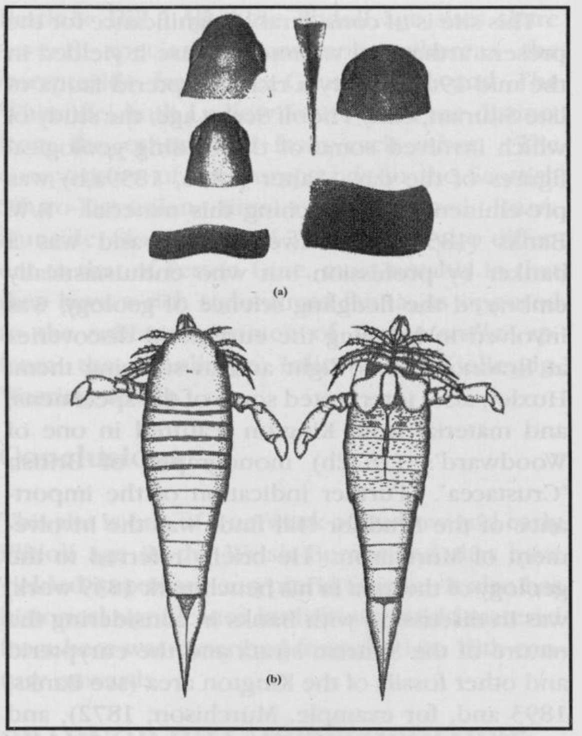


Figure 2.52 *Herefordopterus banksii* (Salter, 1856); Downton Sandstone Formation, Přídolí Series, Kington, Herefordshire. (a) Carapace, body segments and telson, collection of Richard Banks, from Banks (1856, plate 2, figs 5 and 6). (b) Idealized reconstructions, dorsal (left) and ventral views, from Tetlie (2006a, fig. 7).

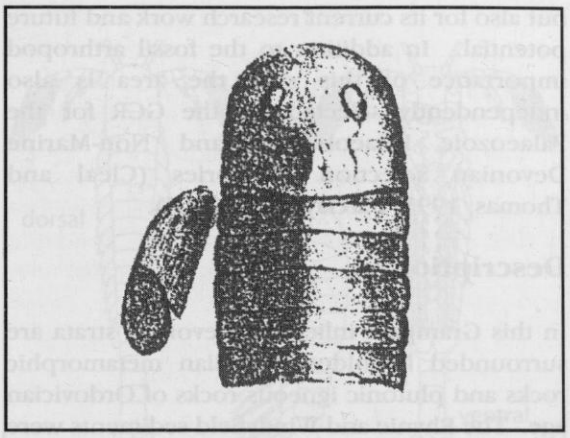


Figure 2.53 *Nanahughmilleria pygmaea* (Salter, 1859); lectotype, British Geological Survey, GSM89483, carapace, partial body and left swimming leg, collection of Richard Banks; Downton Sandstone Formation, Přídolí Series, Kington, Herefordshire. (From Salter, 1859b, plate 10, fig. 4.)

Interpretation

The eurypterid fauna of Bradnor Hill inhabited what by late Silurian times was a largely infilled Anglo-Welsh Basin. This fauna has similarity with those from Ludford Corner and Ludford Lane in the Ludlow Anticline, Tin Mill Race in the Downton Syncline, and Perton Lane in the Woolhope Inlier. All these sites are Přídolí in age and they share several species in common. Bradnor Hill also links with the eurypterid localities of Church Hill in the Leintwardine area and the Whitcliffe site at Ludlow. However the latter two are Ludlow Series sites and in terms of their eurypterid faunas both are distinct from that of Bradnor Hill and all the other Welsh Borderland sites, and also from each other. The lack of stylonuroid eurypterids immediately distinguishes Bradnor Hill from the Scottish Siluro-Devonian eurypterid sites of Gutterford Burn, Dunside, Slot Burn and Turin Hill.

