Chapter 2 Pre-Carboniferous fossil arthropods

Pre-Carboniferous geological history

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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 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 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.

Laurentia

In the present context, the oldest sites are in the Midland Valley of Scotland with Dunside and Slot Burn within the Lesmahagow killer, 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 (Rhyne 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 grap-tolite-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 southwest 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 northeastern 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 P■ídolí 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 P■ídolí time, north-west England in late P■ídolí 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 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.

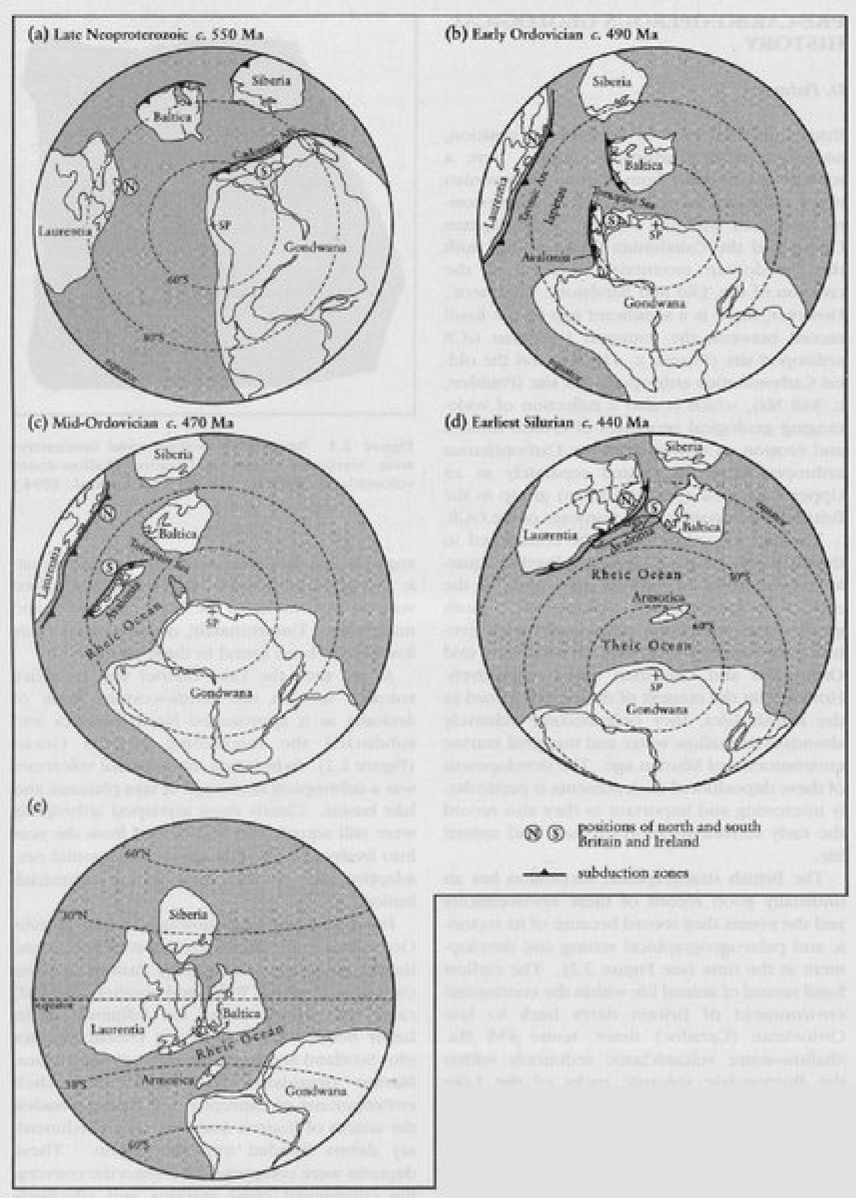
Climate

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. I Iowever, by late Ordovician times, Avalonia was moving towards Laurentia and global climates descended into an ice age and sea levels fell.

