Fossil Arthropods of Great Britain

E.A. Jarzembowski
Maidstone Museum & Bentlif Art Gallery,
Maidstone, UK

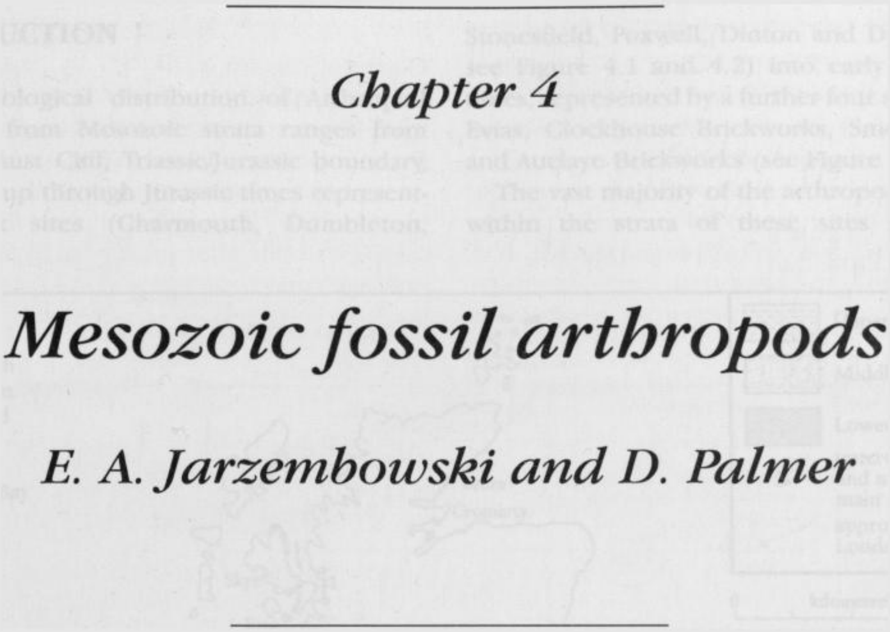
Derek J. Siveter
Oxford University Museum, Oxford, UK

D. Palmer
Cambridge, UK

and

P.A. Selden
Department of Earth Sciences,
University of Manchester, UK

GCR Editors:
Larry Thomas
and
Neil Ellis



Chapter 4

Mesozoic fossil arthropods

E. A. Jarzembowski and D. Palmer

INTRODUCTION

The chronological distribution of Arthropod GCR sites from Mesozoic strata ranges from Rhaetian (Aust Cliff, Triassic/Jurassic boundary, *c.* 200 Ma) up through Jurassic times represented by six sites (Charmouth, Dumbleton, Stonesfield, Poxwell, Dinton and Durlston Bay, see Figure 4.1 and 4.2) into early Cretaceous times, represented by a further four sites, Teffont Evias, Clockhouse Brickworks, Smokejacks Pit and Auclaye Brickworks (see Figure 4.2).

The vast majority of the arthropods fossilized within the strata of these sites are insects.

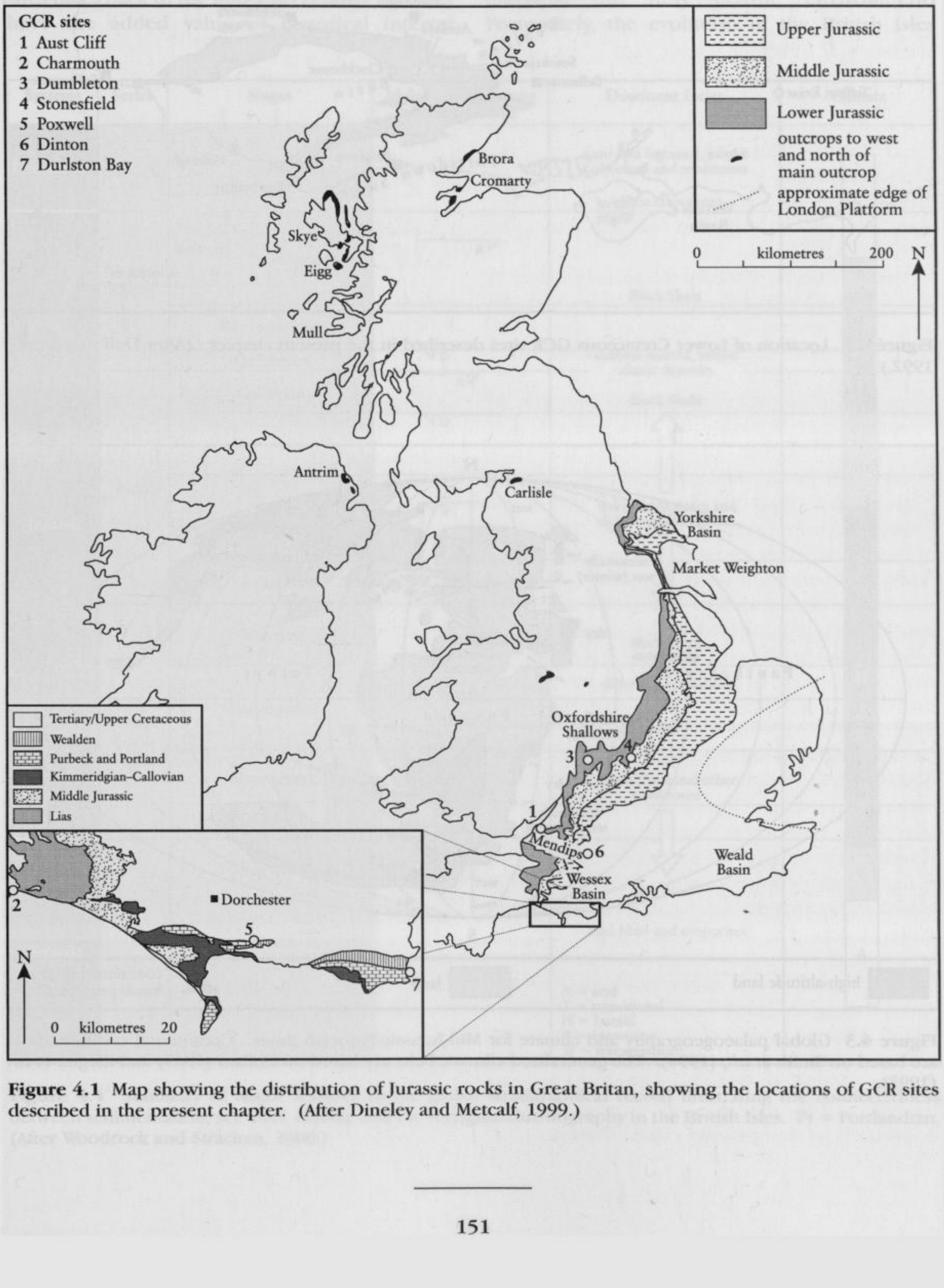


Figure 4.1 Map showing the distribution of Jurassic rocks in Great Britan, showing the locations of GCR sites described in the present chapter. (After Dineley and Metcalf, 1999.)

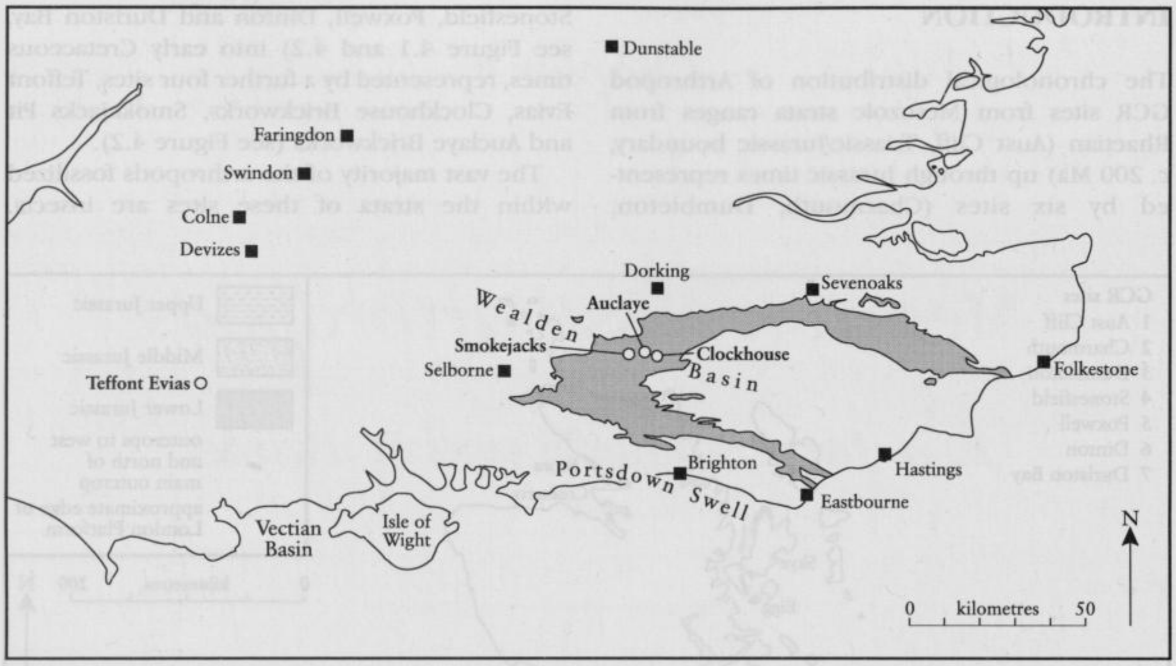


Figure 4.2 Location of Lower Cretaceous GCR sites described in the present chapter. (After Duff and Smith, 1992.)

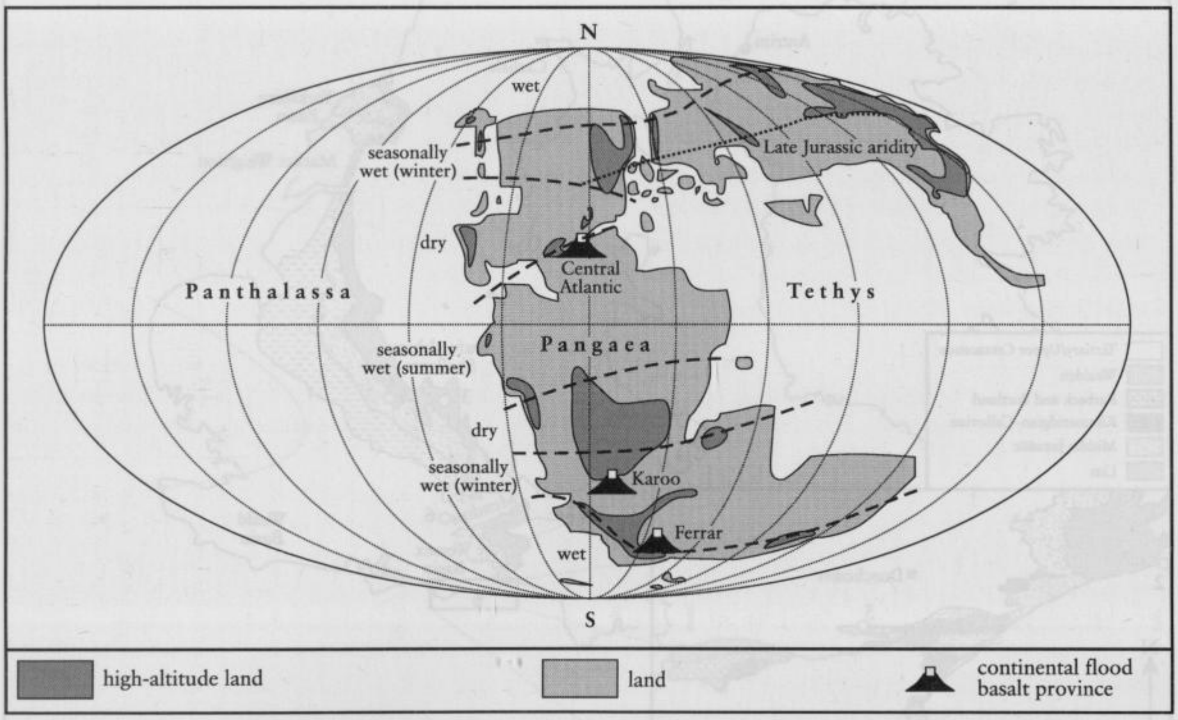


Figure 4.3 Global palaeogeography and climate for Mid-Jurassic/Bajocian times. Continental configurations are based on Smith *et al.*, (1994). The generalized climatic belts are based on Hallam (1985) and Ziegler *et al.* (1993).

Indeed, the primary selection of these sites within the context of this GCR volume is largely based on their insect faunas, although several of the sites have also been selected for the GCR for other palaeontological reasons, especially their fish and reptile faunas (see Dineley and Metcalf, 1999, and Benton and Spencer, 1995, respectively). The discovery of some of these insect sites dates back to the mid-19th century and they have the added value of historical interest associated with pioneers of the study of fossil insects such as the Reverend P.B. Brodie (1845).

Most of the fossil insects considered here are terrestrial, consequently their preservation requires particular environmental conditions within which deposition occurs in freshwater environments. Charmouth is the exception; here the entomofauna has been recruited in a marginal but fully marine environment. Fortunately, the evolution of the British Isles

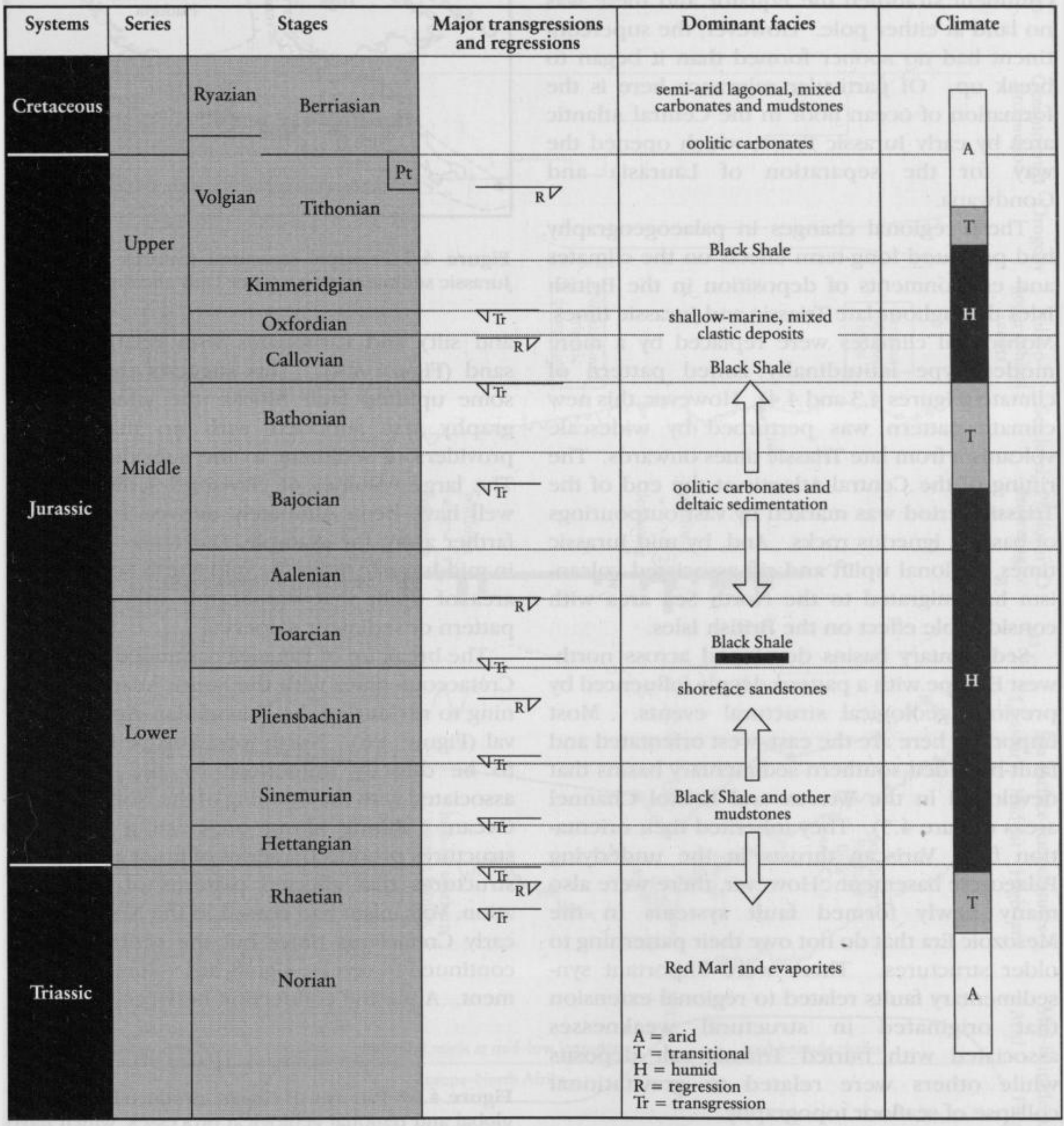


Figure 4.4 Summary of major features in the global stratigraphical record illustrating the connectedness between sedimentation, sea level, climate and the recognized stratigraphy in the British Isles. Pt = Portlandian. (After Woodcock and Strachan, 2000.)

during Mesozoic times saw the development of extensive shallow marine, marginal marine and fluviatile environments, especially in southern England.

REGIONAL SETTING

The regional setting for the late Triassic and Jurassic geological development of the British Isles was the progressive breakup of the supercontinent of Pangaea (Figure 4.3). The supercontinent straddled the Equator and there was no land at either pole. However, the supercontinent had no sooner formed than it began to break up. Of particular relevance here is the formation of ocean floor in the Central Atlantic area by early Jurassic times, which opened the way for the separation of Laurasia and Gondwana.

These regional changes in palaeogeography had profound long-term effects on the climates and environments of deposition in the British Isles throughout late Triassic and Jurassic times. Monsoonal climates were replaced by a more modern-type latitudinally zoned pattern of climate (Figures 4.3 and 4.4). However, this new climate pattern was perturbed by widescale volcanism from late Triassic times onwards. The rifting of the Central Atlantic at the end of the Triassic Period was marked by vast outpourings of basaltic igneous rocks. And, by mid Jurassic times, regional uplift and rift-associated volcanism had migrated to the North Sea area with considerable effect on the British Isles.

Sedimentary basins developed across north-west Europe with a pattern deeply influenced by previous geological structural events. Most important here are the east–west orientated and fault-bounded southern sedimentary basins that developed in the Wessex and Bristol Channel areas (Figure 4.5). They inherited their orientation from Variscan thrusts in the underlying Palaeozoic basement. However, there were also many newly formed fault systems in the Mesozoic Era that do not owe their patterning to older structures. There were important syn-sedimentary faults related to regional extension that originated in structural weaknesses associated with buried Triassic salt deposits while others were related to gravitational collapse of seafloor topography.

Sedimentologically, the late Triassic and Jurassic environments of deposition are dominated by fine-grained clastic deposits (clay and silt) and carbonates with relatively little sand (Figure 4.4). This suggests that despite some uplifted fault blocks, the general topography was subdued with no major local providers of sediment to the subsiding basins. The large volumes of clay-sized sediment may well have been ultimately derived from much farther away, for example, Laurentia. However, in mid-Jurassic times the mid-North Sea was one area of uplift that significantly influenced the pattern of sediment dispersal.