Conclusion

Bradnor Hill forms one of a group of upper Silurian, Ludlow and Přídolí series, Welsh Borderland sites that are important for their eurypterid faunas. It stands as the type locality for many of the eurypterid species that occur there. It is also of historical importance as it represents one of the most significant Anglo-Welsh localities in mid- to late 19th century studies of this arthropod group, and attracted the attention of leading palaeontological/geological commentators of the day.

RHYNIE CHERT, ABERDEENSHIRE (NJ 494 277)

P. A. Selden

Introduction

The Rhynie Chert locality, of Early Devonian (Pragian, about 410 million y ears old) age, is the best known Lagerstätte of early terrestrial biota in the world, with its diversity of arthropods, ranging from tiny collembolans (springtails) to predatory trigonotarbid arachnids. Not only is it the longest known Lagerstätte, having been first described scientifically in the 1920s, but also it preserves the biota in such an exquisite manner that current research is still producing new morphological detail (e.g. Shear *et al.*, 1998; Trewin and Rice 2004). The cherts represent fossilized sinter – hot-spring siliceous deposits that were laid down in a complex of rivers, lakes and floodplains within the vast Laurasian continent. The hydrothermal activity centred on a fault system, mineralizing and altering subsurface strata as well as forming hot springs and geysers at the surface in the Rhynie area (see Figure 2.58).

The deposits surround both upright and fallen stems and other parts of early land plants (see Cleal and Thomas, 1995, for details of plant studies on the Rhynie Chert) such as *Rhynia* and *Aglaophyton*. Together with the petrified plants, animals were discovered in the 1920s, which remained the oldest-known terrestrial animals until 1990 (Jeram *et al.*, 1990). The arthropods found here and their association with other fossils make this one of the world's most important sites for studies of early terrestrial ecosystems, palaeobiology and evolution.

Crustacea were reported in the Rhynie Chert by Scourfield (1920a,b, 1926, 1940a) and Calman (1926), and arachnids by Hirst (1923). Hirst and Maulik (1926) described a possible eurypterid and collembolan 'insects'. With few exceptions, the accuracy of the descriptions and, especially, the detailed drawings of arthropods in these papers has been corroborated by later workers, and the illustrations have been widely reproduced in the literature. Later published

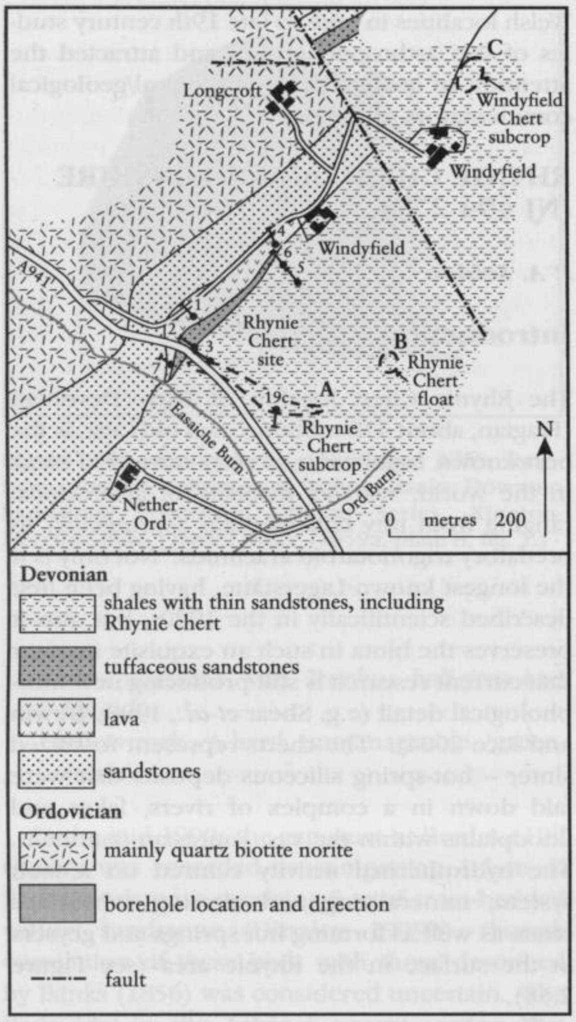


Figure 2.54 Geology of the Rhynie area showing detail of that part of the outlier containing the fossiliferous chert. Based on Trewin and Rice (1992, fig. 1.)

work, for example Claridge and Lyon (1961) and Shear *et al.*, (1987a,b), has only added details to the initial discoveries. Since 1926, new taxa have been described from Rhynie only in the last decade.