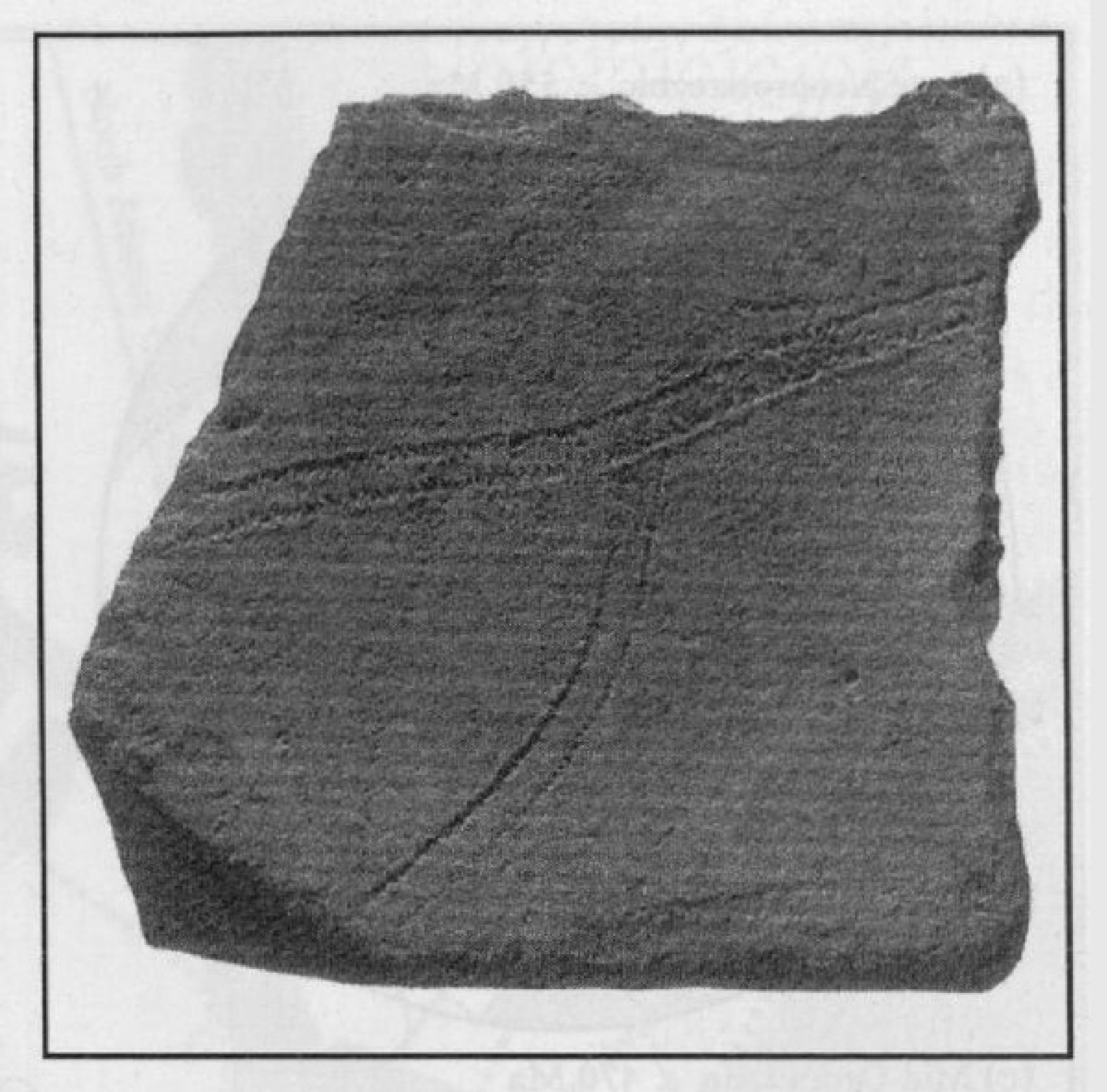
The cooling process climaxed at the end of Ashgill times and the Ordovician–Silurian boundary. By earliest Silurian times, Avalonia had move north of latitude 30° South and was converging on Laurentia when global temperatures rapidly recovered and sea levels rose sharply.

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.