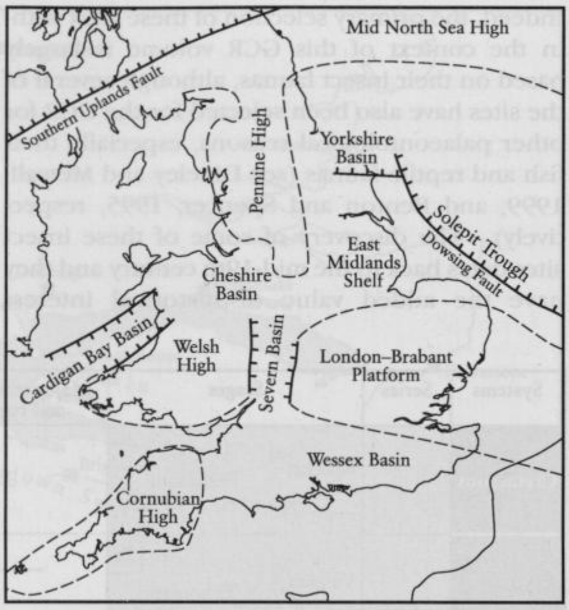
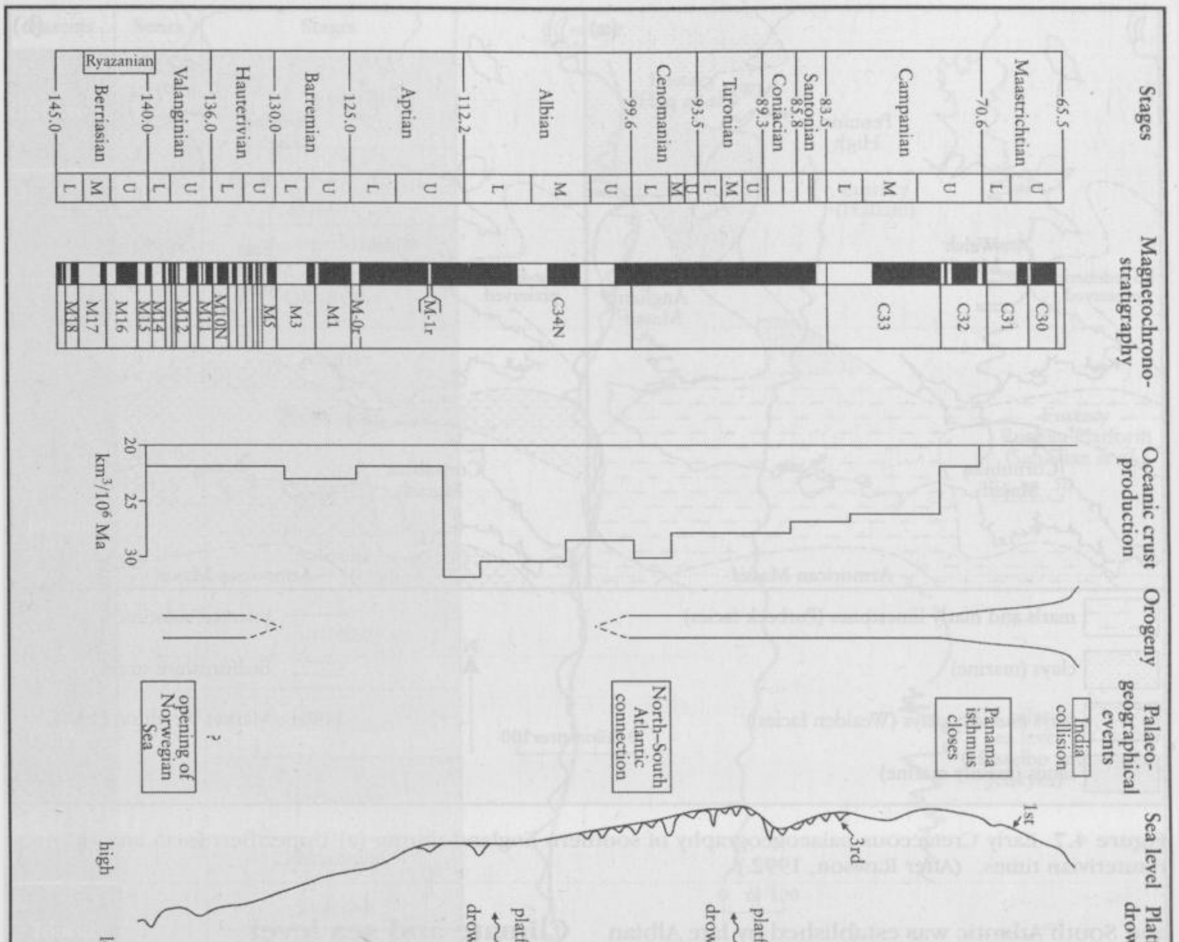


Figure 4.5 Principal structural features controlling Jurassic sedimentation. (After Duff and Smith, 1992.)

The break up of Pangaea continued into early Cretaceous times with the South Atlantic beginning to rift during the Valanginian–Aptian interval (Figure 4.6). North-west Europe continued to be directly influenced by the extension associated with the opening of the North Atlantic Ocean. Rifting along pre-existing basement structures produced a series of horst and graben structures that affected patterns of sedimentation. Volcanism had ceased in the North Sea by early Cretaceous times but the central graben continued to receive significant volumes of sediment. A marine connection between the North

Figure 4.6▸ Patterns of change produced by various global and regional geological processes, which have affected the environment of sedimentation through Cretaceous timesIndicators of global change through Cretaceous times. (Gale, 2000.)


Stages
65.5
Maastrichtian
70.6
Campanian
83.5
Santonian
85.8
Coniacian
89.3
Turonian
93.5
Cenomanian
99.6
Albian
112.2
Aptian
125.0
Barremian
130.0
Hauterivian
136.0
Valanginian
140.0
Berriasian
Ryazanian
145.0
U
L
M
Magnetochrono-stratigraphy
C30
C31
C32
C33
C34N
M-1r
M-0r
M1
M3
M5
M10N
M11
M12
M14
M15
M16
M17
M18
Oceanic crust production
20
25
30
km³/10⁶ Ma
Orogeny
Palaeo-geographical events
India collision
Panama isthmus closes
North–South Atlantic connection
opening of Norwegian Sea
?
Sea level
1st
3rd
high
low
Platform drowning
platform drowning
2
1
O
Preservation of organic matter in ocean basins
δ13 C
–
+
Sea surface temperatures
Low-lat
Mid-lat
High-lat
32°C
28°C
Southern England Blk C and CO3
Israel: fish-teeth
high-lat southern oceans: formas
Mid-latitude A/H
Arid
Humid
evaporites
muds and marls at mid–low latitudes;
mid-latitude chalks
Europe–North Africa

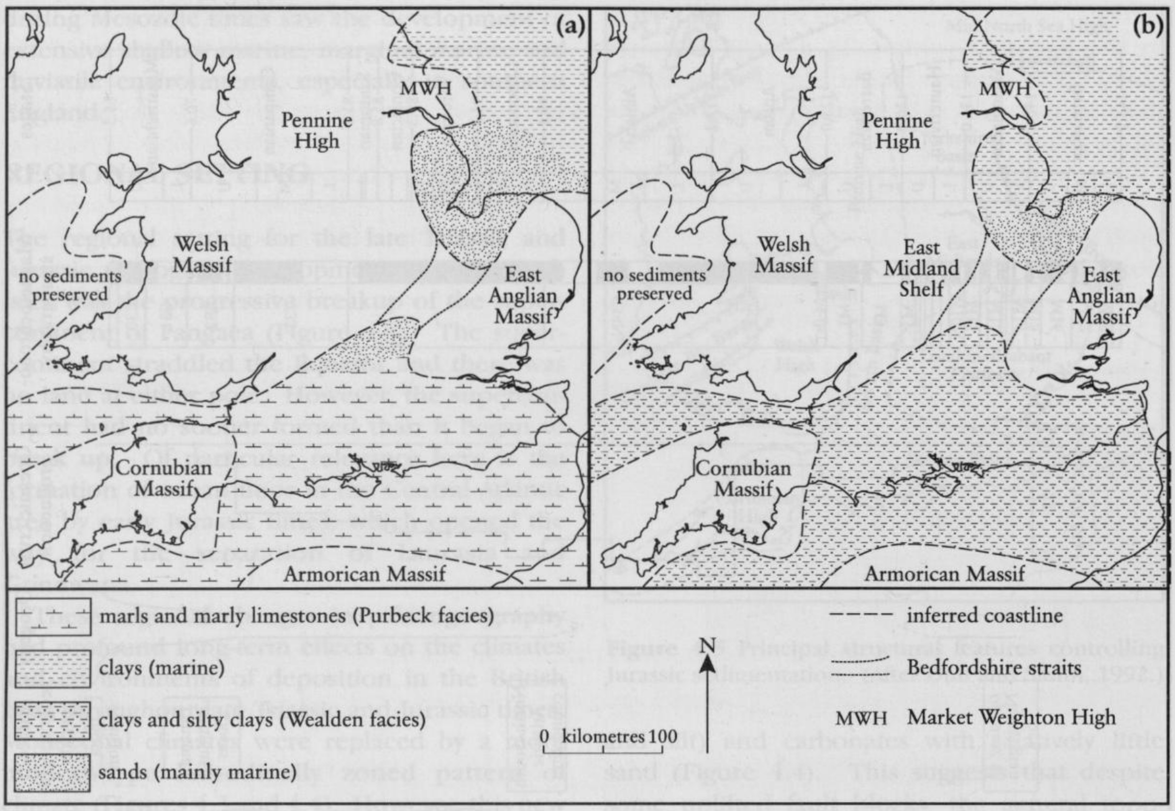


Figure 4.7 Early Cretaceous palaeogeography of southern England during (a) Upper Berriasian and (b) mid-Hauterivian times. (After Rawson, 1992.)

and South Atlantic was established by late Albian times at the end of the Early Cretaceous Epoch (Figures 4.7 and 4.11).

Since there are no fossil arthropod GCR sites subsequent to Barremian times in the British Early Cretaceous strata, geological developments within late Cretaceous times are of no particular importance here. However, the reason why there are no fossiliferous arthropod sites is of passing interest. A significant increase in the rate of production of ocean floor crust occurred between Aptian and early Campanian times (125–183 Ma ago, Figure 4.6) and has been interpreted as resulting from the rise of a mantle superplume in the Pacific Ocean. Associated increases in atmospheric carbon dioxide enhanced the Cretaceous greenhouse climate warming from the Barremian Stage onwards, reaching a maximum in the late Cenomanian times. In addition, there was an overall rise in sea-level that peaked in Turonian times. Consequently, there was a marine transgression and flooding of much of lowland Britain by shallow seas whose faunas were predominantly marine.

Climate and sea level

From latest Triassic through Jurassic times, the British Isles lay between 30° and 40° North (comparable to the Mediterranean today). The region straddled the boundary between a continuously dry 'megamonsoonal' and a more northerly climate with wet winters. The megamonsoonal climate was one of relatively dry high pressure influenced by powerful heating that was in turn induced by the large high latitude continental masses.

The late Triassic and Jurassic sedimentary sequences of the British Isles include excellent records of these changing climates from arid to humid and back to arid (see Figure 4.4). In particular, the return to arid conditions by latest Jurassic and earliest Cretaceous times is marked by the development of carbonates and evaporites (the Purbeck Group facies) in southern England.

Estimated palaeotemperatures for Jurassic times in the British Isles, based on oxygen-isotope studies of marine invertebrates, range between 12 and 29°C. The lack of high seasonal

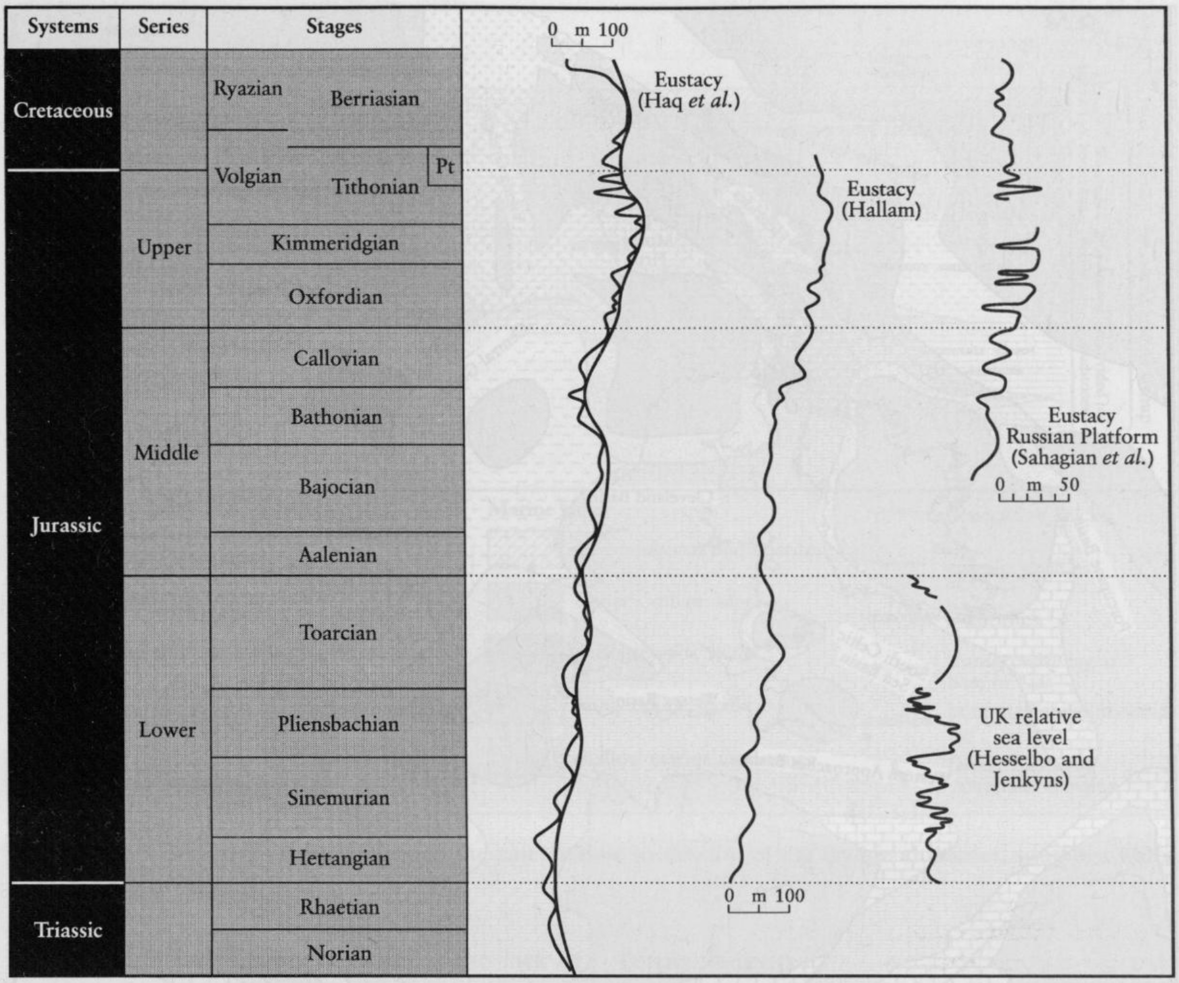


Figure 4.8 Global sea-level curves based on Jurassic Period sedimentary cycles. Pt: Portlandian. (After Haq *et al*., 1987; Hallam, 1996 and Sahagian *et al*., 1996.)

variation may be due to the ameliorating effect of shallow seaways in the region, although the persistence of mean annual tree-rings in Jurassic fossil wood suggests that, nevertheless, there were seasonal variations.

There is good evidence for a general increase in global sea levels throughout the Jurassic Period (Figure 4.8) with a long-term rise in the order of 100 m. However, in detail there is also evidence for a stillstand or even a slight fall in mid-Jurassic (Bajocian–Bathonian) times in north-west Europe. The lack of evidence for any significant volume of polar ice through the period suggests that the rise in sea level is due to increasing rates of production of oceanic crust during the break-up of Pangaea. There were also a number of short-term eustatic changes with rises during early Toarcian, Sinemurian, Pleinsbachian, Bajocian, Callovian and Tithonian times and marked falls in the late Rhaetian, late Sinemurian, Aalenian, early Oxfordian and mid Tithonian (Figure 4.8).

By Cretaceous times, the Earth was entering a 'greenhouse phase' of global warming. There were low thermal gradients between the equator and the poles and an absence of polar ice at sea level. The warming began in Berriasian times and continued through the early Cretaceous (see Figure 4.6). There was a mid-Cretaceous (Cenomanian–Santonian) thermal high with the development of a mid-latitude arid zone across Europe. Sea levels also rose and reached a maximum in Cenomanian–Coniacian times. The contemporaneous widespread epeiric seas were marked by the deposition of a white carbonate coccolith ooze now referred to as 'chalk'.

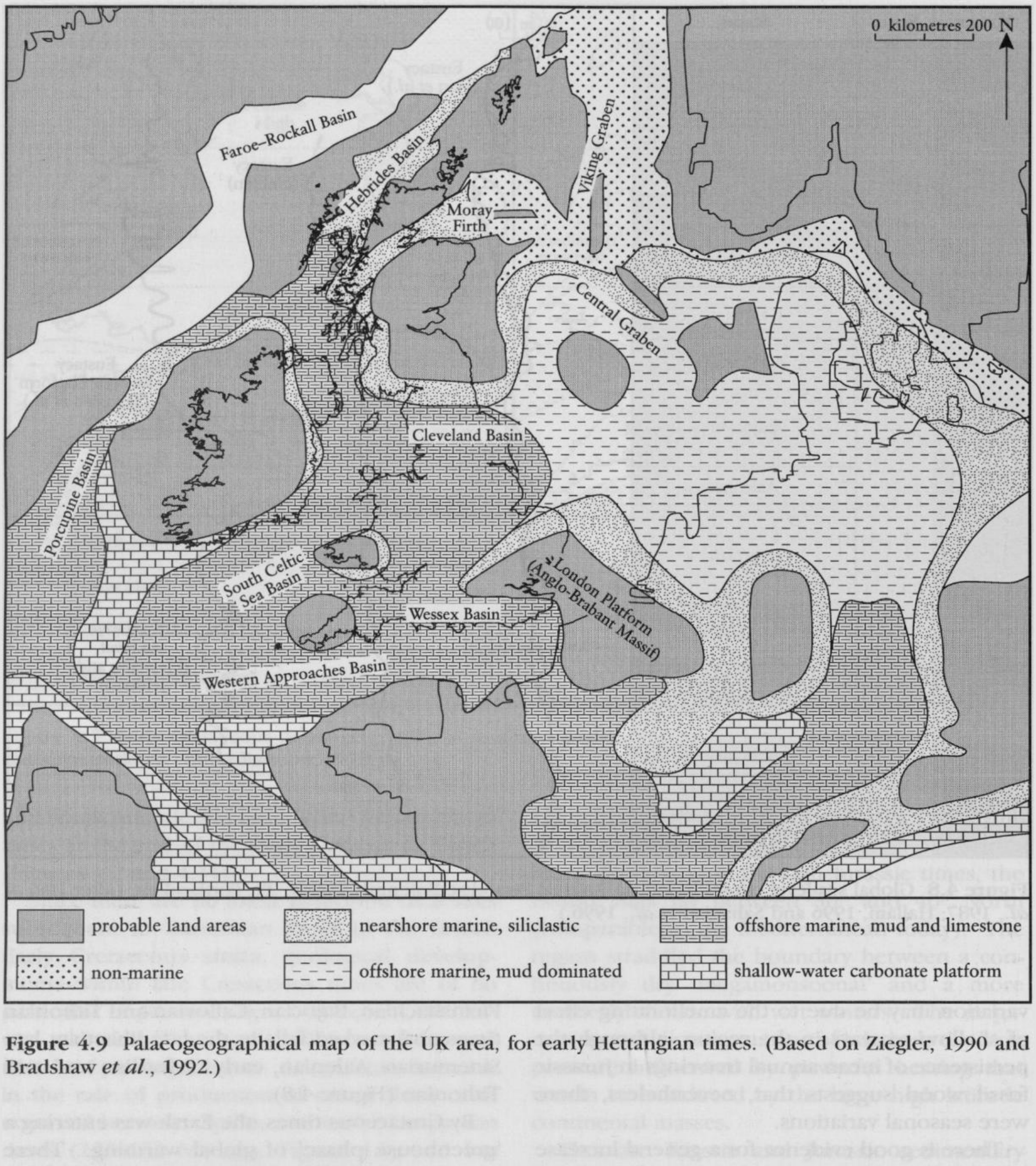


Figure 4.9 Palaeogeographical map of the UK area, for early Hettangian times. (Based on Ziegler, 1990 and Bradshaw *et al.*, 1992.)

Sedimentation – Late Triassic (Rhaetian) to earliest Cretaceous (Berriasian) times

Study of sedimentary basins in the south and west of Britain shows that there was rapid subsidence in early Jurassic times, probably associated with rifting along the northern margin of the Tethys Ocean. Borehole records in southern Britain also demonstrate thickening of Jurassic strata across major fault zones such as the Isle of Wight–Purbeck system in the Wessex Basin. Offshore in the North Sea and Cardigan Bay basins, seismic reflection data commonly show lateral changes in thickness that result from differential subsidence across faults in Jurassic times which are closely associated with crustal extension. The Lower Jurassic strata of Cardigan Bay alone accumulated a thickness of 2.5 km, the thickest yet discovered in the British Isles which suggests that there must have been significant seafloor topography.