Recent work has involved investigation of the stratigraphy, sedimentology, taphonomy, structure, and mineral deposits of the chert (Rice *et al.*, 1995; Trewin 1994b; Trewin and Rice 1992, 2004). This work led to the discovery of a new locality, called the 'Windyfield Chert', some 700m to the east of the Rhynie site. There is little doubt as to the international importance of the Rhynie site, not only for historical reasons but also for its current research work and future potential. In addition to the fossil arthropod importance of this site, the area is also independently selected for the GCR for the Palaeozoic Palaeobotany and Non-Marine Devonian selection categories (Cleal and Thomas, 1995; Barclay *et al.*, 2005).

Description

In this Grampian inlier the Devonian strata are surrounded by older Dalradian metamorphic rocks and plutonic igneous rocks of Ordovician age. The Rhynie and Windyfield sediments were deposited in a narrow north-east to south-west trending faulted, half-graben basin within these older rocks. The western edge was marked by an active fault with the resulting sedimentary wedge lying unconformably on the older basement rocks and decreasing in thickness eastwards. Hydrothermal fluids rose along the fault plane and deposited sinter around geysers and hotsprings at the surface. Subsequent earth movements tilted the strata towards the north-west and folded the chert bearing rocks near Rhynie village into a north-eastwards plunging syncline.

The cherts at Rhynie occur as lenses within the Dryden Flags and Shales of Early Devonian (Pragian) age. The sequence was described in detail by Trewin (1994), and summarized below:

Shales with thin sandstones, including the Rhynie cherts/(alluvial plain and lacustrine)	>30 m
Tuffaceous sandstones	to 40 m
Lava–variably altered andesite	to 20 m
Pre-lava sandstones/(local alluvial fan)	*c.* 30 m

The cherts occur as lenses within shales, and represent fossilized sinters from hot springs, within a dominantly fluvial setting on the Old Red Sandstone continent. Modern analogues for the sedimentological setting of siliceous hot springs occur in Yellowstone National Park, Wyoming, USA. The strata are dated by palynology to Pragian, or possibly late Lochkovian, in age (Rice *et al.* 1995).

Trewin (1994b) summarized the Rhynie faunal list: one crustacean (but it is the commonest arthropod fossil at the site), five trigonotarbid arachnids, one mite (possibly five species), one collembolan and a euthycarcinoid

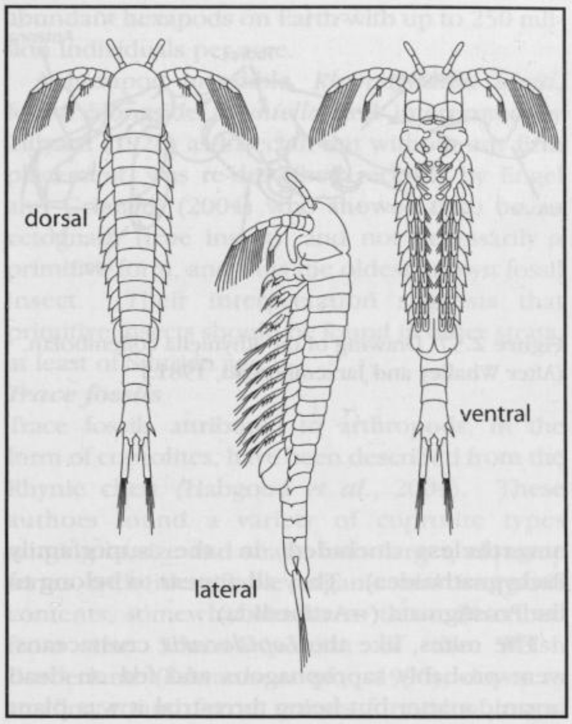


Figure 2.55 *Lepidocaris rhyniensis* reconstruction, based on specimens from the Rhynie Chert. (From Scourfield, 1940.)