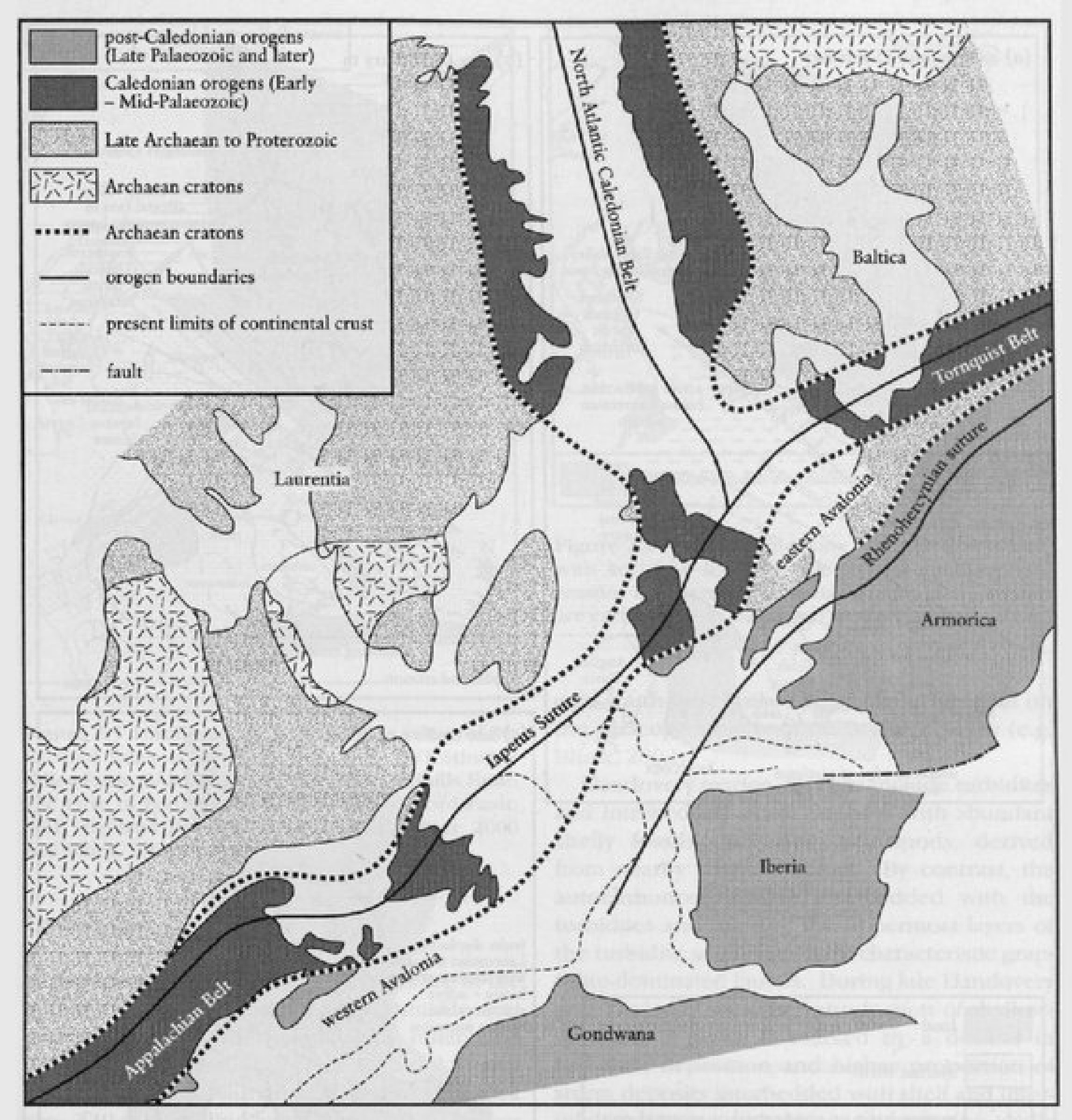
References



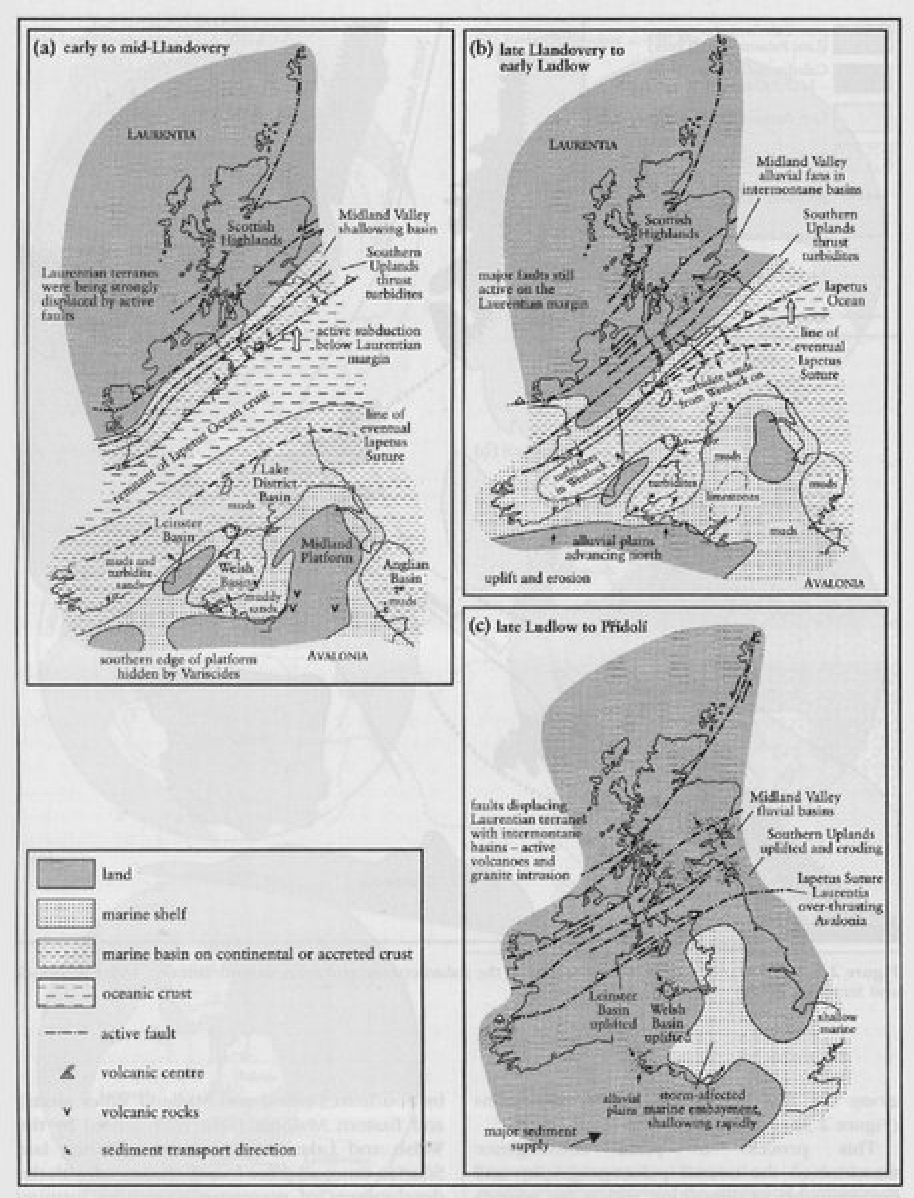
(Figure 2.2) Palaeozoic reconstructions of palaeocontinental positions showing the geological formation of the British Isles following the closure of the Iapetus Ocean. SP = South Pole. (Ater Holdsworth et al., 2000.)