Elevated land areas undoubtedly existed during late Triassic and early Jurassic times but their

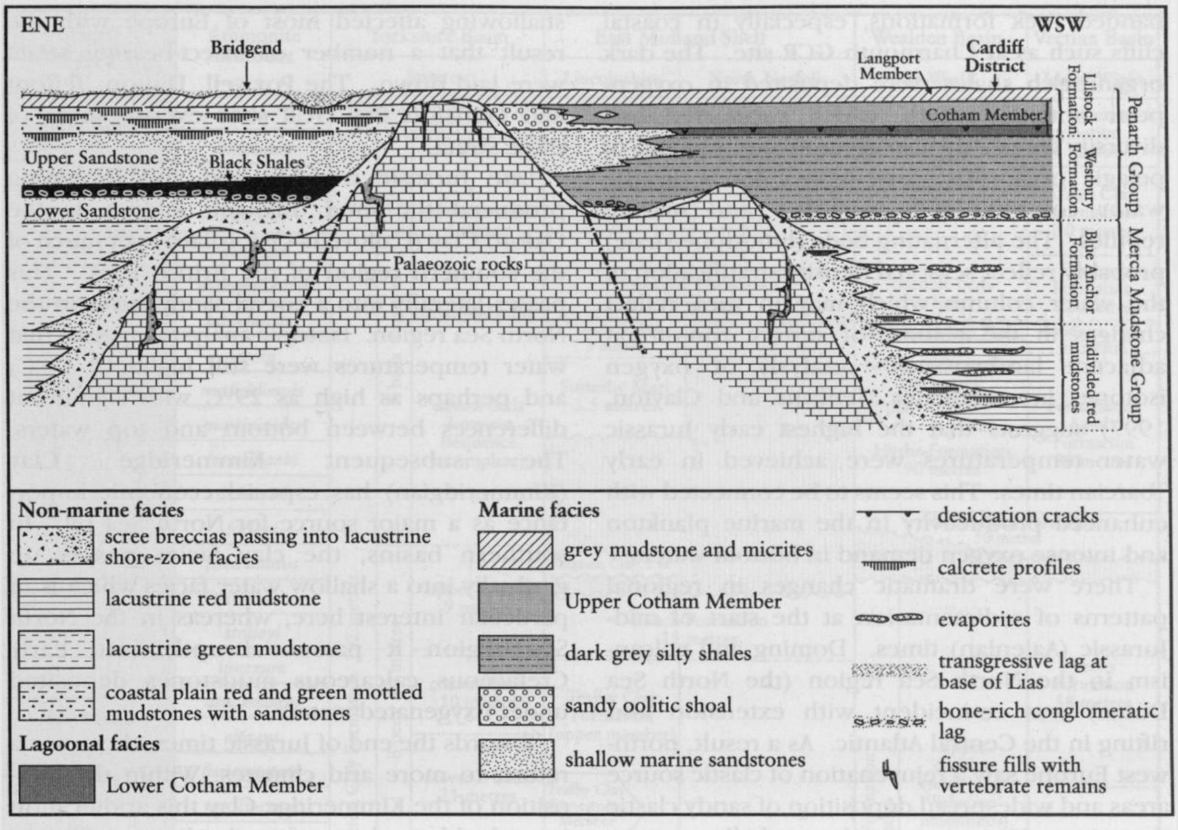


Figure 4.10 Schematic section through the Late Triassic succession of the Bridgend district, southern Wales. (After Wilson *et al.*, 1990.)

extent is unclear largely because of the lack of coarse clastic sediments which would have fringed their coasts. The best-established is the western end of the Anglo-Brabant landmass (also known as the 'London Platform', see Figure 4.9) across which there was a progressive onlap of Lower Jurassic strata. There is also evidence of an uplifted elongate island that marked the northern margin of the Bristol Channel Basin.

Initiation of the latest Triassic passage from non-marine to marine deposition is well preserved in strata exposed today in south-west England and southern Wales (see Figure 4.10). The uppermost strata of the Mercia Mudstone Group are argillaceous red beds with minor coarse-clastic deposits denoting the proximity of an uplifted shoreline. Sulphate evaporites that were deposited in coastal sabkhas bordering hypersaline marine waters are present. A northward expansion of the marine waters is marked by a thin black shale unit known as the 'Westbury Formation' (see GCR site report for Aust Cliff) which is a basal unit within the Penarth Group.

Deposition of the black shales is a precursor to the more-persistent, Jurassic age, organic shales. The formation contains reworked vertebrate and invertebrate fossils of both marine and non-marine origin. In the Bristol area marine deposition was initially in shallow lagoons in which a stromatolite horizon developed (the Cotham 'Marble'). Alternations from brackish through normal marine to hypersaline waters are marked by interbedded sequences of different faunas and floras. Occasional regression and exposure is marked by mudcracked bedding planes. There are also adjacent fissure deposits containing important late Triassic vertebrate remains (reptiles and early mammals, mostly small teeth) which are preserved within Carboniferous limestones.

Mudstone deposition was widespread by early Jurassic (Hettangian–Sinemurian) times with interbedded marls, shales and carbonate muds forming the Blue Lias facies. The rhythmic alternation on a decimetre scale of dark shale and pale-coloured limestones produces strikingly banded rock formations, especially in coastal cliffs such as at Charmouth GCR site. The dark organic-rich shales were deposited in oxygen-poor bottom waters, which supported low diversity faunas but also accumulated remains of pelagic organisms from higher levels in the water column, such as fishes and marine reptiles. The alternating beds (limestone/shale) probably reflect seasonal density stratification of the water column which may in turn reflect changes in the volume of surface run-off on adjacent landmasses. Analysis of oxygen isotopes in carbonates (Jenkyns and Clayton, 1997) suggests that the highest early Jurassic water temperatures were achieved in early Toarcian times. This seems to be connected with enhanced productivity in the marine plankton and intense oxygen demand in bottom waters.

There were dramatic changes in regional patterns of sedimentation at the start of mid-Jurassic (Aalenian) times. Doming and volcanism in the North Sea region (the North Sea Dome) was co-incident with extension and rifting in the Central Atlantic. As a result, north-west Europe saw a rejuvenation of clastic source areas and widespread deposition of sandy clastic deposits. However, southern shallow water areas developed carbonate platform areas instead of siliciclastic shoreline deposits (especially during Aalenian through Bajocian to Bathonian times). They were marked by the deposition of oolitic and bioclastic limestones with intermittent quieter water lagoonal mud deposition. Cross-bedding, sometimes up to a metre or so in amplitude, indicates strong tidally swept seas and perhaps intermittent storm activity. These strata probably reflect sediment-starved environments of deposition which lay beyond the reach of siliciclastic shoreline deposits derived from the North Sea Dome.

There were further significant changes in palaeogeography at the end of mid-Jurassic times largely brought about by a steady rise in sea level that drowned paralic sedimentary environments. A major marine transgression, marking the Bathonian–Callovian boundary, swept across much of Britain and Ireland (see GCR site report for Stonesfield). Marine mudstones were deposited over a wide area with interbedded marine sands which were commonly glauconitic. The subsequent deepening of late Jurassic times meant that no significant arthropod related faunas were fossilized during this latter interval. However, a subsequent Volgian shallowing affected most of Europe with the result that a number of insect-bearing strata were laid down. The Poxwell, Dinton, Teffont and Durlston Bay GCR sites expose some of these strata.

Late Jurassic transgression and drowning produced the mud 'blanket' known as the Oxford Clay (Callovian–Oxfordian) over much of the southern region of the British Isles. This passes laterally into a coeval sandy facies in the North Sea region. Isotopic analysis suggests that water temperatures were still high (12–19°C) and perhaps as high as 29°C with significant differences between bottom and top waters. The subsequent Kimmeridge Clay (Kimmeridgian) has especial economic importance as a major source for North Sea oil. In southern basins, the clay facies passes up gradually into a shallow water facies which is of particular interest here, whereas in the North Sea region it passes abruptly into early Cretaceous calcareous mudstones deposited under oxygenated waters.

Towards the end of Jurassic times, there was a return to more arid climates. Within the deposition of the Kimmeridge Clay this aridification is marked by a change from kaolinite to illite as the dominant clay mineral within the clay-rich facies. In southern England the mudstones give way to the carbonates of the Portland Group strata of Tithonian age. They are oolitic and bioclastic carbonates along with finer-grained dolostones that famously have been used for high-quality monumental building material. Above lie interbedded limestones and shales of the Purbeck Group, which were deposited within lagoons that suffered phases of high evaporation. This environment led to the deposition of some evaporite horizons with minerals such as halite, gypsum, anhydrite and celestite. Significant volumes of salt-rich (haliferous) evaporites were laid down in the area, which now lie in the Porcupine Basin off south-west Ireland.

In southern England, the existence of silicified gymnospern trees within the Purbeck Beds (especially within the 'Dirt Beds', see Cleal and Thomas, 2001 p. 109 ff) of Portland has long been known. More recently, analysis of the growth rings has suggested that there were marginal and variable Mediterranean-type climates with warm wet winters and hot dry summers. It has also been suggested (Francis, 1984) that the growing season was sometimes interrupted by significant dry spells that pro-

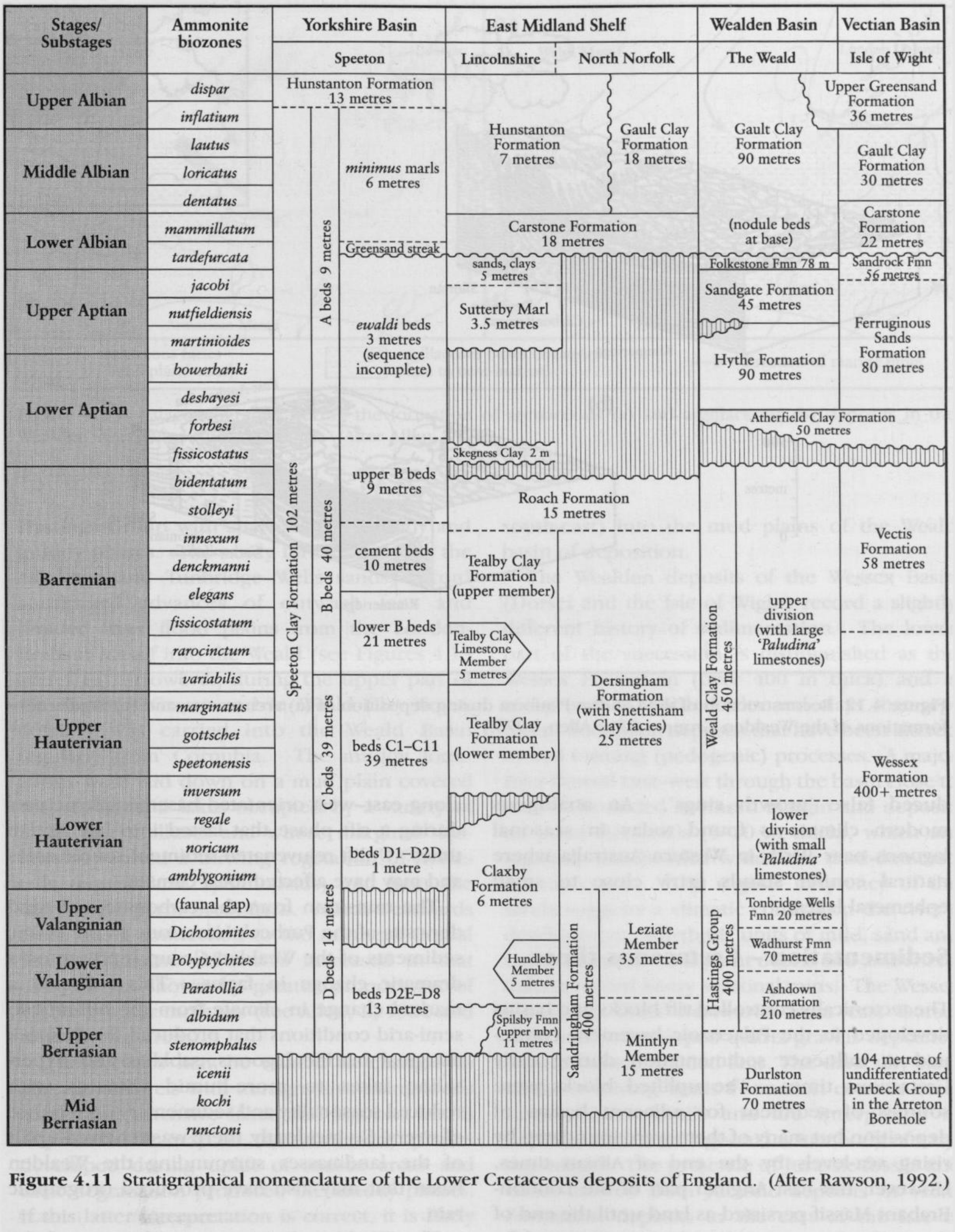


Figure 4.11 Stratigraphical nomenclature of the Lower Cretaceous deposits of England. (After Rawson, 1992.)

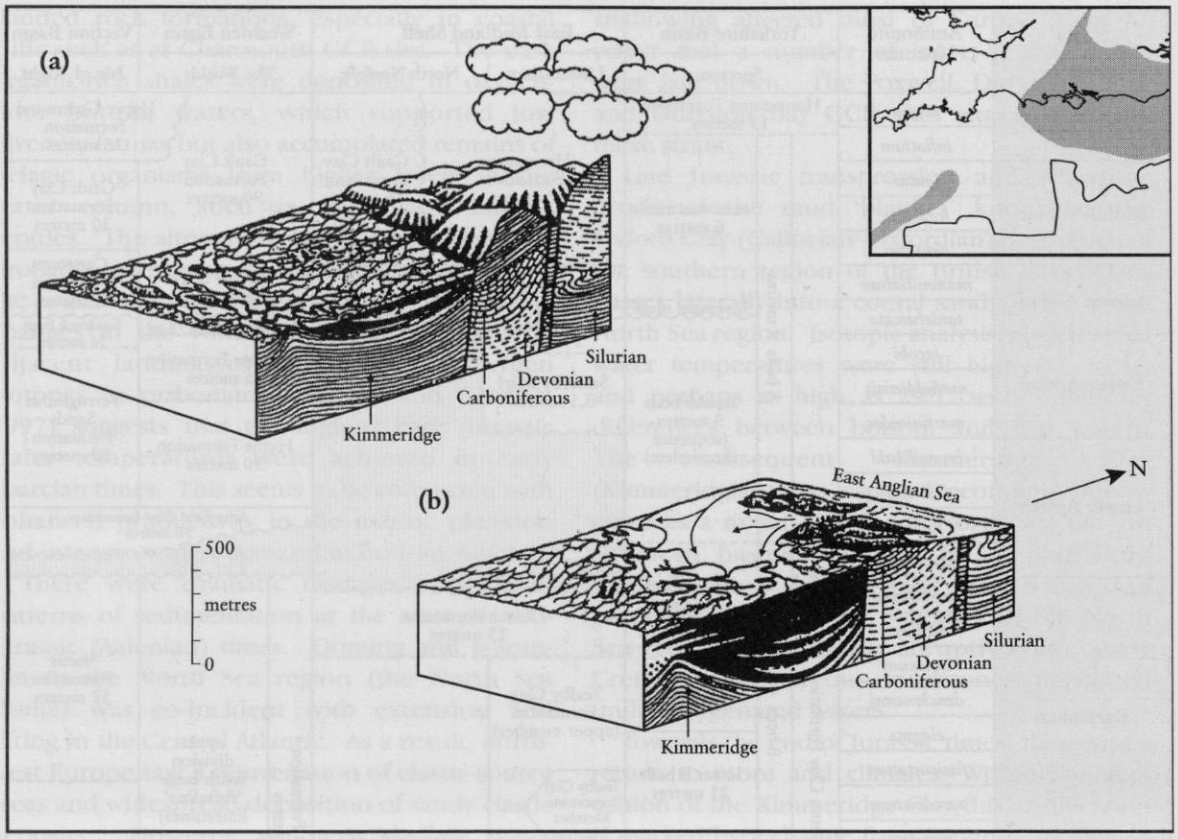


Figure 4.12 Reconstruction of the London Platform during deposition of (a) arenaceous, and (b) argillaceous formations of the Wealden Group. (After Allen, 1975.)

duced false 'growth rings'. An analogous modern climate is found today in seasonal lagoons near Perth in Western Australia where natural conifer stands grow close to small ephemeral lakes.

Sedimentation – Cretaceous times

The tectonically controlled rift blocks and basins developed in the Palaeozoic basement continued to influence sedimentation during early Cretaceous times. The uplifted blocks were sources of sediment for adjacent basins of deposition but many of them were inundated by rising sea-levels by the end of Albian times. However, the East Anglian part of the London-Brabant Massif persisted as land until the end of the Early Cretaceous Epoch (see Figure 4.7). The Cornubian Massif of south-west England and the East Midlands Shelf persisted as a landmass into late Cretaceous times.

Southern England's early Cretaceous structural history was marked by occasional movement along east–west orientated basement structures during a rift phase that lasted into late Aptian times. Uplift rejuvenated sediment source areas and may have affected local climate.

The transition from the carbonate and mud deposits of the Purbeck Limestone to the clastic sediments of the Wealden Group represented a dramatic change in facies. This reflected a marked change in climate from the hot-arid to semi-arid conditions that produced the Purbeck marginal marine lagoons, sabkhas and hypersaline lakes to more-humid climates with reduced seasonality and sedimentary dominance of rivers. Co-incidently, there was renewed uplift of the landmasses surrounding the Wealden basin that may also have produced orographic rain.

The Wealden Supergroup sediments of the Weald area in southern England are subdivided into a lower Hastings Group (*c.* 400 m thick, see Figure 4.11) and a finer-grained, mud-dominated, upper Weald Clay Group (*c.* 450 m thick). There are three major sedimentary cycles in the

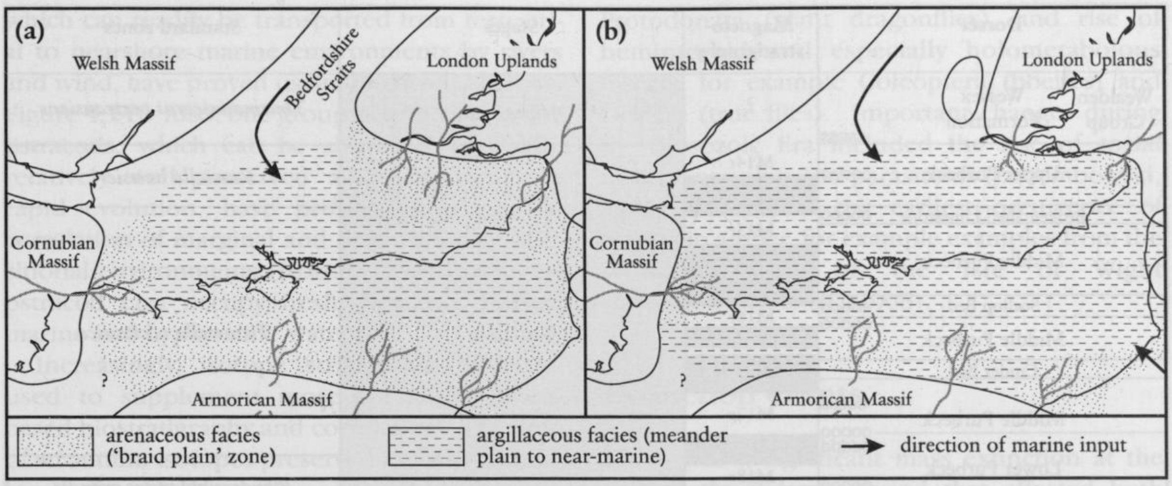


Figure 4.13 Palaeogeography during the formation of arenaceous (a) and argillaceous (b) deposits in the Wealden strata of southern England. (After Allen, 1975.)

Hastings Group with alternations of sandy and muddy phases. The sandy formations (e.g. the Ashdown and Tunbridge Wells sands) record southward advances of outwash fans and braided river flood plains from the London-Brabant Massif into the Weald (see Figures 4.13 and 4.14). However, during the upper part of the Hastings Group and in Weald Clay times, detritus was carried into the Weald Basin regularly from Cornubia. The muddy formations were laid down on a mud plain covered with ephemeral lakes occupied by a variety of freshwater molluscs and whose marginal shallows supported a thriving vegetation of horsetails (equisitalean sphenopsids) and later the early angiosperm *Bevhalstia*. North-westwards there was a connection to the northern Boreal Sea and marine influences increased in that direction as shown by greater proportions of brackish water molluscs (see Allen, P., 1981 and references therein).

These cycles may be related to changes in eustatic sealevels with transgressive rising levels generating extensive lakes and lagoons but is unproven. It may be that the sandy phases developed during uplift of source areas and their degradation produced the muddy phases. If this latter interpretation is correct, it is likely that the mud-dominated Weald Clay Group developed when the London-Brabant massif was in its most eroded and degraded state. A number of near-marine horizons are present in the Weald Clay, representing incursions from the Boreal Sea (in the north) and Tethys (lying to the south-east) into the mud plains of the Weald basin of deposition.

The Wealden deposits of the Wessex Basin (Dorset and the Isle of Wight) record a slightly different history of sedimentation. The lower part of the succession is distinguished as the Wessex Formation (over 400 m thick) and is comprised of mottled silts and clays that represent floodplain deposits that have been altered by soil forming (pedogenic) processes. A major river flowed east–west through the basin close to its fault-bounded northern margin and deposited point bar sands (5–10 m thick), which are regularly interbedded within the mud-dominated succession. The regular frequency of the sands suggests a climatic control on the river's development. Rhythmic units of mud, sand and coarser detritus with plant debris and amberized insects record heavy seasonal rains. The Wessex Formation thins westwards from east Dorset with locally developed quartz gravels deposited from proximal braided fans. The dark silty clays of the overlying Vectis Formation contain occasional insect fossils and are interpreted as deposits of a large lagoonal water body of varying salinity. The presence of Jurassic fossils and clasts derived from Jurassic deposits in Vectis Formation deposits in the east of the Isle of Wight suggests a source in Cornubia to the west and perhaps Armorica to the south. According to Radley (2005) these fossils are probably derived in the main from scarps along the Purbeck/Isle of Wight structure just to the north of the present Wealden outcrop.