(from the Windyfield Chert, Anderson and Trewin, 2003). The poorly preserved remains of a supposed spider and eurypterid described by Hirst (1923) and Hirst and Maulik (1926) have not generally been accepted by later workers (see below). More recently, an opilionid (harvestman) and myriapods have been reported from the chert (Shear *et al*. 1998; Anderson and Trewin 2003; Dunlop *et al*., 2004). The disputed insect *Rhyniognatha hirsti* was shown to be genuine by Engel and Grimaldi (2004), and new crustaceans have been described (Anderson *et al*., 2004; Fayers and Trewin 2003). In spite of the low diversity of the fauna (only arthropods are known) their remains are abundant in some horizons, and the exceptionally fine preservation of detailed morphology has established the Rhynie animals as models for elucidating the anatomy and taphonomy of arthropods in other early terrestrial Lagerstätten. The Windyfield chert biota was described in comparison with that of Rhynie by Fayers and Trewin (2004), whose summary gives the most recent list of the biotas. These authors did not consider there to be any significant difference between the two chert biotas.

Crustacea

The commonest arthropod in the Rhynie chert is *Lepidocaris rhyniensis* Scourfield, 1926 (Figure 2.55). Scourfield (1926) erected a new crustacean order, Lipostraca, for the new animal, and later he described some new specimens, including young stages Scourfield (1940a). *Lepidocaris* is a tiny, multi-segmented form with 11 pairs of phyllopods (leaf-like limbs), long branched antennae and a pair of caudal appendages. It lived in water and fed on organic detritus in ephemeral pools within the hot-spring environment much like fairy shrimps do today. More recently, other branchiopod species have been described by Fayers and Trewin (2003) and Anderson *et al*. (2004).

Euthycarcinoidea

Hirst and Maulik (1926) described *Heterocrania rhyniensis*, represented by scattered fragments of body and appendages, and referred it, with considerable doubt, to the Eurypterida. *Heterocrania* was largely ignored by later workers; it was not, for example, included in Waterston's review of Devonian eurypterids (in Rolfe and Edwards 1979). However, the discovery of more-complete specimens in the Windyfield Chert by Anderson and Trewin (2003) revealed that the animal was an euthycarcinoid and was the first known from Devonian rocks. The systematic position of this group is problematic as they have similarities to both crustaceans and insects. Like the crustacean *Lepidocaris*, they lived in ephemeral freshwater pools and were probably detritus feeders.

Arachnida

The remains of trigonotarbids (Figure 2.56) are fairly common in the Rhynie chert and their spider-like appearance was described by Hirst (1923) and Hirst and Maulik (1926). Despite this similarity they lack definitive spider features such as poison glands and silk producing glands. The discovery of well-preserved book-lungs in Rhynie trigonotarbids (Claridge and Lyon 1961, see also Størmer 1976) removed any possible doubt that these were truly terrestrial air-breathers. Further morphological details were added by Shear *et al*., (1987) and Dunlop (1994a). Trigonotarbids belong to the arachnid taxon Tetrapulmonata, as the sister group to spiders, amblypygids, uropygids and schizomids. They occur in all of the main early terrestrial

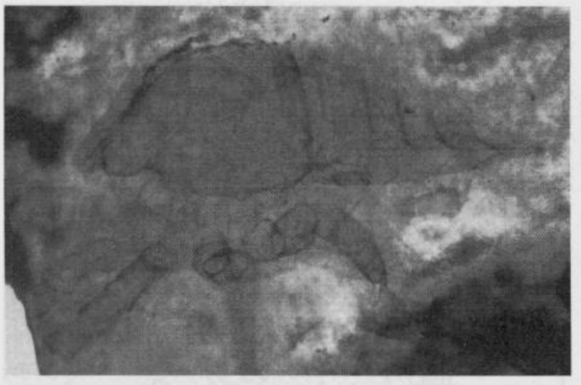


Figure 2.56 A triognotarbid specimen from the Rhynie Chert. (Photo: P. Selden.)