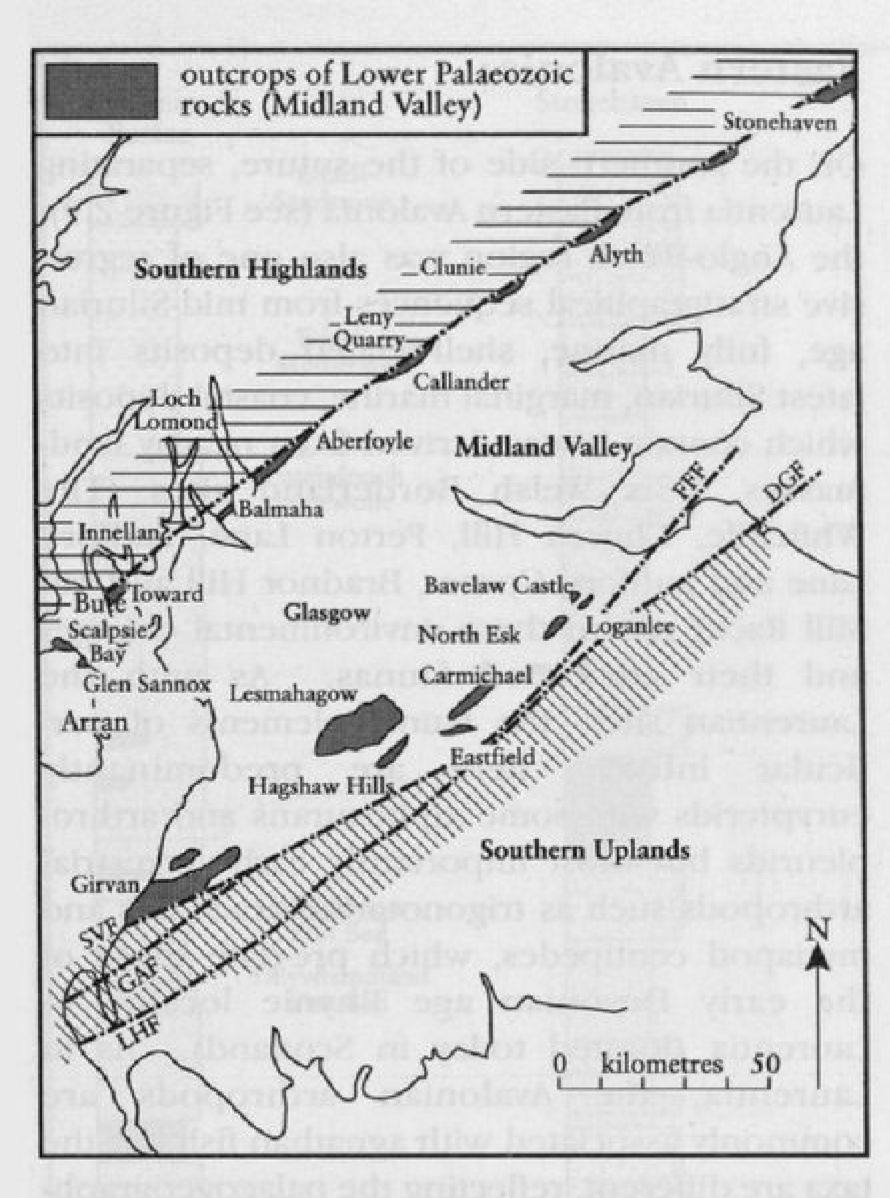
(Figure 2.1) Remarkably well-preseved centimetre-wide myriapod tracks in Caradoc shallow-water volcaniclastic sediments. (From Johnson et al., 1994.)