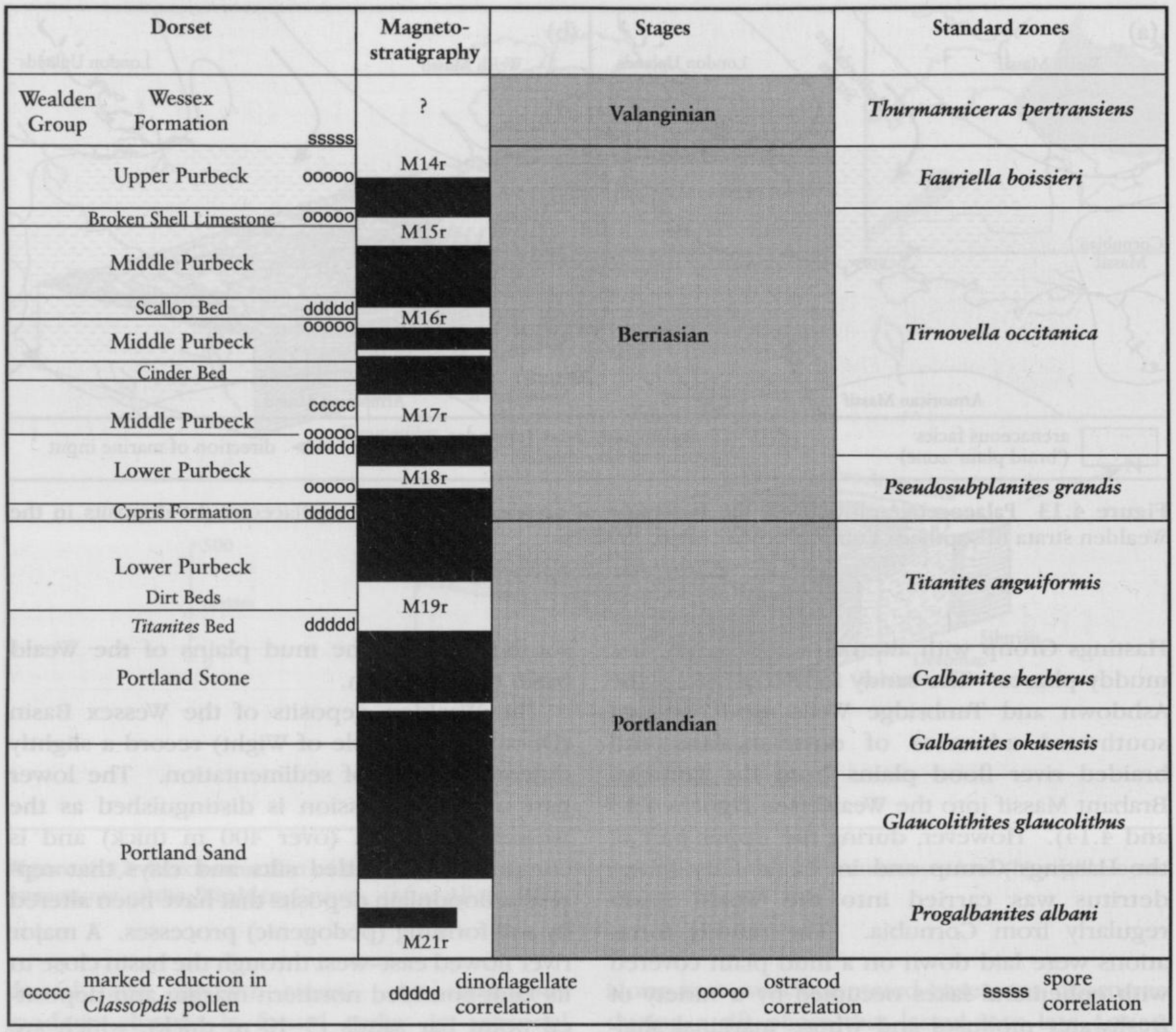


Figure 4.14 Summary of the Jurassic–Cretaceous boundary interval in Dorset. (After Ogg *et al.*, 1995.)

Correlation

Jurassic strata have had a basically stable system of subdivision into stages with groupings into Lower, Middle and Upper since the mid 19th century when it was first introduced by d'Orbigny (1850). Biostratigraphical zonation has been developed using changes in marine ammonite faunas which were first recognized around the same time in German Jurassic strata by Oppel (1857). Ammonite biostratigraphy was subsequently also successful in helping subdivide Cretaceous strata (see Figure 4.11). The relative abundance, wide distribution, rapid evolution, ease of recognition and preservability of ammonite fossils has made them particularly useful as biozonal indicators. Subdivision is now so well developed that the average duration of an ammonite biozone is about one million years. In some instances, biostratigraphical resolution may be as fine as 70 ka.

However, ammonites are not always common in all parts of the Cretaceous succession and other biozonal indices have proved more useful. Recently, complementary biozonal schemes based on microfossils have been developed, especially calcareous nannofossils (coccoliths). The schemes are especially important for the correlation of borehole information where macrofossils such as ammonites are not always recognizable. Of importance here is the problem of correlation between marine and terrestrial facies and the potential difficulties introduced by diachroneity of marginal facies between marine and terrestrial deposits, especially when sea levels are changing. Plant spores and pollen, which can readily be transported from terrestrial to nearshore marine environments by rivers and wind, have proved useful in correlation (see Figure 4.14). Also, one group of arthropods, the ostracods, which can be abundant as fossils, relatively well preserved and with relatively rapid evolution, have proved useful in the correlation of marginal and diachronously transitional environments (Horne, 1995). Different ostracod taxa occupy fresh, brackish, normal marine and hypersaline waters.

Increasingly, isotope stratigraphy is being used to supplement more traditional fossil-based biostratigraphy and correlation. The ratio of strontium isotopes preserved in fossil carbonate shells varies over time and records the radiogenic strontium composition of the seawater the organisms lived in. The ratio of ^{87}Sr to ^{86}Sr, is relatively high in strontium derived from the weathering of continental rocks, and relatively low in strontium derived from mantle sources such as mid-ocean ridge lavas. Strontium isotope composition curves have been developed from analysis of strontium ratios in biostratigraphically well-constrained Jurassic oyster and belemnite shells and show distinctive changes between early, mid and late Jurassic times. The early ratios reflect the dominance of rifting processes whereas the late ratios show increased rates of ocean-floor magmatism. Analysis of carbon isotopes is also proving useful, especially as there have been significant short term perturbations of ^{12}C to ^{13}C ratios in ocean waters (see Figure 4.6). These are due to rapid changes in the burial and release of light carbon derived from organic matter and are recorded as carbon isotope excursions in both carbonate fossil shells and organic fossil carbon.

Arthropods in Mesozoic times

The transition from the Permian to the Triassic periods is an important point in arthropod evoution, despite the lack of Permo-Triassic insects in Great Britain (Aust Cliff GCR site excepted), because the Permian/Triassic extinction is the most significant one in insct evolutionary history (Jarzembowski, 2005), Contrasting entomofaunas such as those from Writhlington Rock Store and Aust Cliff, however, show the significant changes. These changes include the disappearance of various palaeopterous insects such as Palaeodicytopteroidea Protodonata (giant dragonflies), and rise of hemipteroid and especially holometabolous insects, for example Coleoptera (bbetles) and Diptera (true flies). Important changes during the Mesozoic Era included the rise of social insects, parasites and parasitoids (Jarzembowski, 1981) as well as the earliest occurrence of insects in amber, for example examples from the Wealden strata of the Isle of Wight (Jarzembowski *et al.*, 2008).

Extinction events

There was a significant mass extinction at the end of the Triassic Period that affected both marine and terrestrial organisms, but there is little evidence that the insects were significantly reduced in abundance or diversity. Some Palaeozoic groups that had survived the Permo-Triassic boundary extinction finally became extinct (conodonts and strophomenid brachiopods). Although there is evidence that the extinction may have been rapid (i.e. within a stratigraphical resolution of *c.* 40 000 years) and catastrophic, there is, as yet, no evidence for any impact associated debris in Triassic–Jurassic boundary sediments. The Rhaetian sequence of the Bristol Channel Basin has been carefully searched for such evidence but to no avail so far. The outpouring of extensive flood basalts associated with the opening of the Central Atlantic Ocean is a more likely cause but the evidence for link is still largely circumstantial.

AUST CLIFF, AVON
(ST 565 895)

Introduction

Aust Cliff, at the eastern end of the Severn Road Bridge, is famous for its excellent exposure of Rhaetian and Liassic strata (*c.* 200 Ma) between the Upper Triassic and Lower Jurassic. From this cliff and foreshore exposure (Figures 4.15 and 4.16), first described by Buckland and Conybeare (1824), a prolific fossil biota has been obtained over the intervening years. Some fossil elements have attained international importance such as the reptiles and fishes. Accompanying the vertebrates is an abundant invertebrate fauna that also includes a nationally important

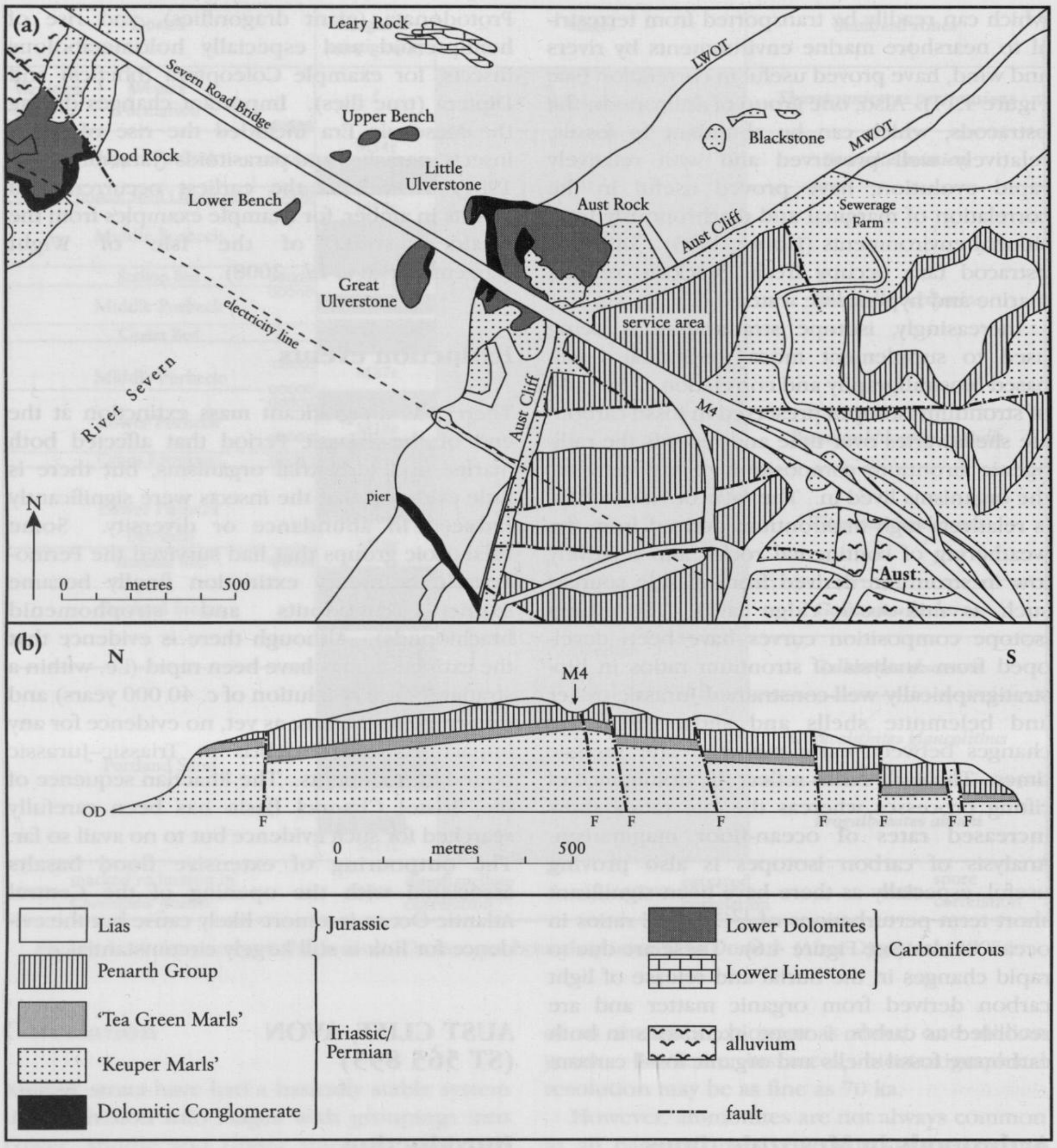


Figure 4.15 Triassic and Jurassic strata at Aust Cliff (a) geological map, and (b) the broad anticlinal structure. (After Hamilton, 1977.)

and diverse insect fauna. The constant erosion of the site produces new exposures and fossiliferous material from cliff falls on the foreshore, creating a considerable potential for new finds. In addition to the fossil arthropod importance of this site, the area is also independently selected for the GCR for the Permian–Triassic, Permian-Triassic Reptilia and Rhaetian selection categories.

Description

The Aust Cliff section is an eroded and truncated NW–SE-trending anticlinal ridge of Triassic and Lower Jurassic strata cut by a series of small faults downthrowing to the south. The folding and faulting have been explained by compaction and thermal subsidence of the Triassic age Mercia Mudstone following Permo-Triassic

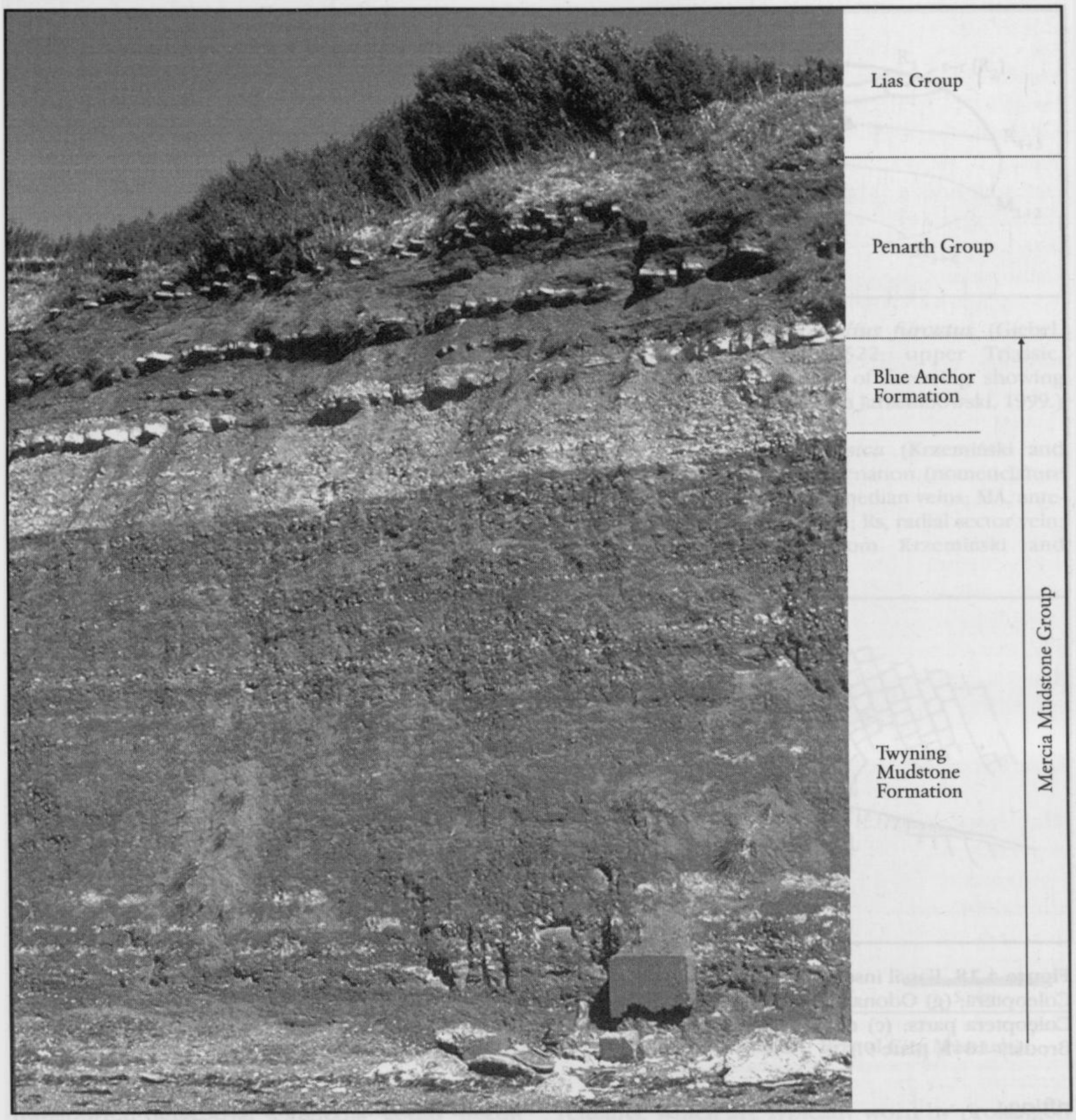


Figure 4.16 Aust Cliff: view on the north-eastern side of the Severn Bridge, looking south-east. (Photo: Andrew Swift.)

			Thickness (metres)
Jurassic	Lower Lias	Blue Lias (Hettangian)	(variable)
		planorbis Beds	
		pre-*planorbis* Beds	(variable)
Penarth Group		Lilstock Formation	*c.* 3.40
		Westbury Formation	*c.* 4.30
Mercia Mudstone Group		Blue Anchor Formation	*c.* 7.0
		red mudstones	*c.* 30.0
Carboniferous		Carboniferous Limestone	(variable)

Figure 4.17 A representative section for Aust Cliff. The Penarth Group and Mercia Mudstone Group are Triassic in age. (After Warrington *et al.*, 1980.)

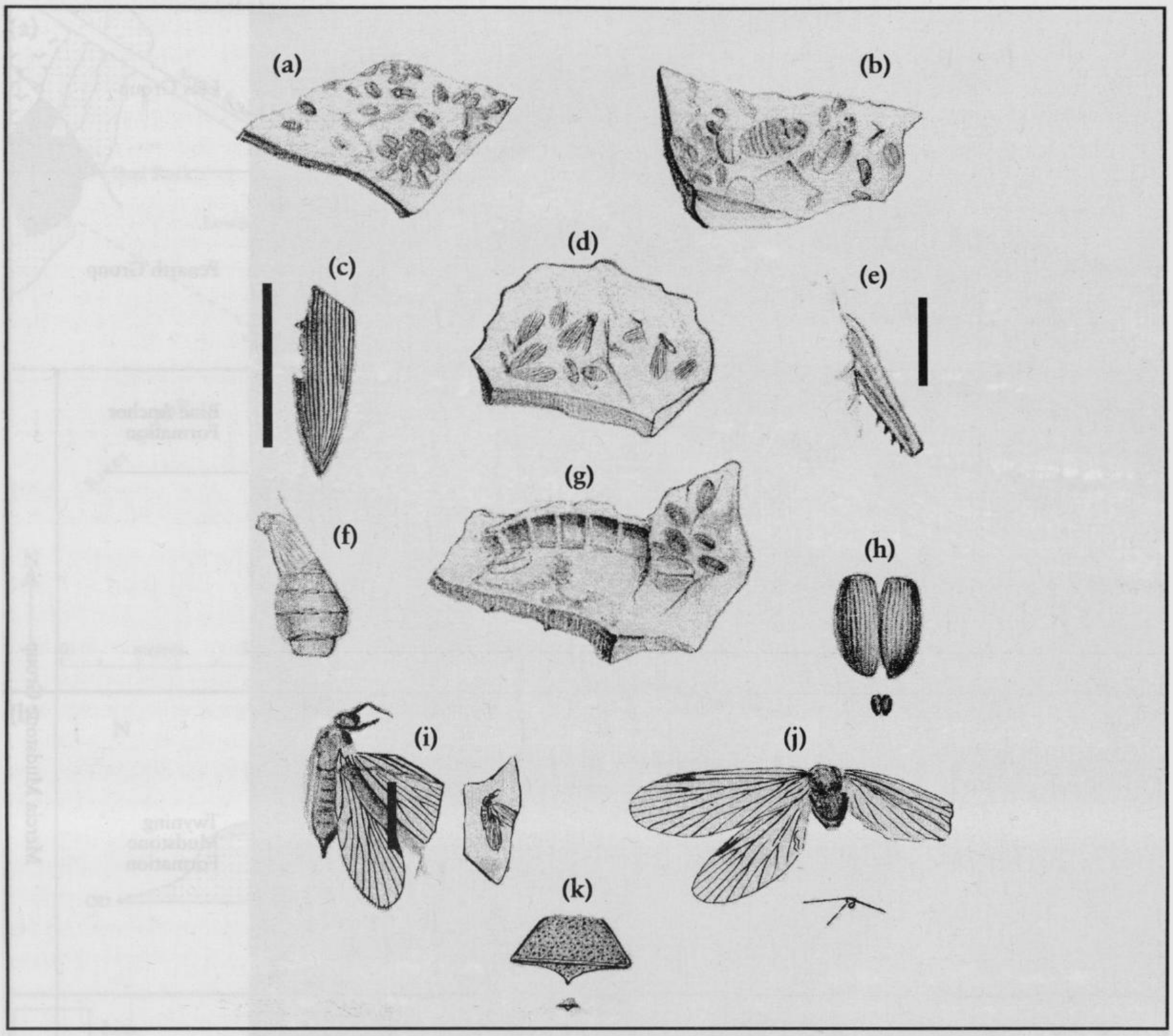
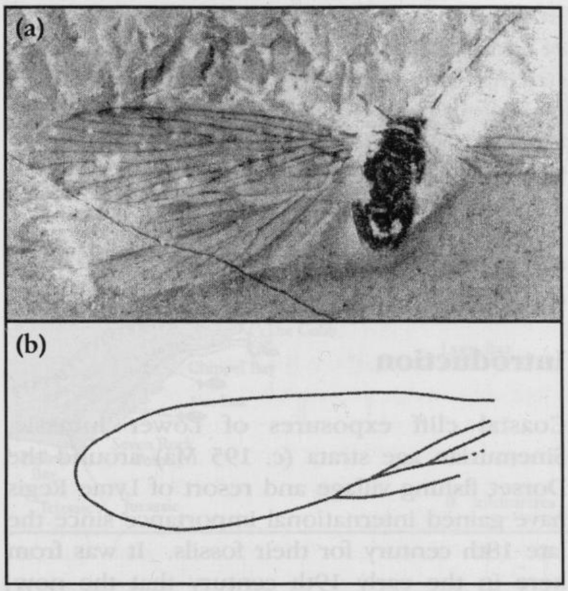


Figure 4.18 Fossil insects from the Lias and Trias of Aust Cliff. (a, b) Coleoptera; (d) Amphiesmenoptera and Coleoptera; (g) Odonata and Coleoptera; (h) *Hydrobiites giebeli* (Rhaetian).
Coleoptera parts: (c) elytron; (f) abdomen; (k) thorax; (e) Orthoptera leg; (i, j) Amphiesmenoptera. (From Brodie, 1845, plate 9.)