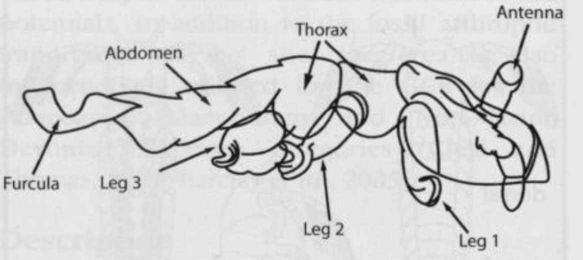


Figure 2.57 Drawing of the Rhyniella collembolan. (After Whalley and Jarzembowski, 1981.)

Lagerstätten.

Trigonotarbids, like almost all arachnids, were carnivores and presumably fed on any animals they could catch. Having caught their prey they would have injected it with digestive enzymes through the wounds made by their biting cheliceral fangs. The enzymes would liquefy the flesh of the prey so that it could be sucked out.

Palaeocteniza crassipes, described as a spider by Hirst (1923), was re-studied by Selden *et al.* (1991) who concluded that it was not a spider but probably the moult of a juvenile trigonotarbid. The oldest known spider is therefore the Upper Devonian *Attercopus fimbriunguis* (Shear, Selden and Rolfe, 1987) (Shear *et al.*, 1987a,b).

The oldest known mites (Acari) occur in the Rhynie chert and like trigonotarbids and spiders, mites are arachnids. Hirst (1923) thought the specimens were conspecific; he named them *Protacarus crani* which he placed, with some doubt, in the modern family Eupodidae. Dubinin (1962) considered they represented five species belonging to four families: *Protacarus crani* (Pachygnathidae), *Protospeleorchestes pseudoprotacarus* (Nanorchestidae), *Pseudoprotacarus scoticus* (Alicorhagiidae), and *Paraprotacarus hirsti* and *Palaeotydeus devonicus* (Tydeidae). John Kethley (Field Museum of Natural History, Chicago) has restudied the specimens and questioned the alicorhagiid affinity of *Pseudoprotacarus scoticus* because of its pretarsal morphology (in Kethley *et al.*, 1989). He considered all to belong to the family Pachygnathidae (pers. comm. in Norton *et al.*, 1989) except the nanorchestid (a family which is nevertheless included in the superfamily Pachygnathoidea). They all appear to belong to the Prostigmata (=Actinedida).

The mites, like the *Lepidocaris* crustaceans, were probably saprophagous and fed on dead organic matter but being terrestrial it was plant litter and other soil organic detritus. However, it is also possible that some mites were sap-suckers who sucked juices from living plant tissue.

Myriapoda

A short piece of leg probably belonging to a predatory scutigerimorph centipede was identified in a piece of Rhynie chert by Shear *et al.*, (1998) and Anderson and Trewin (2003). Detritivorous eoarthropleurids have also been found (Fayers and Trewin (2004).

Hexapoda

The earliest known hexapod, the collembolan *Rhyniella praecursor* Hirst & Maulik, 1926 (Figure 2.57), 1.5 mm long was described from multiple specimens originally found by the Revd W. Cran (Jarzembowski, 1989). *R. praecursor* had a furca as in living Collembola and evidently belongs to the extant family Isotomidae (Whalley and Jarzembowski 1981; Greenslade and Whalley 1986). Such an early (Pragian) date for *Rhyniella* and the mite *Protacarus* has been controversial (Crowson 1970; Greenslade 1988), but there is no evidence that *Rhyniella* is anything other than an extinct genus and species of early Devonian springtail. *Rhyniella* was probably adapted for walking on water as it has elongate claws, which are characteristic of Collembola, which live in a semi-equatic environment. Collembola are the most abundant hexapods on Earth with up to 250 million individuals per acre.

A hexapod mandible, *Rhyniognatha hirsti*, found alongside *Rhyniella* and interpreted by Tillyard (1928) as insectan but without any firm placement, was re-described recently by Engel and Grimaldi (2004) who showed it to be an ectognath (true insect), and not necessarily a primitive form, and thus the oldest known fossil insect. Their interpretation suggests that primitive insects should be found in older strata, at least of Silurian age.