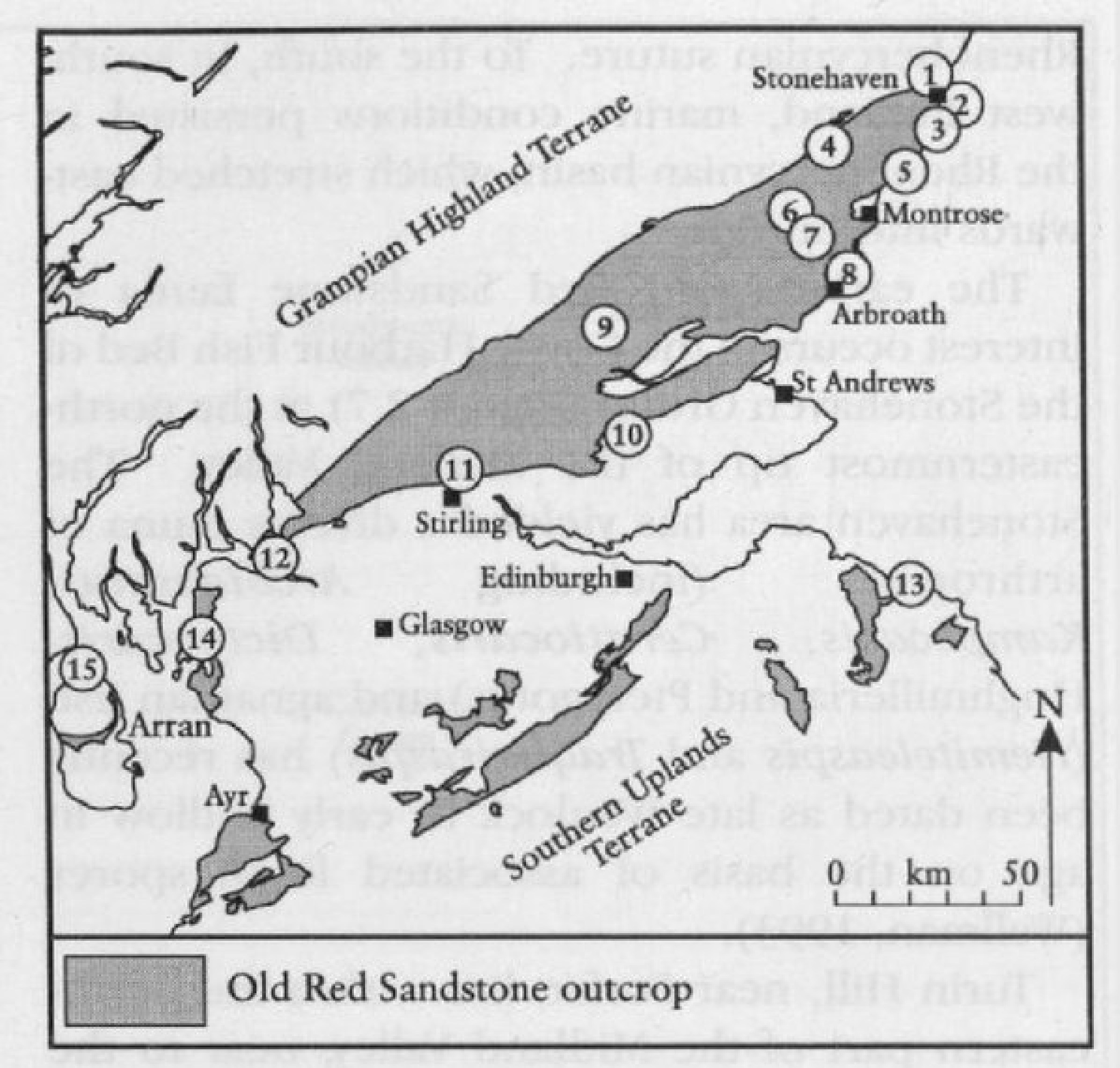
(Figure 2.3) A pre-Atlantic Ocean reconstruction of the palaeocontinental areas around 'Britain'. (After Woodock and Strachan, 2000.)



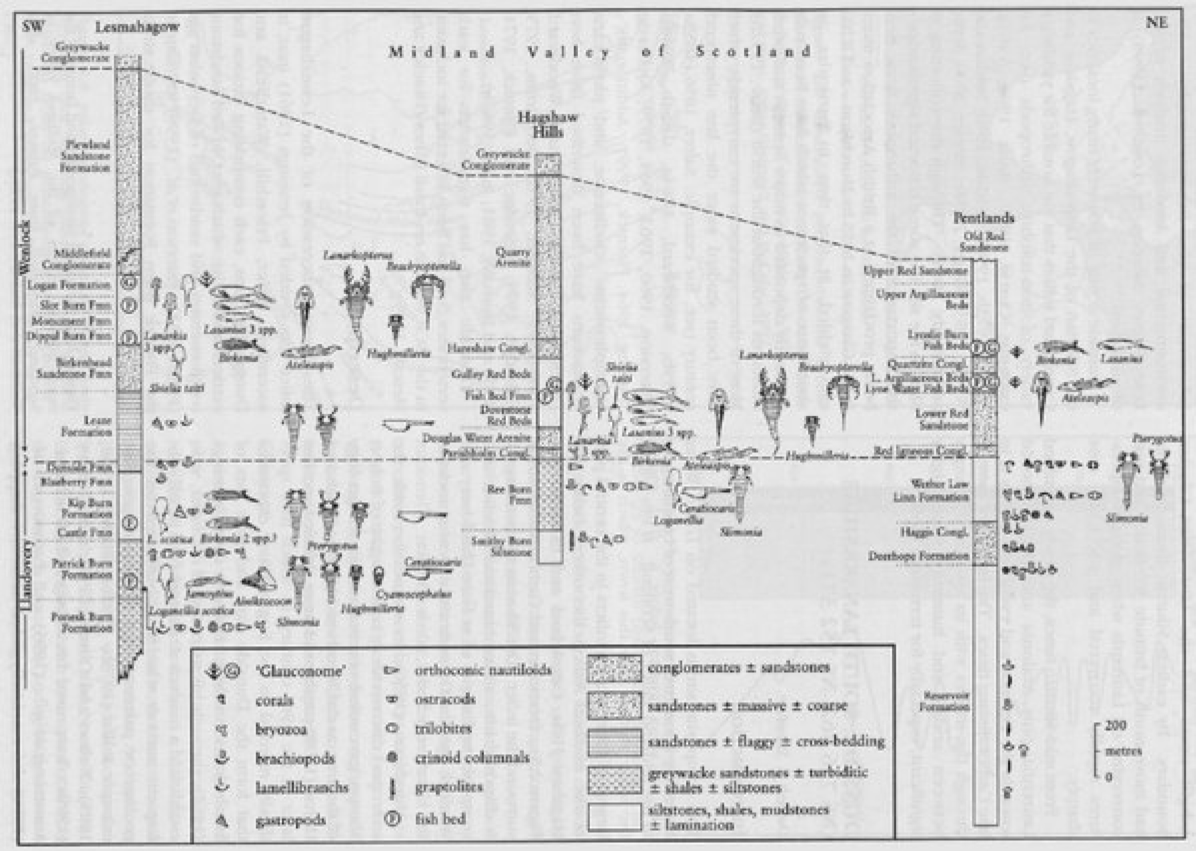
(Figure 2.4) Palaeogeographical maps of Britain for three intervals of Silurian time (a) early to mid-Llandovery; (b) late Llandovery to early Ludlow and (c) late Ludlow and P■ídolí. (After Aldridge et al., 2000.)