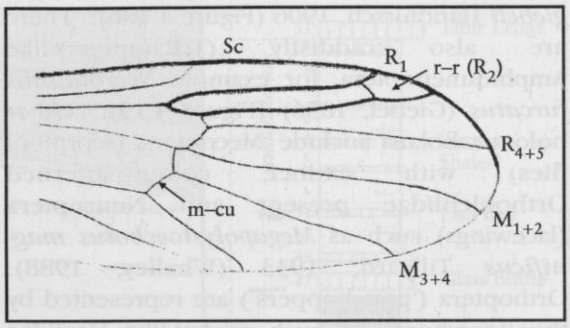
rifting.

The Mesozoic cliff succession lies with angular unconformity upon gently folded Carboniferous Limestone that dips at 15° to the south-west. Triassic age mudrocks belonging to the Mercia Mudstone Group include Red Mudstones overlain by the 'Tea Green Marls' of the Blue Anchor Formation (Figure 4.17). Above lie the grey shales and limestones of the Triassic age Penarth Group (including the Rhaetian strata) followed by more limestones and shales of the lowest Blue Lias of early Jurassic (Hettangian) age.

Fossil insects occur sporadically in the various limestone developments in the Rhaetian Penarth Group and are occasionally concentrated at certain horizons (Figure 4.18 g,h,i). The main source of specimens is the distinctive strata of the Cotham Member, including the Cotham Marble (Lower Lilstock Formation). Insects in these beds are often associated with freshwater ostracods, conchostracans (clam shrimps) and sometimes the aquatic liverwort *Naiadita lanceolata* Buckman, 1850 [emend. Harris]; rarer marine elements (vertebrates and molluscs) may also be present (Jarzembowski, 1999). The environment in which these insects were fossilized was paralic with land to the west of the Severn Valley (supplying rare charcoal) and probably consisted of marginal freshwater, brackish lagoonal or estuarine areas where mixing of freshwater, marine and blown-in or otherwise



◂**Figure 4.19** (a) *Necrotaulius furcatus* (Giebel, 1856); adult BMNH I 11522; upper Triassic, Gloucestershire. (b) Outline of forewing showing looped anal veins × 6. (From Jarzembowski, 1999.)



▴**Figure 4.20** *Aenne triassica* (Krzemiński and Jarzembowski, 1999). Wing venation (nomenclature of veins: Cu, cubital veins; M, median veins; MA, anterior median vein; R, radial vein; Rs, radial sector vein; Sc, subcostal vein). (From Krzemiński and Jarzembowski, 1999.)

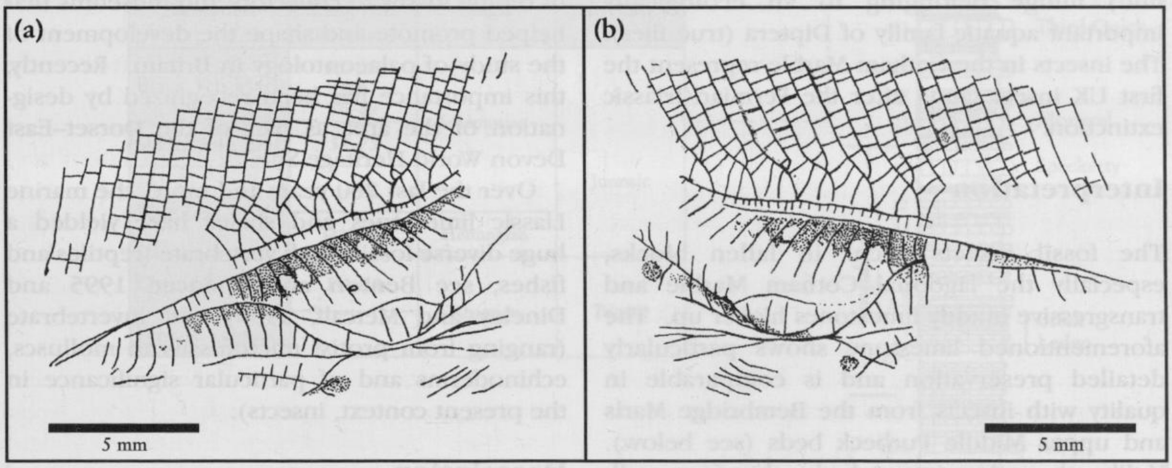


Figure 4.21a,b Male forewing of undescribed haglid by Paul Stevenson (AST4, Bristol City Museum).

transported terrestrial elements could occur. Succeeding Lias Group beds have yielded a richer entomofauna and at least some of this material from basal levels has been considered of Rhaetian age.

Fauna

Aust Cliff is world famous for its exposures of Rhaetian near-shore marine bonebeds and the diversity of fossils they contain. The site is Britain's most prolific locality for fossil reptiles of Rhaetian age, yielding important collections of both marine and terrestrial reptiles. Most of the reptile fossils are of marine ichthyosaurs and plesiosaurs but some rare terrestrial dinosaur remains, which are typically worn by prolonged transport, have also been found (see Benton and Spencer, 1995, p. 75 *et seq*.). In addition, the site has as yielded abundant and diverse fish remains including those of hybodont sharks, actinopterygians and lungfish (see Dineley and Metcalf, 1999, p. 342ff).

The most distinctive insect fossil remains are wings, usually forewings, although bodies and body parts also occur. Fossils range in size from a few millimetres to several tens of millimetres long. At least nine major groups (orders) of insects are represented at Aust Cliff. The insects occur in fallen blocks from the top of the cliff. Coleoptera (beetles) are the commonest insects, especially elytra, for example, *?Hydrobiites* *giebeli* Handhirsch, 1906 (Figure 4.18h). There are also caddisfly (Trichopters)-like Amphiesmenoptera, for example *Necrotaulius furcatus* (Giebel, 1856) (Figure 4.19). Other holometabolans include Mecoptera (scorpionflies) with extinct, colour-patterned Orthphlebiidae present and Neuroptera (lacewings) such as *Megapolystoechotus magnificus* Tillyard, 1933 (Whalley, 1988). Orthoptera ('grasshoppers') are represented by the 'long-horn' or bush cricket-like Haglidae (Figure 4.21). Other non-holometabolans recorded are Blattodea (cockroaches), Odonata (dragonflies) and Hemiptera (bugs).

Aust Cliff provided material during the pioneer phase of Mesozoic palaeoentomology (Brodie, 1845). It is still producing significant new finds, for example *Aenne triassica* Kzremiński and Jarzembowski, 1999 (Figure 4.20) currently the earliest non-biting (chironomid) midge belonging to an ecologically important aquatic family of Diptera (true flies). The insects in the Cotham Marble represent the first UK insect fauna after the Permian/Triassic extinction.

Interpretation

The fossil insects occur in fallen blocks, especially the lagoonal Cotham Marble and transgressive muddy limestones higher up. The aforementioned limestone shows particularly detailed preservation and is comparable in quality with insects from the Bembridge Marls and upper Middle Purbeck beds (see below). Unlike the other insect beds, this is a well-marked horizon. At present, disarticulated remains can be found, but historical data (Brodie, 1845) shows that richer concentrations can be exposed due to the continuing erosion of the cliff line. The insects provide data for the end-Triassic extinction and early Mesozoic radiation and recovery after the Permian–Triassic mass extinction.

Conclusion

The conservation value of this site is based on several aspects of its geology and palaeontology, especially the fishes, reptile and insect fossils. The insect fauna obtained from Rhaetian and earliest Jurassic strata (late Triassic–early Jurassic, *c.* 201 Ma) here is of national importance. This is the most productive site in Britain for Rhaetian–earliest Hettangian insects of which scorpionflies (mecopterans) are most striking, with some of the fossils preserving original colour patterning. Furthermore, the site has considerable potential for significant finds of fossil insects in the future.

CHARMOUTH–PINHAY BAY, DORSET (SY 359 931 AND SY 369 930)

Introduction

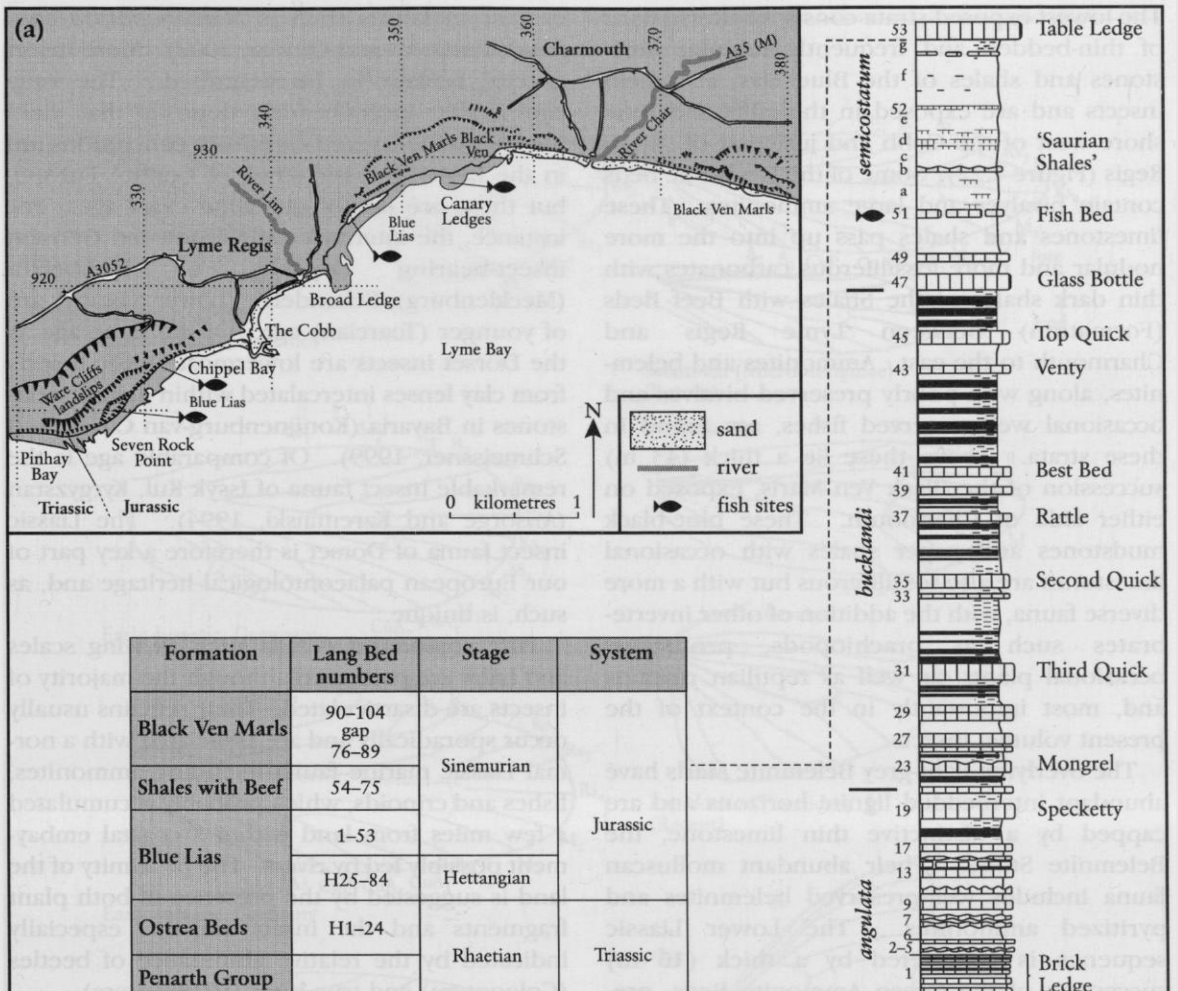
Coastal cliff exposures of Lower Jurassic, Sinemurian age strata (*c.* 195 Ma) around the Dorset fishing village and resort of Lyme Regis have gained international importance since the late 18th century for their fossils. It was from here in the early 19th century that the now-famous Anning family collected and sold a series of reptile fossils to collectors and museums that helped promote and shape the development of the study of palaeontology in Britain. Recently, this importance has been recognized by designation of the area as part of the Dorset–East Devon World Heritage Site.

Over the last 200 years and more, the marine Liassic limestones and shales have yielded a huge diverse fossils both vertebrate (reptiles and fishes, see Benton and Spencer, 1995 and Dineley and Metcalf, 1999) and invertebrate (ranging from protist microfossils to molluscs, echinoderms and of particular significance in the present context, insects).

Description

The abundance of ammonites within the Lower Liassic strata allowed the early application of Oppel's German biozonal scheme (Oppel, 1857) to the Lyme Regis sequence. Numerous detailed accounts have built on these early foundations (e.g. Lang and Spath, 1926), more recently by Getty (1980).

	Thickness (m)
unconformity	
Green Ammonite Beds	32
Belemnite Stone	0.15
Belemnite Marls	23
Armatus Limestone	0.4
Black Ven Marls	43
Shales with Beef Beds (Formation)	23
Blue Lias	27
Ostrea Beds (= Pre-planorbis Beds)	2.5



Formation	Lang Bed numbers	Stage	System
Black Ven Marls	90–104 gap 76–89	Sinemurian	
Shales with Beef	54–75		Jurassic
Blue Lias	1–53 H25–84	Hettangian	
Ostrea Beds	H1–24		
Penarth Group		Rhaetian	Triassic

Figure 4.22 (a) Map of the coastal outcrop of the Lower Lias, Charmouth to Lyme Regis (after Benton and Spencer, 1995); (b) rock succesion (after House, 1993).

The lowest exposed strata consist of alternations of thin-bedded and frequently nodular limestones and shales of the Blue Lias, also yield insects and are exposed in the cliffs and foreshore west of the Cobb and just east of Lyme Regis (Figure 4.22). Some of the limestone beds contain bivalves and large ammonites. These limestones and shales pass up into the more nodular and more fossiliferous carbonates with thin dark shales of the Shales with Beef Beds (Formation) between Lyme Regis and Charmouth to the east. Ammonites and belemnites, along with poorly preserved bivalves and occasional well-preserved fishes, are found in these strata. Above these lie a thick (43 m) succession of the Black Ven Marls, exposed on either side of Charmouth. These blue-black mudstones and paper shales with occasional limestones are also fossiliferous but with a more diverse fauna, with the addition of other invertebrates such as brachiopods, protistans, occasional plants, as well as reptilian remains and, most importantly in the context of the present volume, insects.

The overlying light-grey Belemnite Marls have abundant interbedded lignite horizons and are capped by a distinctive thin limestone, the Belemnite Stone. Their abundant molluscan fauna includes well-preserved belemnites and pyritized ammonites. The Lower Liassic sequence is completed by a thick (16 m) succession of the Green Ammonite Beds, predominantly grey mudstones with limestone nodules containing well-preserved ammonites.

Fauna

The majority of the fossil insects found here occur in the Woodstones and Flatstones (parts of bed 83, e.g. Lang Bed 83h, Black Ven Marls) of Upper Sinemurian age (obtusum Biozone) that are naturally exposed on the coast at Black Ven and Stonebarrow, either side of Charmouth. A few insects have also been found the older turneri Biozone in the birchi Nodules (bed 75a of the Lower Sinemurian Shales with Beef). The Black Ven Marls contain the best-known Lower Liassic entomofauna (see Table 4.1).

The insects have been the subject of modern investigation that has recognized a number of new genera and species known only from Dorset, including the earliest-known Lepidoptera – the moth *Archaeolepis mane* (Figure 4.23). Charmouth has also yielded the earliest snakeflies such as *Metarhaphidia confusa* (Rasnitsyn and Quicke, 2002). More insect species remain to be described. The only comparable insect-bearing deposits that yield insects in fine-layered carbonate concretions are in the Lower Jurassic strata of Central Europe, but these are not of the same exact age. For instance, the internationally renowned German insect-bearing deposits of Dobbertin (Mecklenburg), Schandelah (Lower Saxony) are of younger (Toarcian) age. Of the same age as the Dorset insects are lowermost Liassic insects from clay lenses intercalated within deltaic sandstones in Bavaria (Konijnenburg-van Cittert and Schmeissner, 1999). Of comparable age is the remarkable insect fauna of Issyk Kul, Kyrgyzstan (Ansorge and Kzremiński, 1994). The Liassic insect fauna of Dorset is therefore a key part of our European palaeontological heritage and, as such, is unique.

Fine anatomical details such as wing scales and hairs are preserved although the majority of insects are disarticulated. Their remains usually occur sporadically and are associated with a normal Liassic marine fauna including ammonites, fishes and crinoids, which probably accumulated a few miles from land within a coastal embayment possibly fed by rivers. The proximity of the land is suggested by the presence of both plant fragments and the insect remains especially indicated by the relative abundance of beetles (Coleoptera) and true bugs (Heteroptera).

The insects are terrestrial and non-marine aquatic, but no larval stages have been described. Aquatic insects include Odonata, Heteroptera (true bugs) and some beetles (Coleoptera). The majority, however, are terrestrial, inhabiting 'bush'-type vegetation such as ferns (Ficales), Bennettitales, seedferns, Cycadales and Coniferales (gymnosperms). The fauna is dominated by beetles (Coleoptera, 40% i.e. 66 species), 'grasshoppers' and crickets (22%) followed by true bugs and dragonflies .

The insects probably lived on the Cornubian landmass with the alternative terrestrial sources of the Welsh Massif or Western Approaches being less likely, since distinctive families from these regions such as the Bintoniellidae (Orthoptera) are absent in the Dorset strata. The endemic dragonfly *Dorsettia laeta* shows sexual dimorphism, and elaterid beetles preserve the 'click' escape mechanism of these Coleoptera. The extinct Pseudpolycentropidae would have been true fly-like scorpionflies.