Trace fossils

Trace fossils attributed to arthropods, in the form of coprolites, have been described from the Rhynie chert (Habgood *et al.*, 2004). These authors found a variety of coprolite types ranging in size and shape from larger, elongate forms with identifiable organic and inorganic contents, somewhat similar to those described from the Siluro-Devonain of the Welsh Borderland (Edwards *et al.*, 1990), down to smaller, round faecal masses formed of amorphous organic matter. The producers of the larger coprolites were considered to be mainly detritivores, whereas the smaller masses were likely to have been produced by microherbivores (e.g. collembolans and mites, feeding on microbes and fungi).

Interpretation

Taphonomy and palaeoecology

The Rhynie arthropods appear as thin films of cuticle, which may be preserved complete or as irregular patches. Maceration of the chert in hydrofluoric acid can yield complete podomeres, but the preservation differs from bed to bed (Trewin, 1994b). Both complete and disarticulated arthropod remains occur, including a trigonotarbid specimen showing leg podomeres inside the abdomen; this is presumably a moult. Crowson (1970, 1985) put forward the idea that the Rhynie arthropods could be much younger animals that crawled into fissures in the chert and were sealed in by re-mobilization of the silica, perhaps in Tertiary times, since their modern aspect might not be expected in such ancient rocks. Rolfe (1980), Kühne and Schlüter (1985), and Greenslade (1988) have argued persuasively on geological and palaeontological grounds that the Rhynie fauna is genuinely Devonian in age, and finds of very similar Devonian faunas from elsewhere support this (for example, terrestrial Lagerstätten reported, from Germany (Størmer, 1977), New York (Shear *et al.*, 1987a,b), and Shropshire (Jeram *et al.*, 1990)).

It is quite clear that most of the Rhynie arthropods, with the exception of the freshwater crustaceans, are terrestrial animals, living in Devonian times much as their present-day relatives do. An interesting question then arises: how much of the total terrestrial biota of the area at the time is preserved in the Rhynie chert? As far as the fauna is concerned, most of the terrestrial arthropods belong to primarily carnivorous groups. The mites and collembolan could be herbivores or decomposers. What little is known about the food of Collembola (Christiansen, 1964) indicates a wide variety of foods including fungal hyphae, bacteria, decaying plant material, frass, algae and spores. Similarly, little is known about the food preferences of living pachygnathoid mites, but Krantz and Lindquist (1979) reasoned that pachygnathoids probably feed by sucking fluid from algal cells; they pointed to the sharply pointed mouthparts of these mites, thought by Trägårdh (1909) to be a piercing organ, and work by Schuster and Schuster (1977) who observed nanorchestids feeding on algal mats and refusing animal food. The preponderance of carnivores was discussed by Kevan *et al.* (1975), who suggested three possible explanations: (a) small, soft-bodied prey animals were not preserved in the chert; (b) some of the arthropods were facultative herbivores; or (c) some of the predators were amphibious and returned to the water to feed. Reviews of early terrestrial ecosystems by Shear (1991), Edwards and Selden (1993) and Shear and Selden (1999) concluded that the decomposer/microherbivore food chain, such as occurs in modern soil and litter communities, predominated in Devonian terrestrial Lagerstätten. The Rhynie fauna may be a litter community; on the other hand, macroherbivory may not have been widespread at the time.

The unique preservation of the arthropods in the Rhynie chert, as three-dimensional moulds, means that they complement, and in most cases help to interpret, studies on similar arthropods from the other contemporaneous localities yielding terrestrial biotas. Interestingly, the studies on these other localities have confirmed the lack of macroherbivores among these early arthropods (see above).