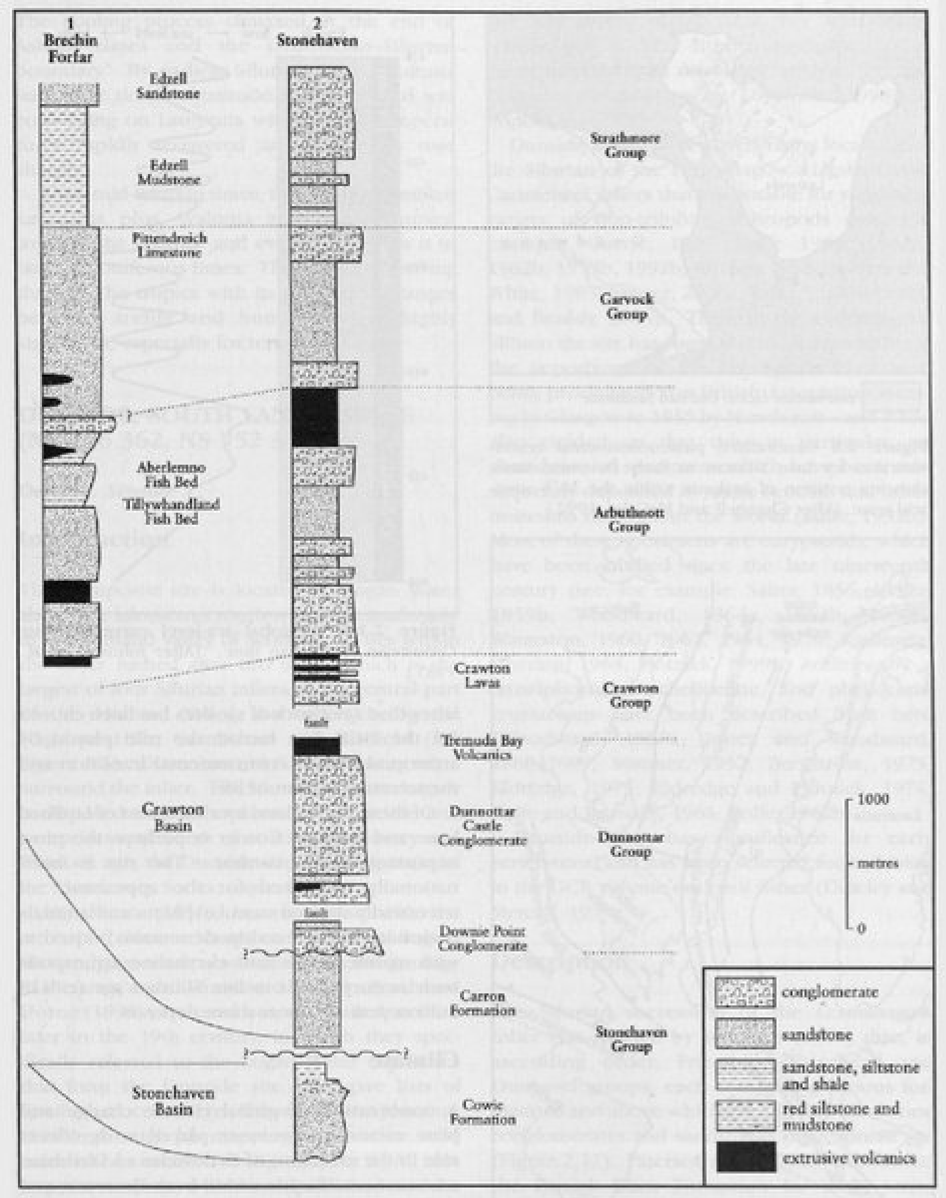
(Figure 2.5) Location of the main Silurian inliers of the Midland Valley of Scotland, and faults. SVF Stinchar Valley Fault; GAF Glen App Fault; LHF Leadhills Fault; FFF Firth of Forth Fault; DGF Dunbar–Gifford Fault; HBF Highland Boundary Fault. (After Palmer, 2000 and Bluck, 2002.)