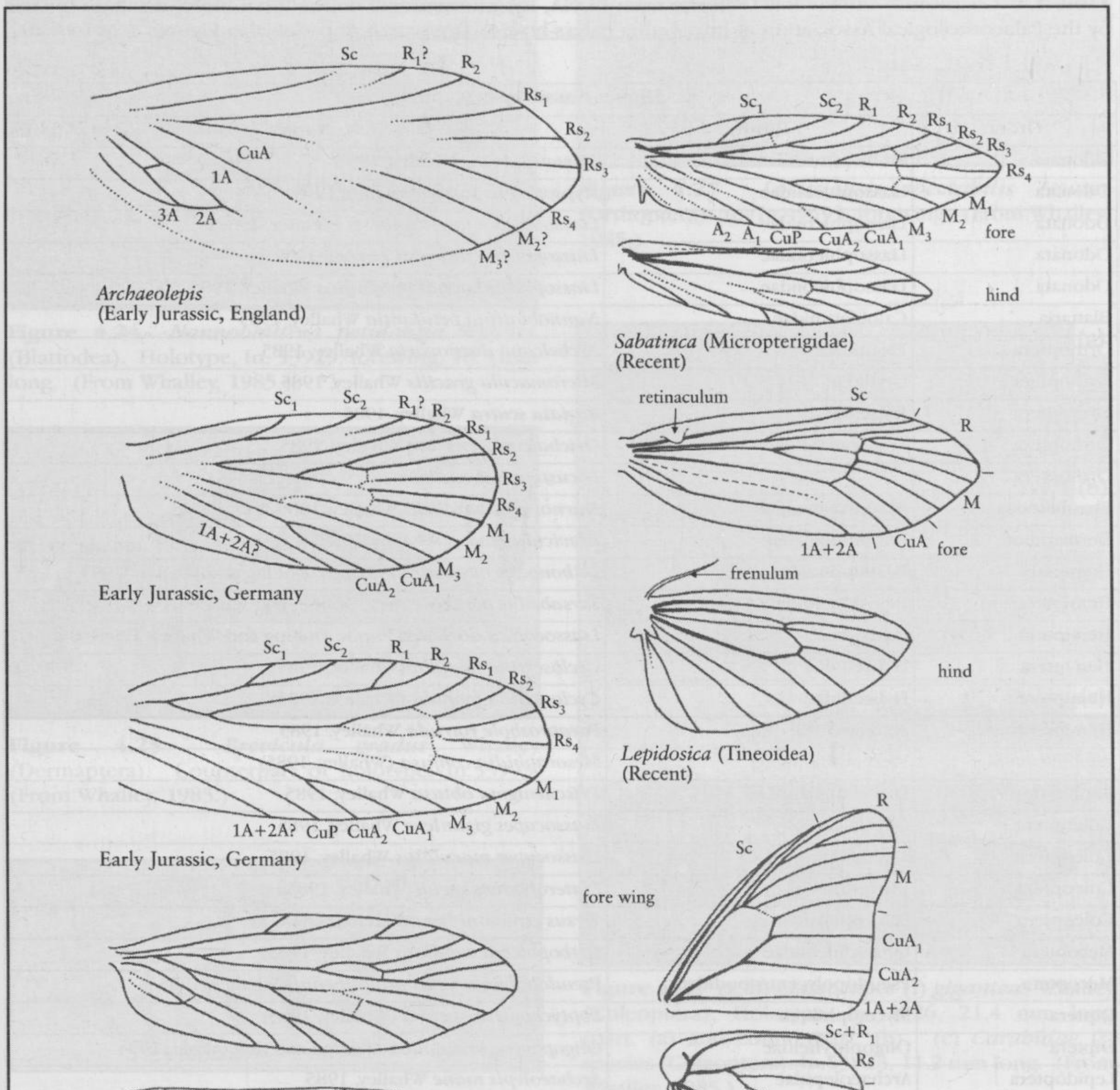


Figure 4.23 Wing venation of early fossil Lepidoptera (left column) and assorted Holocene Lepidoptera (right column). (Nomenclature of veins: A, anal veins; Cu, cubital veins; M, median veins; R, radial vein; Rs, radial sector; Sc, subcostal vein.) Not to the same scale. The oldest Lepidoptera are known from wing fossils with primitive venation from the Early Jurassic deposits of England (*Archaeolepis*) and Germany (undescribed). *Archaeolepis* venation is revised based on new observations (Grimaldi and Engel, 2005); the German Jurassic wings are based on Ansorge (2003).

Table 4.1 Charmouth–Pinhay Bay GCR site from EDNA, the international online fossil insect database hosted by the Palaeontological Association at http://edna.palass-hosting.org/search.php. See also Figures 4.24 to 4.29.

Dorset Liassic Insects		
Order	**Family**	**Name**
Odonata	Archithemistidae	*Dorsettia laeta* Whalley, 1985
Odonata	Liassophlebiidae	*Hypsothemis fraseri* Whalley, 1985
Odonata	Liassophlebiidae	*Liassophlebia anglicanopsis* (Zeuner, 1962)
Odonata	Liassophlebiidae	*Liassophlebia jacksoni* Zeuner, 1962
Odonata	Liassophlebiidae	*Liassophlebia pseudomagnifica* Whalley, 1985
Blattaria	Caloblattinidae	*Nannoblattina petulantia* Whalley, 1985
Orthoptera	Elcanidae	*Archelcana durnovaria* Whalley, 1985
Orthoptera	Gryllidae	*Micromacula gracilis* Whalley, 1985
Orthoptera	Haglidae	*Regiata scutra* Whalley, 1985
Orthoptera	Triassomantidae	*Orichalcum ornatum* Whalley, 1985
Orthoptera		*Locustopsis spectabilis*
Phasmatodea	Aerophasmatidae	*Durnovaria parallela* Whalley, 1985
Dermaptera	Protodiplatyidae	*Brevicula gradus* Whalley, 1985
Hemiptera	Belostomatidae	*Lethonectes naucoroides* Popov, Dolling and Whalley, 1994
Hemiptera	Belostomatidae	*Tarsabedus menkei* Popov, Dolling and Whalley, 1994
Hemiptera	Corixidae	*Liassocorixa dorsetica* Popov, Dolling and Whalley, 1994
Hemiptera	Hylicellidae	*Cycloscytina fennahi* (Whalley, 1985)
Hemiptera	Hylicellidae	*Cycloscytina fennahi* (Whalley, 1985)
Hemiptera	Tettigarctidae	*Paraprosbole rotruda* Whalley, 1985
Raphidioptera	Mesoraphidiidae	*Mesoraphidia confusa* (Whalley, 1985)
Raphidioptera	Priscaenigmatidae	*Priscaenigma obtusa* Whalley, 1985
Coleoptera	Cupedidae	*Liassocupes giganteus* Whalley, 1985
Coleoptera	Cupedidae	*Liassocupes maculatus* Whalley, 1985
Coleoptera	Elateridae	*Elaterophanes regius* Whalley, 1985
Coleoptera	Schizophoridae	*Tersus crowsoni* Ponomarenko, 2006
Mecoptera	Orthophlebiidae	*Orthophlebia capillata* Whalley, 1985
Mecoptera	Pseudopolycentropodidae	*Pseudopolycentropus prolatipennis* Whalley, 1985
Diptera	Mycetophilidae	*Eoptychoptera spectra* (Whalley, 1985)
Diptera	Oligophryneidae	*Oligophryne britannica* Ansorge and Krzemiński, 1994
Lepidoptera	Archaeolepidae	*Archaeolepis mane* Whalley, 1985

In addition, about 100 new 'species' of fossil fish have been recovered and named from the sequence around Lyme Regis, but only about 50 of these are now recognized (see Dineley and Metcalf, 1999). Similarly, about 100 new 'species' of fossil reptile were also named in the 19th century when virtually every bone was given a new name. These have now been rationalized down to about 14 species (see Benton and Spencer, 1995, p. 109) but nevertheless include internationally important specimens, especially of plesiosaurs and ichthyosaurs. The presence of occasional dinosaur remains also has considerable significance, especially for interpretation of the changing environment of deposition in the succession, since their remains indicate the presence of nearby land.

Of the invertebrates, the ammonites have been of particular biostratigraphical importance. Some of the other fossil molluscs have historical and interpretative importance. The presence of plant and insect remains in the Black Ven Marls, Shales with Beef and Blue Lias also supports the conclusion that although still essentially marine, land cannot have been far away.

Interpretation

Renewal of marine deposition in Britain began with the Rhaetian transgression in latest Triassic

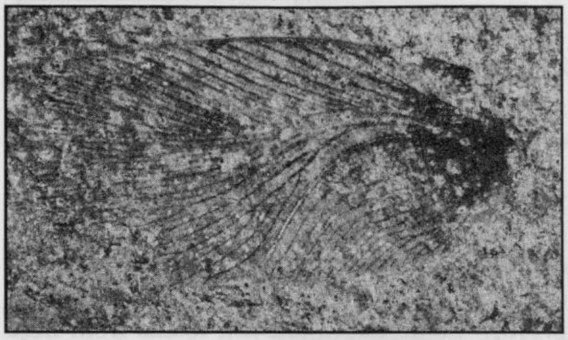


Figure 4.24 *Nannoblattina petulantia* Whalley (Blattodea). Holotype, In. 53929. forewing, 16.3 mm long. (From Whalley, 1985.)

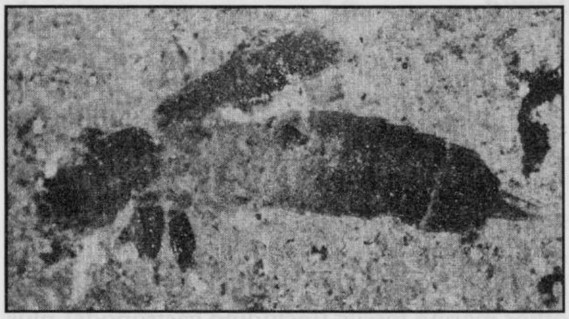


Figure 4.25 *Brevicula gradus* Whalley (Dermaptera). Counterpart of holotype, In.53993. (From Whalley, 1985.)

Figure 4.26 *Archelcana durnovaria* Whalley (Orthoptera) paratype, In.53922, forewing. (From Whalley, 1985.)

times as documented by strata exposed to the west of Lyme Regis and by the Penarth Group strata seen at localities such as Aust Cliff and west of Lyme Regis. By early Jurassic times fully marine conditions were established with a shallow epicontinental sea flooding much of northern Europe to form a huge area of shelf sea. Within this region, largely protected from strong tidal or storm influences, distinctive facies of laminated bituminous shales and rhythmic sequences of lime mud and marl were laid down. Lyme Regis lies in the south of the region and its Lower Liassic biota suggests that seabed

Figure 4.27 *Locustopsis spectabilis* Zeuner (Orthoptera). (c) In.49593, forewing. (From Whalley, 1985.)

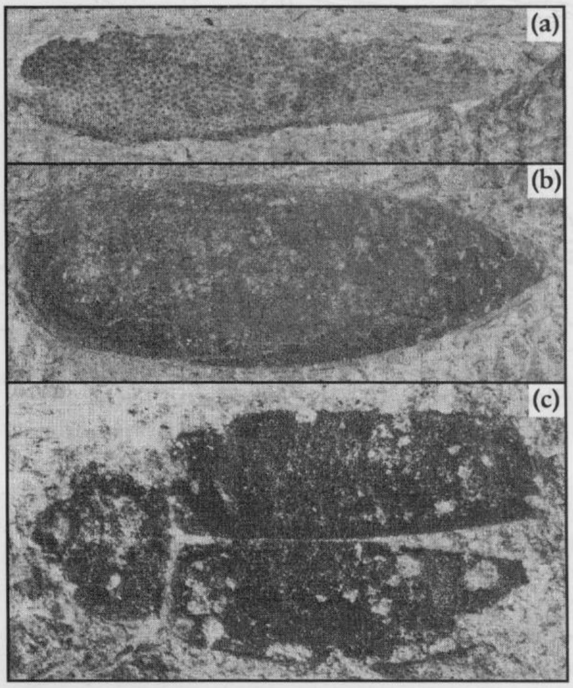


Figure 4.28 (a, b) *Liassocupes* (?) *giganteus* Whalley (Coleoptera), Holotype, In.51026, 21.4 mm long (part, (a) and counterpart, (b). (c) *Carabidae* (?) species (Coleoptera). In.53923, 11.2 mm long. (From Whalley, 1985.)

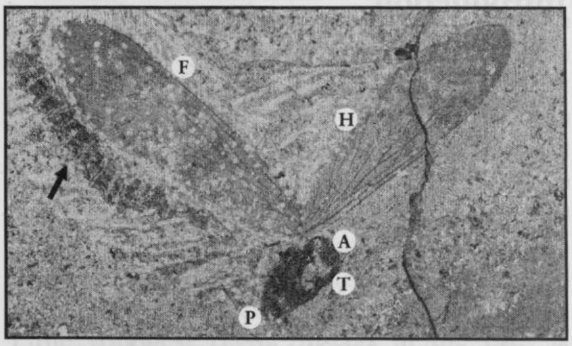


Figure 4.29 *Orthophlebia capillata* Whalley (Mecoptera), holotype, In.53924. A = anterior of thorax; P = posterior of thorax; F = forewing; H = hindwing; T = thorax. Arrow indicates chisel marks, not abdomen. (From Whalley, 1985.)

conditions were often inimical to benthic life. It was mostly the remains of free-swimming organisms such as marine reptiles, fish, ammonite and belemnite cephalopods that accumulated within seabed sediments and were recruited to the fossil record.

The presence of insect fossils within the Black Ven Marls, Shales with Beef Beds and Blue Lias along with other fossils, such as plant remains and the skin impressions of the terrestrial dinosaur *Scelidosaurus* (Martill, 1991), shows that there was land nearby.

Conclusions

Charmouth lies within the Dorset to east Devon World Heritage Site which is inscribed in particular for its geological value. In addition to its international renown and conservation value as a site that preserves a diverse fish and reptile fauna, and indeed its marine invertebrate fauna, Charmouth is one of the most productive sites for fossil insects of Liassic age (Lower Jurassic, Sinemurian, *c.* 197 Ma) in Britain. These terrestrial arthropods are fossilized in marine deposits and include dragonflies (odonatans), bugs (hemipterans), beetles (coleopterans) and crickets (orthopterans) some of which are unique to the site. The exposure is maintained by coastal erosion so there is the potential for new finds to be made at any time.

DUMBLETON AND ALDERTON, GLOUCESTERSHIRE

(SP 006345)

Introduction

The village of Dumbleton lies between the northern flank of Alderton Hill and the Vale of Evesham to the north. Dumbleton and Alderton have been treated as two separate localities in the literature (e.g. Brodie, 1845a) but Dumbleton Pit is actually less than 100 m east of Alderton Hill Quarry (Dr M.J. Simms, pers. comm.). This composite site is critically important for the study of Lower Jurassic (early Toarcian age, *c.* 182 Ma) insects and has provided the type species of important genera of Mesozoic dragonflies *Heterophlebia* and *Liassogomphus*.

Description

The Upper Lias outlier caps the summit of Alderton Hill in the northern Cotswolds (Figure 4.30). Pale limestone nodules from the so-called 'Fish and Insect Beds' (Dumbleton Member) of Toarcian age, Harpoceras falciferum Biozone and H. exaratum Subzone have been known to contain abundant fish and some insect fossils since the mid 19th century (Wright, 1865, p.156). Some important fish fossils from here are recorded by Dineley and Metcalf (1999, p. 380).

Fauna

Dumbleton Pit and Alderton Hill Quarry, survived for the purposes of fossil collecting into the late twentieth century (Simms *et al.*, 2004, p. 186).

The Fish Bed here is about 4 m above the base of the Upper Lias. Insects occur in brown-weathering, blue-centred, early diagenetic nodular limestone 5–20 cm thick associated with fish and other marine fossils (including gastropods) plus occasional plant fossils. No comparable limestone bed was exposed on Dumbleton Hill (contra Brodie, 1845a).

Insects from the Alderton GCR site include:

Odonata (dragonflies) e.g. *Heterothemis brodiei*, *Heterophlebia buckmani* (Brodie, 1845a; Carpenter, 1992; Nel *et al.*, 1993, see Figures 4.33 and 4.34);
Blattodea (cockroaches);
Orthoptera ('grasshoppers' and crickets) e.g. crickets (Zeuner, 1939);
Grylloblattida (rock crawlers) e.g. *Geinitzia carpentieri* (Zeuner, 1939);
Hemiptera (bugs) e.g. cicadas;
Neuroptera (lacewings) e.g. *Actinophlebia intermixta*, (Tillyard, 1933, see Figure 4.33); *Archeosmylus complexus*; (Jarzembowski, 1999)
Coleoptera (beetles)
Diptera (true flies) e.g. crane-fly (Tillyard, 1933, see Figure 4.34)
Mecoptera (scorpionflies) e.g. Tillyard, 1933, (see Figure 4.35)
Amphiesmenoptera (Trichoptera plus Lepidoptera) e.g. *Necrotaulius parvulus*; (Tillyard, 1933, see Figure 4.36.)

The entomofauna has not been monographed

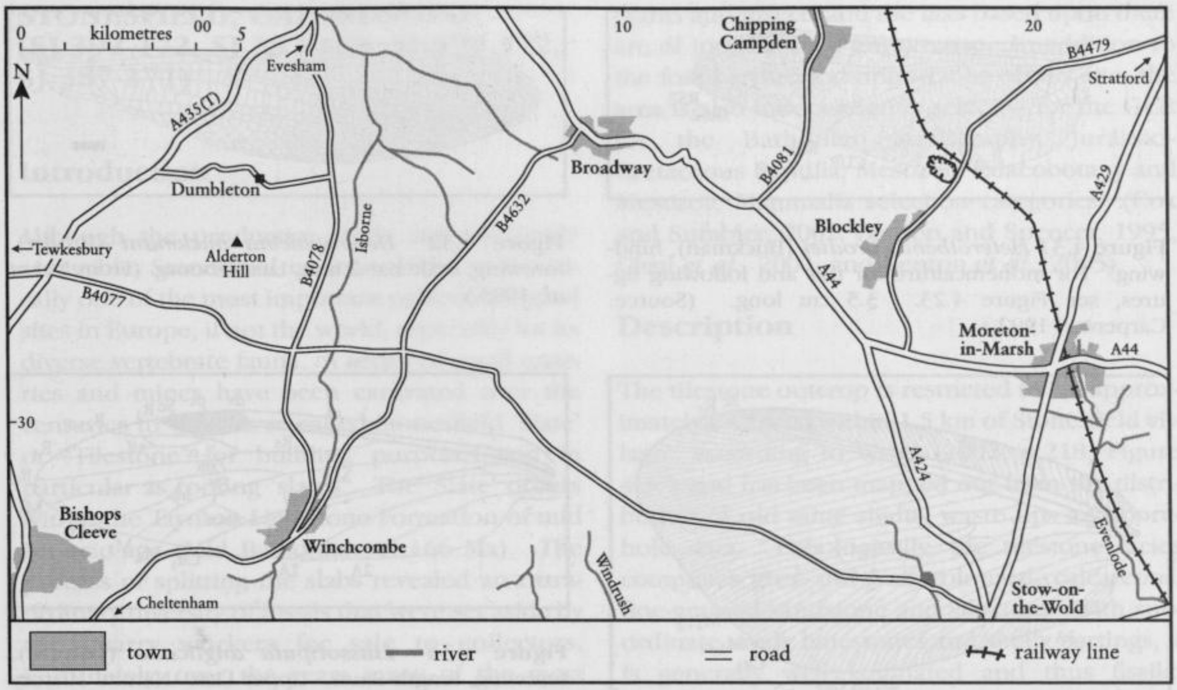


Figure 4.30 Sketch map of the area around the village of Dumbleton. (After Dineley and Metcalf, 1999.)

but the dragonflies are relatively well known. In addition to showing sexual dimorphism, they are also recorded from the continent. Thus *Heterophlebia buckmani* (Brodie) is known from Germany and Luxembourg (Nel *et al.*, 1993) and the famous Posidonia Shale of Holzmaden; *Heterothemis brodiei* (Buckman) is also known from Germany plus the Posidonia Shale of Switzerland (Ansorge, 2003). Blattodea have been revised recently by Vršanský and Ansorge (2007).

The Lower Toarcian insects were preserved as part of a transgressive Oceanic Anoxic Event in the European epicontinental seas under calm conditions resulting in fine-grained, micritic limestone formation in the absence of sediment bioturbation (Ansorge, 2003). The insect remains are mainly just the wings of good fliers (although articulated specimens do occur) drowned during dispersal flights or blown off course by offshore winds. It seems that few insect remains were washed down by rivers because aquatic larvae and ground-dwelling arthropods are either absent or rare.

Those ground-dwelling arthropods that do rarely occur include crickets and grylloblattidans.

Interpretation

The insects probably lived on the London-Brabant Massif (Ansorge, 2003: fig.1) which was evidently well vegetated, judging by the presence of plant-feeding insects such as 'grasshoppers' and plant bugs. Flying insects included forms capable of migration (dragonflies) and those that were perhaps capable of swarming, for example extinct orthopterans such as the Elcanidae and amphiesmenopterans such as the Necrotaulidae. The caddisfly-like necrotauliids (actually stem Amphiesmenoptera) were possibly terrestrial (and not aquatic) as larvae. Cockroaches and some beetles fed on rotting vegetation, the former inhabiting different ecological niches with different size leaf litter. Predatory insects such as Odonata, Mecoptera and Neuroptera were not top predators as they, in turn, were preyed upon by pterosaurs whose remains have been found in the Posidonia Shale.

Alderton is the most productive site in the UK for Upper Liassic insects and has yielded some of the youngest Liassic insects in the UK. The British Lower Jurassic strata are renowned for their insects, a fossil record that extends down into the Upper Trias. The quarry is thus part of a network of sites that include Charmouth

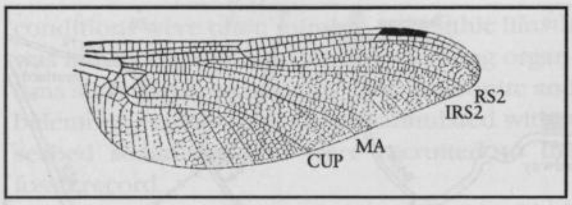


Figure 4.31 *Heterothemis brodiei* (Buckman), hindwing. For monemcalture for this and following figures, see Figure 4.23. 3.5 cm long. (Source: Carpenter, 1992.)

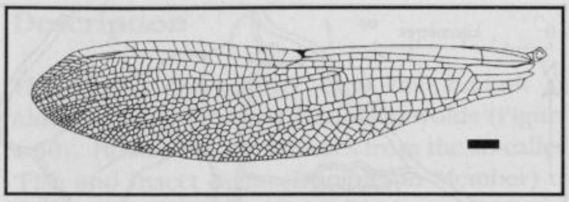


Figure 4.32 *Heterophlebia buckmani* (Brodie), forewing, scale bar 2 mm, Luxembourg. (From Nel *et al.* 1993.)