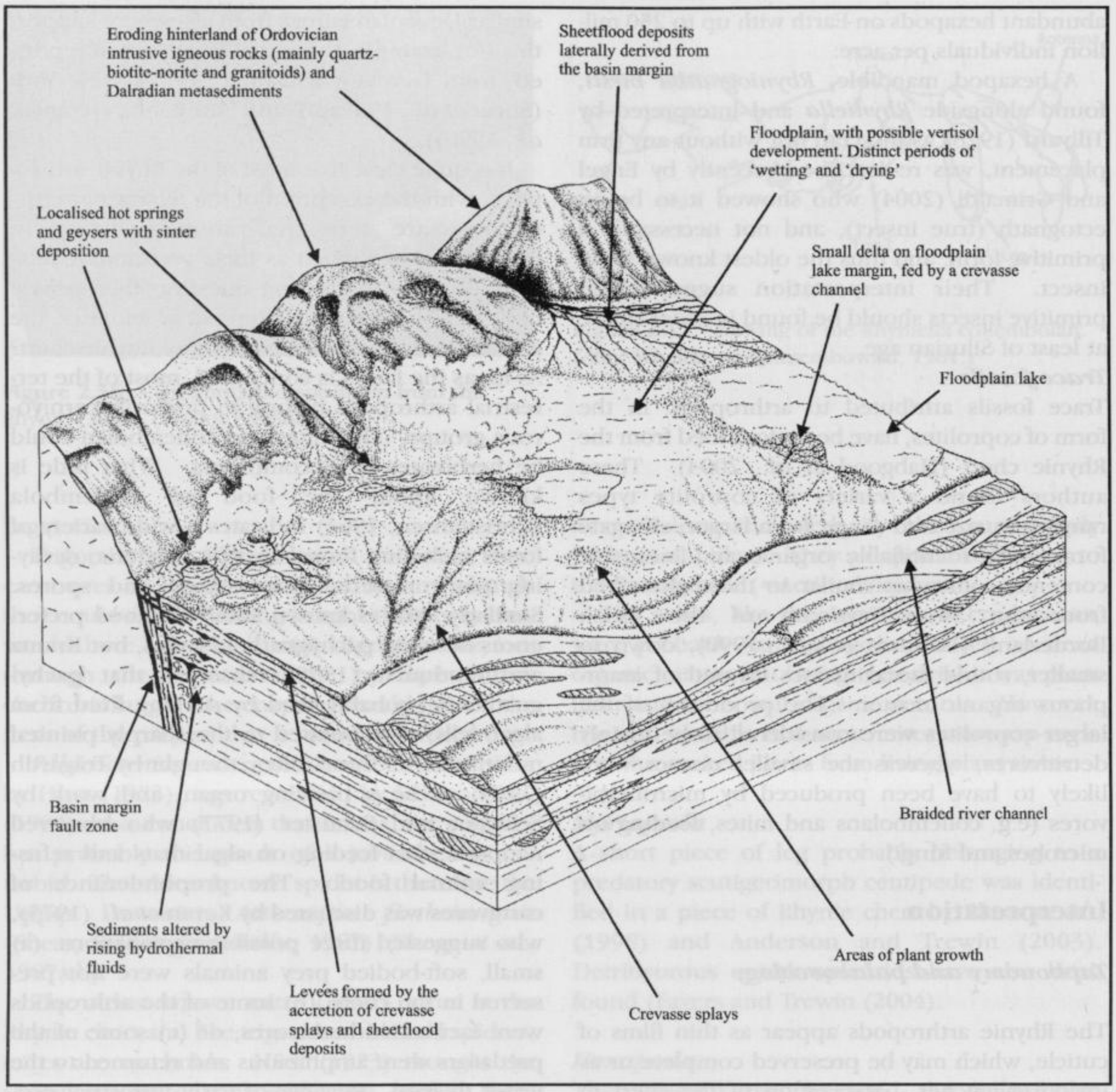


Figure 2.58 Reconstruction of the Rhynie environment. (After Fayers and Trewin, 2004.)

Conclusions

The Rhynie Chert locality is of international importance for the study of terrestrial arthropods, being the first discovered locality, yielding the best-preserved fossils, showing a relatively diverse fauna, and being readily accessible for future work. Apart from some small, concealed sites nearby, the Rhynie chert is unique; no other site in the world has yielded the same types of animals with the same type of high quality preservation in three dimensions. Conservation of the site is essential both for historical interest and to support current and future work being carried out in laboratories throughout the world.