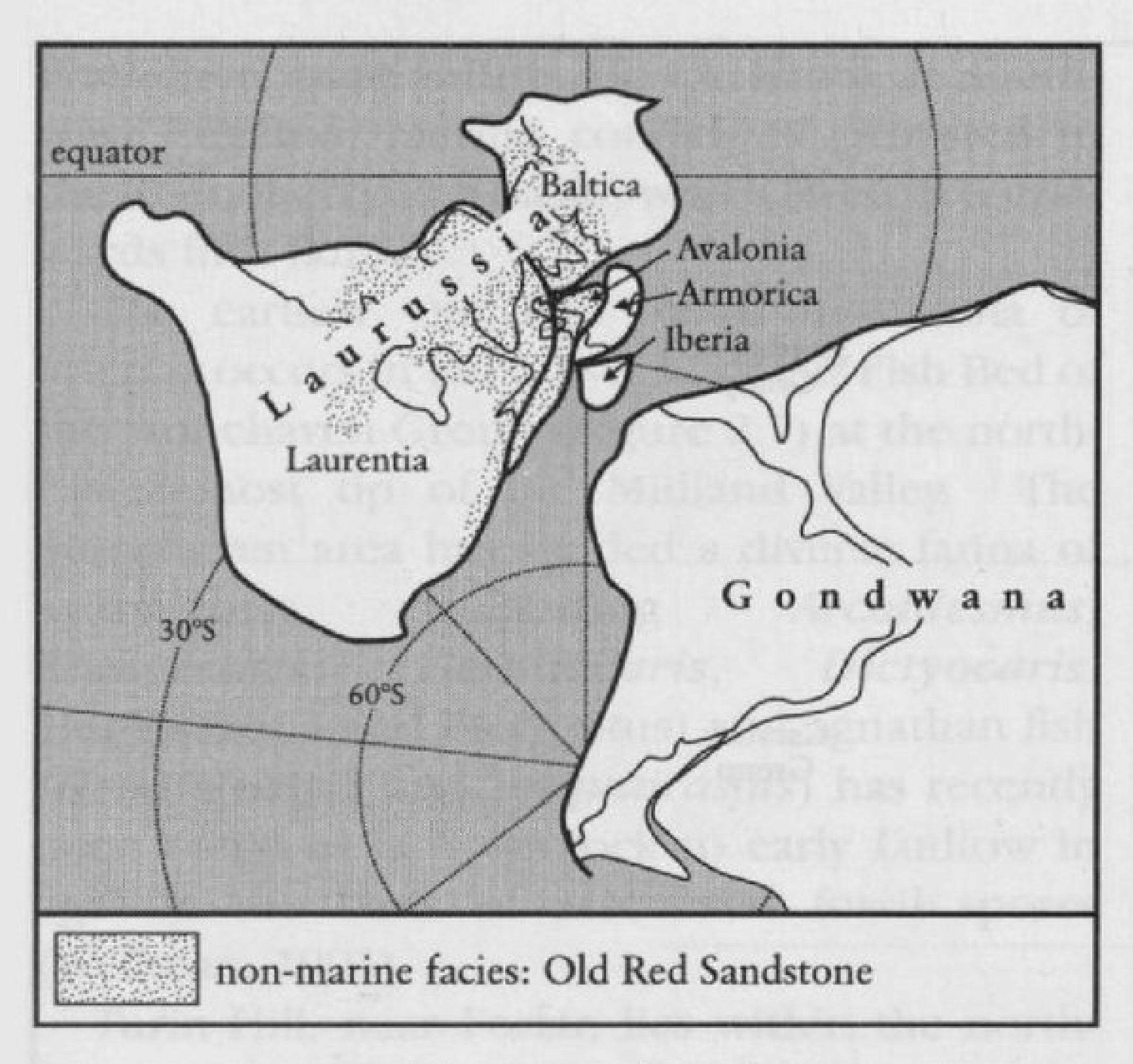
(Figure 2.6) Old Red Sandstone outcrops in Scotland, with key GCR localities selected for stratigraphical reasons numbered. Note that Orkney and Shetland are excluded from this map. (See Barclay et al., 2005.)



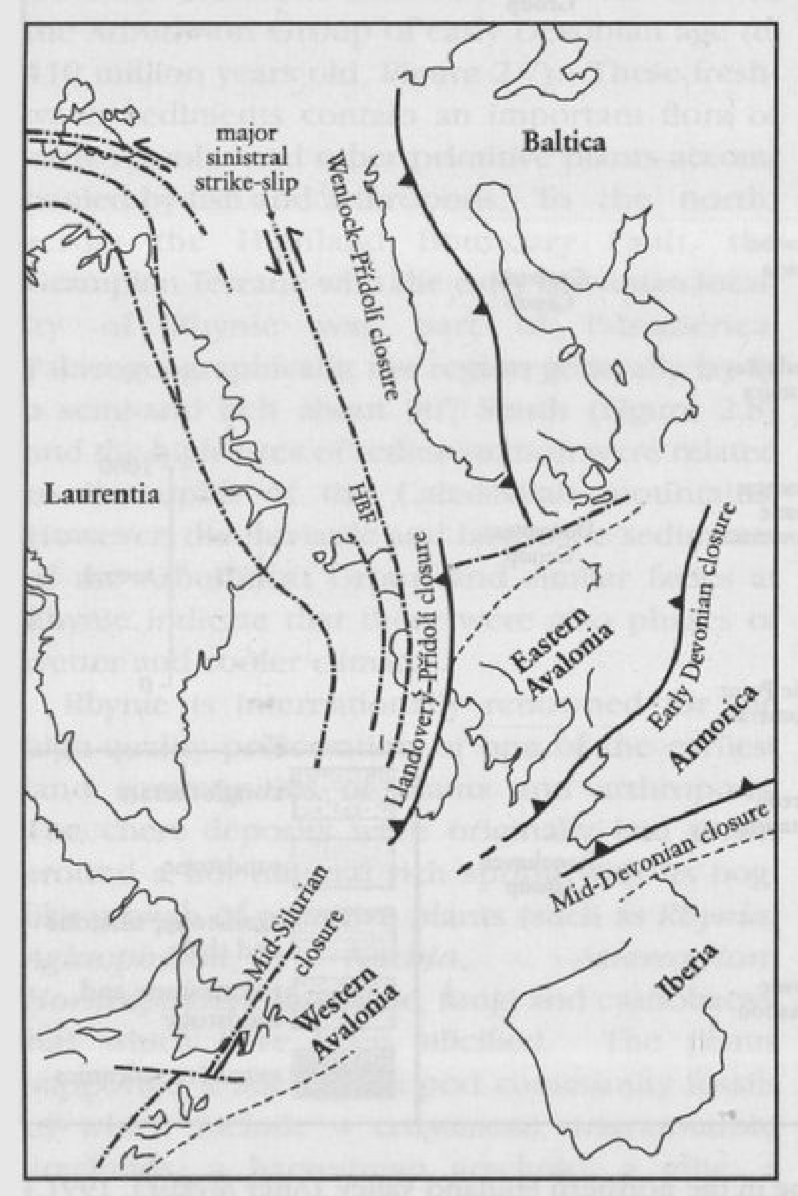
(Figure 2.11) (overleaf) Stratigraphy and faunas of the main Silurian inliers of the Midland Valley of Scotland. (Modified from Palmer, 2000, after Wellman and Richardson, 1993.)