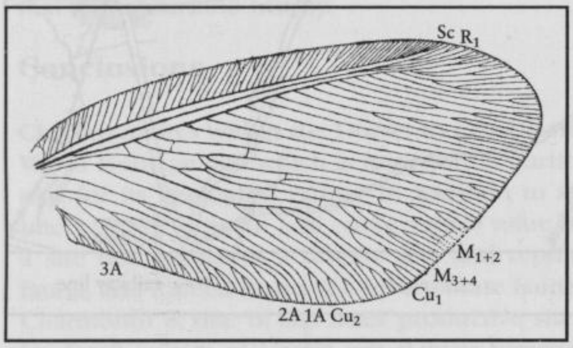


Figure 4.33 *Actinophlebia intermixta* (Scudder), forewing. Length, 11mm, Upper Lias. Natural History Museum I.11346. (From Tillyard, 1933.)

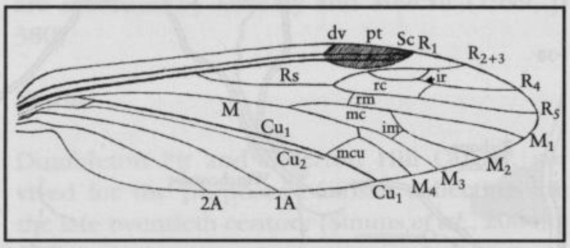


Figure 4.34 *Liassotipula anglicana* (Tillyard), forewing, length 8mm. Upper Lias. Natural History Museum. (From Tillyard, 1933.)

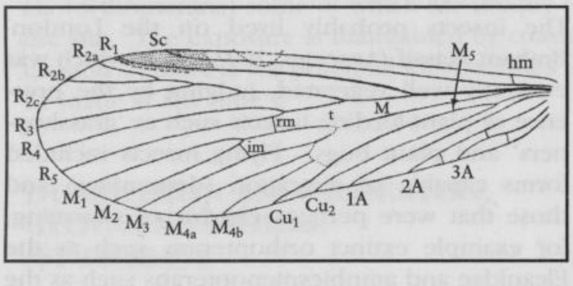


Figure 4.35 *Orthophlebia brodiei* (Tillyard), forewing, length 10.7 mm. Upper Lias. Natural History Museum I.15017. (From Tillyard, 1933.)

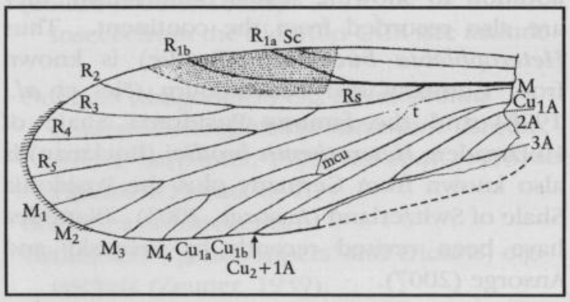


Figure 4.36 *Necrotaulius parvulus* (Geinitz), forewing, length 3.5 mm. Upper Lias. Natural History Museum, I.15014. (From Tillyard, 1933.)

(Lower Lias) and Aust Cliff (Rhaetian).

Conclusion

The conservation value of the Dumbleton and Alderton GCR site lies in the palaeontological significance of its insect fauna. The type specimens and species of some important Mesozoic dragonfly genera (*Heterophlebia* and *Heterothemis*) were found in the Upper Lias strata of Lower Jurassic age (Lower Toarcian, *c.* 185 Ma) which are exposed here. Face clearance of the disused clay pits on Alderton Hill would enhance their geological potential.

STONESFIELD, OXFORDSHIRE (SJ 392 172, SJ 387 168, SJ 379 172, SJ 387 171)

Introduction

Although the productive strata are not easily accessible, Stonesfield in Oxfordshire is historically one of the most important palaeontological sites in Europe, if not the world, especially for its diverse vertebrate fauna. A series of small quarries and mines have been excavated over the centuries to win the so-called Stonesfield 'Slate' or 'Tilestone' for building purposes and in particular as roofing 'slates'. The 'Slate' occurs within the Taynton Limestone Formation of mid Jurassic age (Mid Bathonian, *c.* 166 Ma). The process of splitting the slabs revealed an extraordinary diversity of fossils that were set aside by the quarry workers for sale to collectors. Fortunately, over the years many of the most interesting fossils found their way into museum collections and these include a diverse fauna of fossil insects. The overall fossil biota comprises an unusual mixture of marine, freshwater and terrestrial organisms. Many of the Stonesfield specimens of fossil fishes, reptiles, mammals, plants and insects and the taxa based upon them are of international importance. In addition to the fossil arthropod importance of this site, the area is also independently selected for the GCR for the Bathonian stratigraphy, Jurassic–Cretaceous Reptilia, Mesozoic Palaeobotany and Mesozoic Mammalia selection categories (Cox and Sumbler, 2002, Benton and Spencer, 1995, Cleal *et al.*, 2001, and Benton *et al.*, 2005).

Description

The tilestone outcrop is restricted to 'an approximately oval area within 1.5 km of Stonesfield village', according to Wyatt (2002, p.218; Figure 4.37) and has been mapped out from the distribution of old mine shafts, waste tips and borehole data. Lithologically, the tilestone facies comprises grey and buff coloured, calcareous, fine-grained sandstone and siltstone. With subordinate sandy limestones and shelly partings, it is generally well laminated and thus fissile, which is why it was exploited as a roofing material since Roman times. There are both laminae and scattered oolitic grains and sometimes small-scale, current cross-bedding. The maximum thickness of the most productive 'slate' horizon was stated to be 1.8 m (Fitton, 1828)

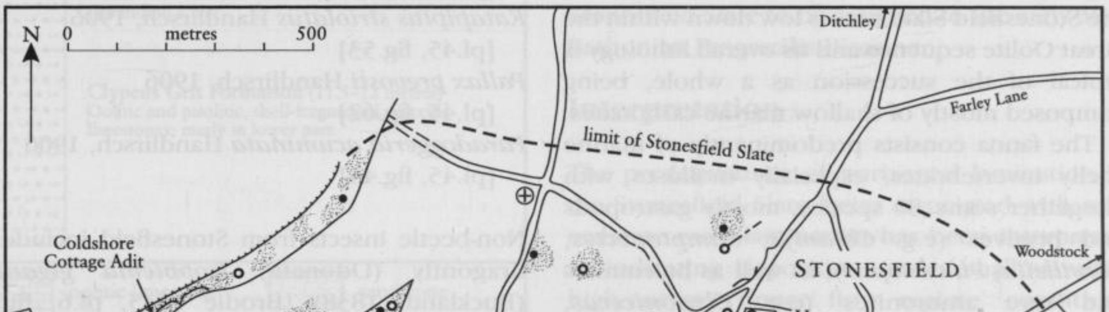


Figure 4.37 Sketch map showing the distribution of the Stonesfield Slate. (After Benton and Spencer, 1995.)

but, more commonly, was less than half a metre. Details of individual shafts and adits are given by Wyatt (2002, p.219–220) and a measured section from Home Close Shaft, Stonesfield by Sumbler (in Boneham and Wyatt, 1993, see Figure 4.38) is as follows:

	Thickness (m)
Hampen Marly Formation	7.75
Taynton Limestone formation	
Limestone – oolitic, bioclastic, sparry, cross-bedded	1.13
Marl – oolitic, bioclastic; pebbles of limestone and sandstone in lower part	0.31
Limestone – oolitic, bioclastic, sparry	0.27
Stonesfield slate	
Sandstone – fine-grained, hard, calcareous, scattered ooliths; soft, cross-laminated and fissile at adit depth of 12.78–13.13m; continuing below in hard, laminated, fissile sandstone with strings of ooliths; variably oolitic from 13.30m with oyster shells	1.06
Limestone – coarse-grained oolitic, bioclastic, sparry	0.28

The Taynton Limestone Formation that includes the Stonesfield Slate occurs low down within the Great Oolite sequence and its overall lithology is typical of the succession as a whole, being composed mostly of shallow marine carbonates.

The fauna consists predominantly of marine shelly invertebrates, especially molluscs with altogether some 80 species, mostly gastropods and bivalves (e.g. *Chlamys*, *Camptonectes*, *Gervillella*, *Placunopsis*), as well as belemnites and rare ammonites (e.g. *Clydoniceras*, *Micromphalites*, *Oppelia*) accompanied by a variety of brachiopods (commonly the rhynchonellid *Kallirhynchia*), crustaceans, annelids and corals. In addition, some 23 species of terrestrial plants (such as ferns, cycads, ginkgos and conifers, Cleal *et al*., 2001), at least 14 species of insects, and three species of mammals (including the first pre-Tertiary mammals to be recognized such as *Amphilestes broderipi* (Owen) have been described along with 40 species of fish (including numerous sharks, rays and bony fishes, see Dineley and Metcalf, 1999) and 14 reptile species (e.g. turtles, crocodilians, ichthyosaurs and the first dinosaur to be recognized and accepted as such – *Megalosaurus bucklandi* Meyer – see Benton and Spencer, 1995).

The faunal element of greatest significance in the present context is the entomofauna, which includes large beetles and dragonflies some of which are found in the slightly older Charlbury Formation of Gloucestershire (Figure 4.38). Even early palaeoentomologists like Brodie (1845b) noted that the Stonesfield insects are uncommonly large (>15 mm or more in length), that is on a centimetric, rather than millimetric, scale. This large scale of the remains is presumably the result of a taphonomic filter generated by the high-energy, shallow-marine environment.

Most of the remains are beetle (Coleoptera) elytra – but not all – see below. Most of the finds were made in the Victorian heyday of the historic tilestone quarrying. The following beetles have been recorded from Stonesfield:

Adikia punctulata Handlirsch, 1906
[pl.45, fig.52]
Bucklandia striata Handlirsch, 1906
[pl.45, fig.45]
Doggeria bucklandi (Mantell,1844)
[pl.45, fig.42]
Doggeriopsis stonesfieldiana Handlirsch, 1906
[pl.45, fig.43]
Katapiptus striolatus Handlirsch, 1906
[pl.45, fig.53]
Pallax prevosti Handlirsch, 1906
[pl.45, fig.62]
Paradoggeria acuminata Handlirsch, 1906
[pl.45, fig.44]

Non-beetle insects from Stonesfield includes a dragonfly (Odonata) *Isophlebia gigantea* (Buckland, 1838) [Brodie 1845, pl.6, fig.22 Figure 4.39]

Furthermore there is the cicada-like (Hemiptera: Homoptera) *Palaeontina oolitica* Butler, 1873 [pl.49, figs 1-7]

P. oolitica was famously misidentified originally as a Jurassic butterfly (Lepidoptera): the error persisted well into the 20th Century. For instance, Handlirsch (1906–8, pl. 49) reconstructed these insects as hirsute Lepidoptera despite the lack of scales or hairs in the fossils. In reality, fossil butterflies are not found until Cenozoic times and *P. oolitica* is the type species

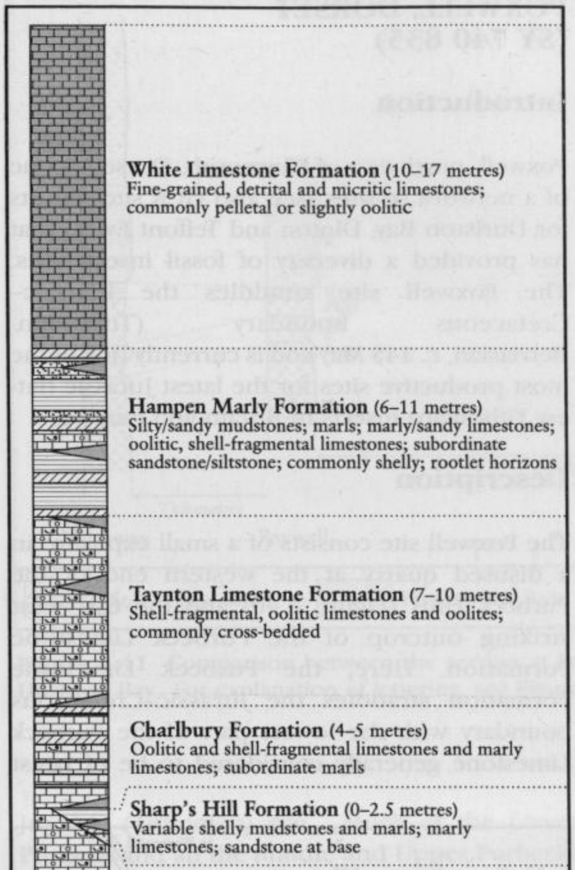


Figure 4.38 Generalized sequence through the Great Oolite Group of the Stonesfield area, showing the different levels at which the Stonesfield 'Slate' facies is developed. (After Boneham and Wyatt, 1993.)

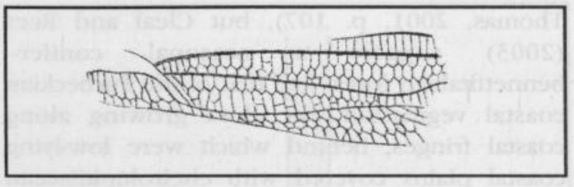


Figure 4.39 Wing of dragonfly *Isophlebia gigantea* × 0.3. (From Brodie, 1845b.)

of the type genus *Palaeontina* of the extinct family Palaeontinidae (now known as 'butterfly bugs') which consists of cicada-like plant bugs of the Mesozoic Era. The error originated earlier with misidentification of the open venation (through convergence) and the large size of the palaeontinid forewings.

One of the species found at this classic site by Brodie (1845b) was the large beetle *Kibdelia oolitica* (Brodie, 1845b) which has also been found at Eyeford and Sevenhampton in Gloucestershire (Brodie pl.6, fig.15; Handlirsch 1906–8, pl.45, fig.61). From the plants found in the Stonesfield tilestones, Brodie (1845b) concluded that the insects inhabited a well-vegetated coastal or island environment not far away, in a 'gulf' (Cleal and Rees, 2003).

Identification of rare ammonites (Torrens, 1974) such as *Procerites mirabilis* Arkell and the biozonal index *P. progracilis* allows the Stonesfield Slate to be assigned to the early Mid-Bathonian Progracilis Biozone.

Interpretation

The predominance of horizontal lamination in the Stonesfield Slate facies associated with subordinate cross-lamination has been interpreted as indicating deposition under shallow-water, high-energy, 'upper flow regime'- conditions (Sellwood and McKerrow, 1974). The quartzose tilestones represent influxes of sand and silt into the otherwise carbonate-dominated sedimentary environment in which the oolitic and bioclastic deposits of the Taynton Limestone Formation accumulated. The provenance of the clastic debris is uncertain, but may have been from the erosion of sandstones on the London Landmass, which lay to the east.

The Stonesfield fossil flora gives some indication of the topography and vegetation of that landmass. Some interpretations suggested that the most-common plant fossils were derived from mangrove-like vegetation (Cleal *et al.*, Thomas, 2001, p. 107), but Cleal and Rees (2003) suggest a seasonal conifer–bennettitalean forest like that of the Purbeckian coastal vegetation, the flora growing along coastal fringes, behind which were low-lying coastal plains covered with cheirolepidiacean forests that were periodically inundated. However, another common element of the flora (*Pelourdea*) might have grown in slightly drier marginal habitats, suggesting that there were some areas of slight elevation.

The presence and proximity of this subaerial landmass is supported by the occurrence of terrestrial remains such as dinosaurs, small mammals, land plants and insects. Sellwood and McKerrow (1974) suggested that the diversity of the Stonesfield biota was enhanced by the re-deposition of concentrations of strandline flotsam under the influence of storm-induced currents. Rapid burial is indicated by the preservation of some otherwise relatively delicate organisms such as dragonflies.

Because of the lack of surface exposures, the biostratigraphical position of the Stonesfield Slate was, until relatively recently, uncertain. However, the drilling of four boreholes in 1991 and re-assessment of old shaft and adit sections revealed that the Stonesfield Slate was originally worked from three separate levels within the Taynton Limestone Formation. Furthermore, all three levels were impersistent and localized, thus it is not possible to allocate fossils from historical collections to any particular bed because the specific horizon from which they were originally collected was not recorded. Also, insects were collected from several localities in the Cotswold region of Oxfordshire and Gloucestershire.

Conclusion

Although largely inaccessible today, the importance of the Middle Jurassic (Bathonian, *c.* 166 Ma) Stonesfield Slate fossil biota is so great that the site retains considerable conservation value, especially as it retains some potential for future work. Diverse elements of the biota such as the fishes, reptiles, mammals and plants have a recognized international significance. The fauna of beetles (coleopterans), dragonflies (odonatans) and bugs (hemipterans) is of particular interest for the description of British fossil insects.

POXWELL, DORSET (SY 740 835)

Introduction

Poxwell, north-east of Weymouth, Dorset, is one of a network of sites (see also GCR site reports for Durlston Bay, Dinton and Teffont Evias) that has provided a diversity of fossil insect beds. The Poxwell site straddles the Jurassic–Cretaceous boundary (Tithonian/Berriasian, *c.* 145 Ma) and is currently one of the most productive sites for the latest Jurassic (latest Tithonian) insects in Britain and Europe.

Description

The Poxwell site consists of a small exposure in a disused quarry at the western end of the Purbeck Hills (Figure 4.40) and the east–west striking outcrop of the Purbeck Limestone Formation. Here, the Purbeck Limestone Formation straddles the Jurassic–Cretaceous boundary with the lowest part of the Purbeck Limestone generally considered to be of latest

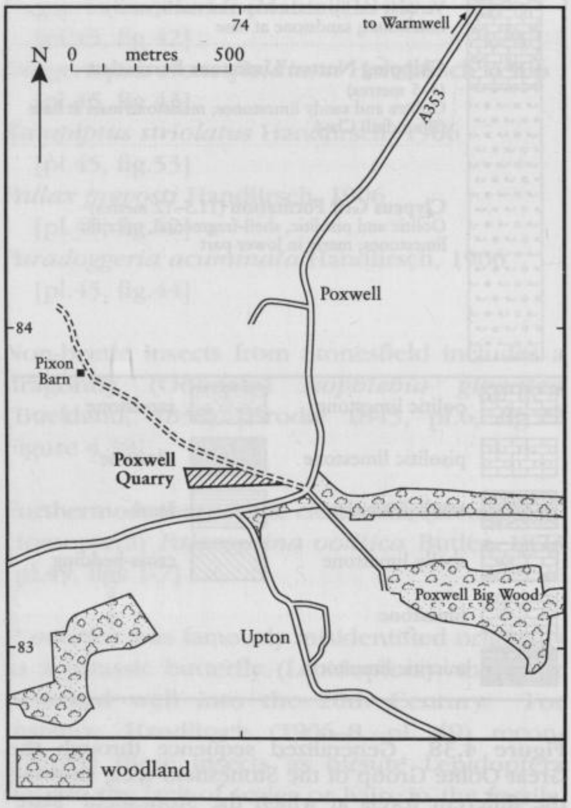


Figure 4.40 Location map for Poxwell Quarry GCR site.

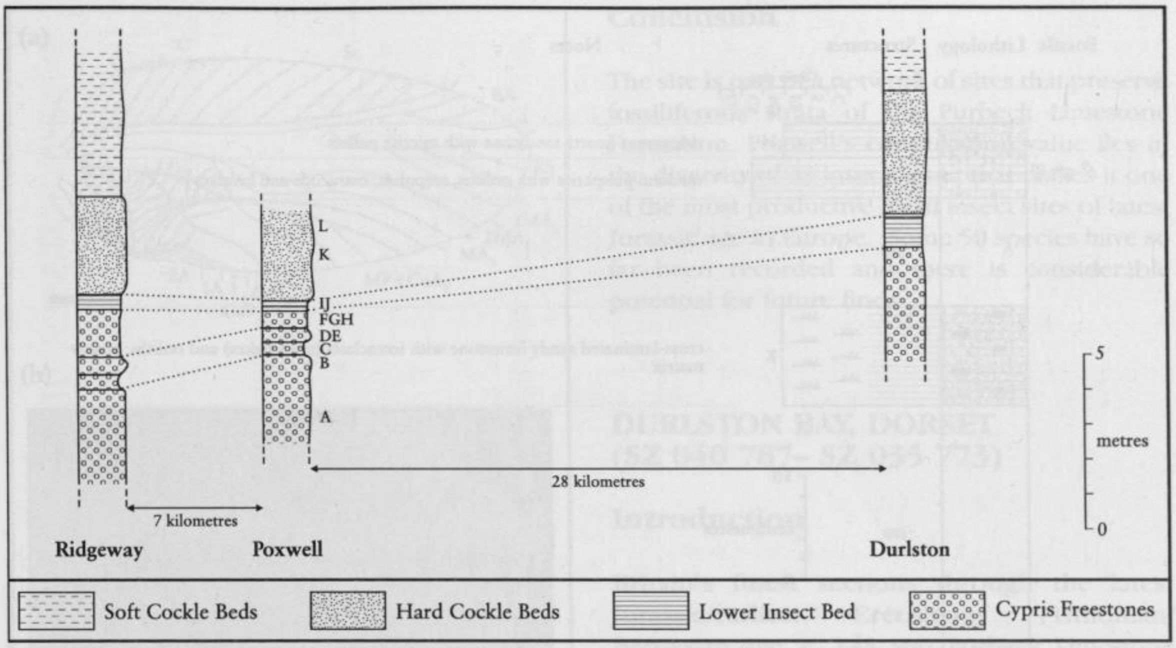


Figure 4.41 Comparison between the section at Poxwell Quarry and related sections at Ridgeway Hill and Durlston Bay. For explanation of lettering, see Figure 4.42. (After Fisher, 1856; Barton, 1978.)