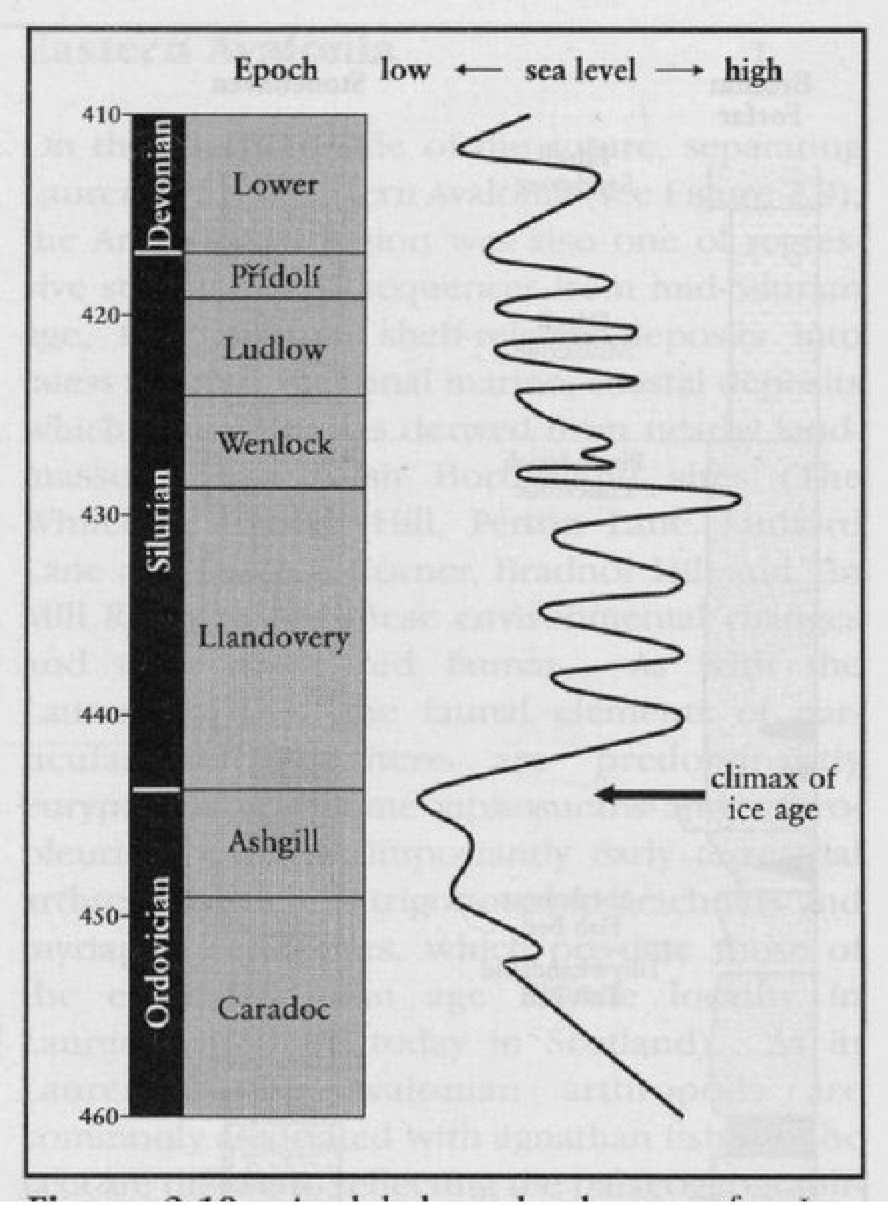
(Figure 2.7) Selected sections of Lower Old Red Sandstone in the northern Midland Valley. (After Mykura, 1991.)



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



(Figure 2.9) Palacocontinental 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.)