Jurassic (Tithonian) age. Much of the Lower Purbeck and all the Middle and Upper Purbecks are Early Cretaceous (Berriasian) in age. The fossil insects are preserved in a soft white micrite (limestone) with pseudomorphs after halite and gypsum assigned to the Lower Insect Bed (Barton, 1978, Figures 4.41 and 4.42).

Fauna

Some 50 species of terrestrial and aquatic insects have been found so far in the Lower Purbeck strata exposed at Poxwell and include forms not previously known from any other Purbeck localities. Overall, the entomofauna includes fossil cockroaches (blattodeans), dragonflies (odonatans), bugs (hemipterans), beetles (coleopterans), true flies (dipterans), wasps (hymenopterans), 'grasshoppers' (orthopterans), lacewings (neuropterans) and caddisflies (trichopterans). Species found here include a unique species of caddisfly (*Pteromixanum poxwellense* Sukatsheva and Jarzembowski, 2001), an extinct false cranefly (*Brodilka mitchelli* Lukashevich, Jarzembowski and Coram, 1997; Figure 4.44), an enigmatic Purbeck whitefly-like larva (Jarzembowski and Coram, 1997, fig. 6) and the unique, bush cricket-like ?*Cyrtophyllites cretaceus* Gorochov, Jarzembowski and Coram (2006) (Figure 4.43).

Interpretation

The evaporites in the Insect Bed recorded by Barton (1978; pseudomorphs after gypsum and halite) suggest hypersalinity during or subsequent to deposition of the bed. The absence of molluscs and infrequency of ostracods suggests a stressful environment, probably due to fluctuating salinities. This is supported by a restricted aquatic insect fauna dominated by a single species of water bug (*Nepidium stolones* Westwood). This fauna also suggests brackish rather than freshwater conditions. So, the insects are probably preserved due to brackish, stressful and even hypersaline conditions limiting the infauna and inhibiting organic decay. The water body was subject to varying degrees of salinity and therefore varying marine influence, suggesting a lagoonal environment.

Comparison with other localities

This small field outcrop is the finest inland exposure of the historically important Lower Insect Bed (Lulworth Formation), first recognized in

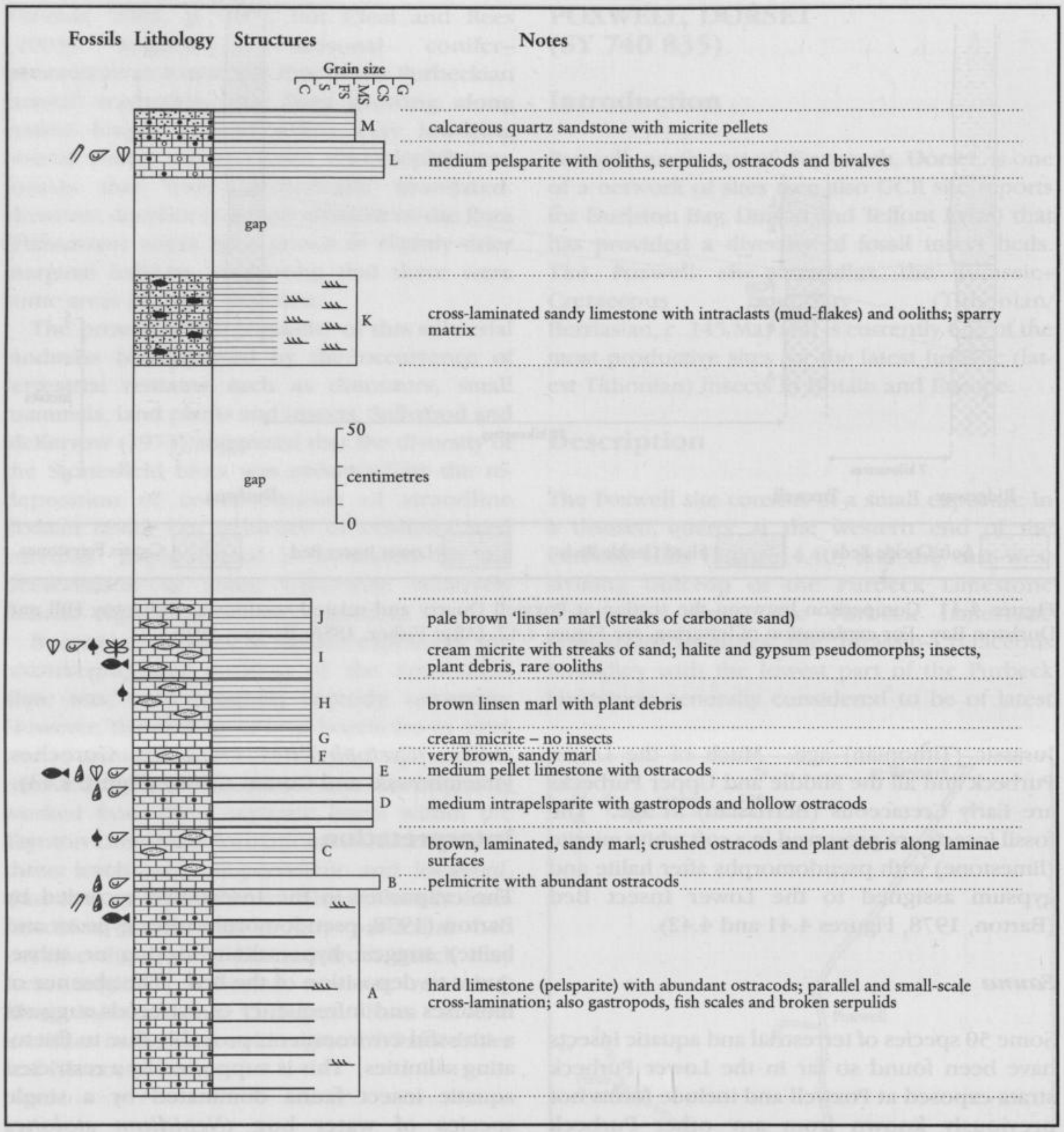


Figure 4.42 Graphic log of the Poxwell 'Insect Quarry'. For lithology: C, clay; CS, coarse sand; FS, fine sand; G, gravel; MS, medium sand. The horizons where various types of fossils are found are shown by symbols for gastropods, fish, plants, insects, ostracods, serpulids and bivalves. (After Barton, 1978.)

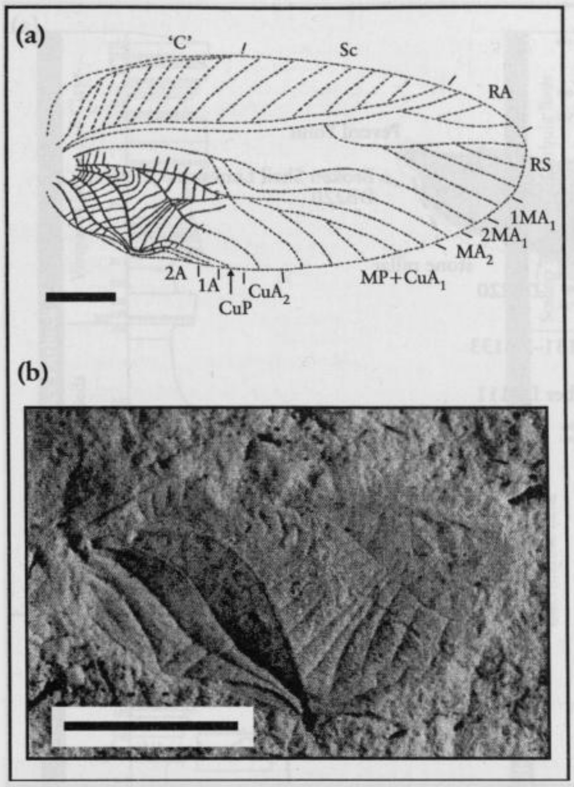


Figure 4.43 (a,b) *?Cyrtophyllites cretaceous* Gorochov *et al.*, 2006, male forewing (holotype). Bar 5 mm. For venation abbreviations see Figure 4.23. (From Gorochov *et al.*, 2006.)

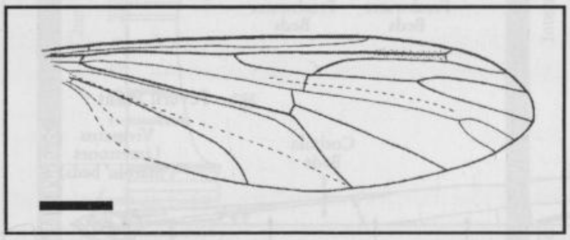


Figure 4.44 *Brodilka mitchelli* Lukasevich *et al.*, 2001, holotype MNEMG 2000.50; Poxwell, Dorset; Upper Tithonian.

the Weymouth area by Fisher (1856). The only other equivalent horizon in Durlston Bay has been degraded by modern coastal defence works, so it supplements the bay which is the type section of the Purbeck Limestone Formation.

Conclusion

The site is part of a network of sites that preserve fossiliferous strata of the Purbeck Limestone Formation. Poxwell's conservation value lies in the diversity of its insect fauna that makes it one of the most productive fossil insect sites of latest Jurassic age in Europe. Some 50 species have so far been recorded and there is considerable potential for future finds.

DURLSTON BAY, DORSET (SZ 040 787– SZ 035 773)

Introduction

Britain's finest sections through the latest Jurassic/earliest Cretaceous (Tithonian/Berriasian age, *c*. 145 Ma) Purbeck Limestone Group are exposed in the 2 km coastal cliffs between Peveril Point and Durlston Head near Swanage in Dorset (Figure 4.45). The section is famous for its exceptionally diverse fauna, especially the vertebrates such as the fossil fishes (both marine and freshwater, see Dineley and Metcalf, 1999, pp. 405–15), reptiles (including 36 species of lizards, turtles, crocodilians, pterosaurs and dinosaurs) see Benton and Spencer, 1995, pp. 203–14) and mammals (see Benton *et al.*, 2005). It is also the most productive site in Europe for Tithonian/Berriasian age insects with about 200 described species belonging to 17 different orders being recorded from a number of different horizons within the Lower and Middle Purbeck strata.

Historically, many of the fossils, insects excepted, were recovered during commercial working of the limestones for building stone. The outcrop of some of the higher quality Purbeck 'Building Stones' was even pursued in underground workings. However, many other important finds were made in the 19th century by enthusiastic local collectors such as S.H. Beckles who collected 170 'lizard' specimens from the section, now recognized as belonging to seven genera. The section includes the type locality for the Purbeck Limestone Group (see Figure 4.46).

Durlston Bay is one of a network of Jurassic/Cretaceous boundary sites (see also the GCR site report for Poxwell, Dinton and Teffont Evias that preserve insects from within the

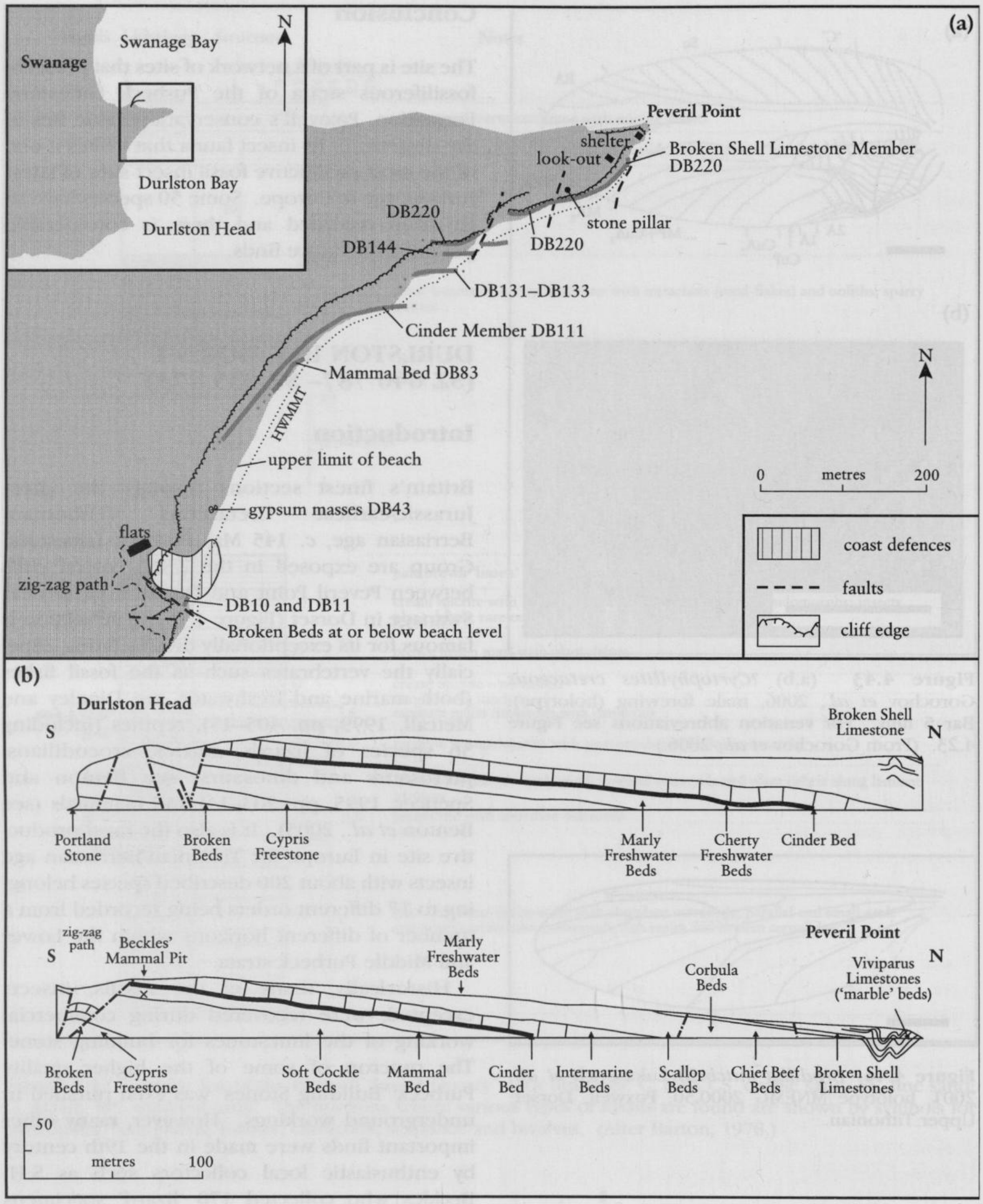


Figure 4.45 (a) Sketch map of the northern part of Durlston Bay (after Clements, 1993); letters and numbers refer to Clements' labelling of the beds. (b) Cliff profile at Durlston Bay. (After Benton and Spencer, 1995.)

Purbeck beds (Purbeck Limestone Group). In addition to the fossil arthropod importance of this site, the area is also selected for the GCR for the Mesozoic-Tertiary Fish/Amphibia, Mesozoic Mammalia, Portlandian–Berrisian and Jurassic-Cretaceous Reptilia selection categories.

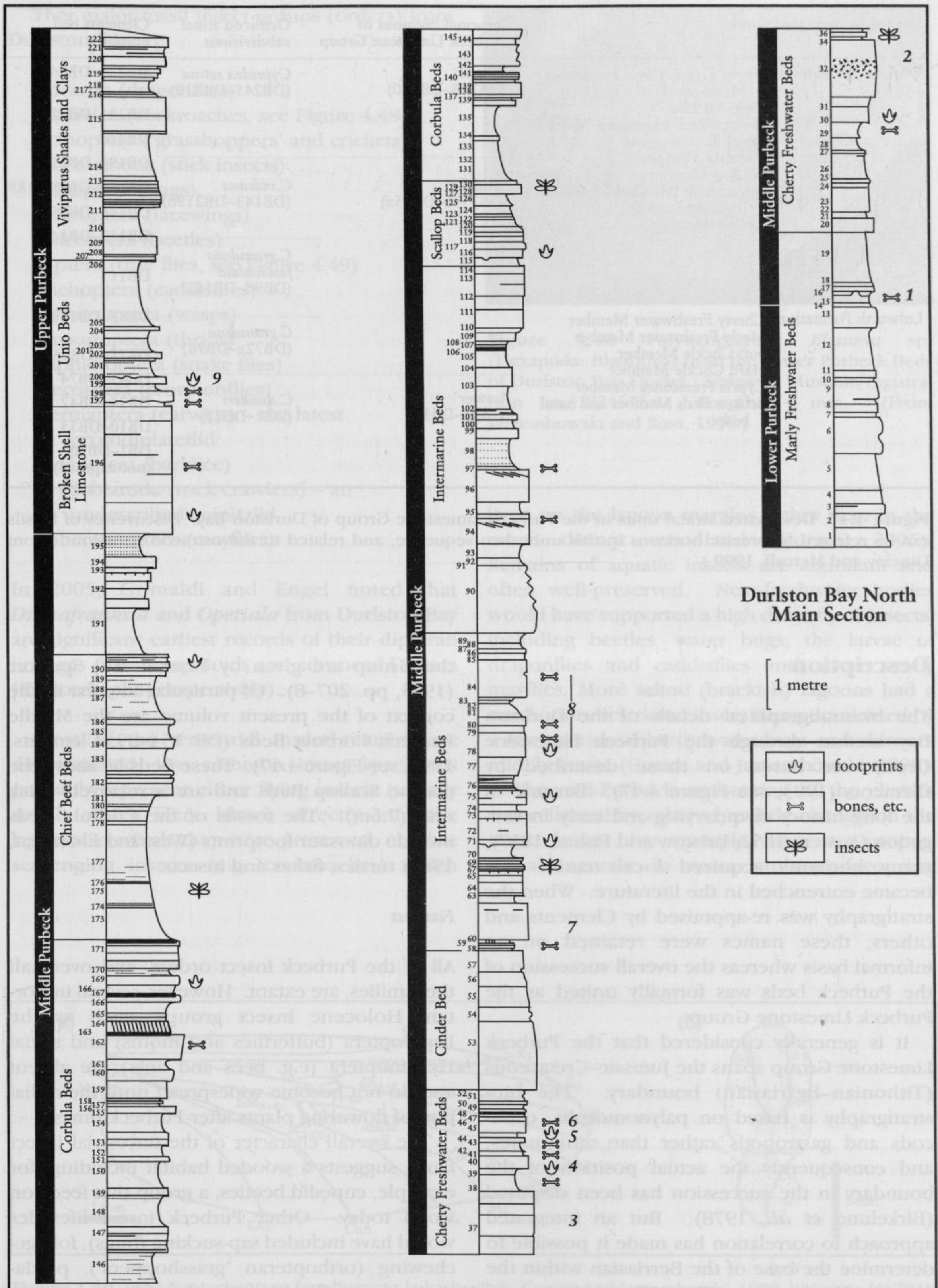


Figure 4.46 Stratigraphical section through the Purbeck strata at Durlston Bay. Numbers are those of Clements. (After Benton and Spencer, 1995; Coram and Jarzembowski, 1998.)

Formal stratigraphic terms		Informal divisions of Purbeck Limestone Group	Ostracod zonal subdivisions	Clements bed numbers
Durlston Formation	Upper Cypris Clays and Shales Member	'Upper' (DB246–DB220)	*Cypridea setina* (DB245–DB220)	DB224–DB245
	Unio Member			DB221–DB223
	Broken Shell Limestone Member			DB220
	Chief Beef Member			DB190–DB219b
	Corbula Member	'Middle' (DB219b–DB75a)	*C.vidrana* (DB143–DB219b)	DB154–DB188/189
	Scallop Member			DB146–DB153
	Intermarine Member (or Upper Building Stones)			DB112–DB145
	Cinder Member		*C.granulosa fasciculata* (DB97–DB142)	DB111
Lulworth Formation	Cherty Freshwater Member		*C.granulosa* (DB72a–DB96)	DB87–DB110
	Marly Freshwater Member			DB75a–DB86
	Soft Cockle Member			DB43–DB74
	Hard Cockle Member	'Lower' (DB74–DB1)	*C.dunkeri* (DB1–DB71)	DB34–DB42
	Cypris Freestones Member			DB10–DB33
	Broken Beds Member and basal beds			DB1–DB10 (not exposed)

Figure 4.47 Designated stratal units in the Purbeck Limestone Group of Durlston Bay. Discoveries of fossils can be referred to precise horizons in this unbroken sequence, and related to the ostracod zonation. (From Dineley and Metcalf, 1999.)

Description

The biostratigraphical details of the Durlston Bay section through the Purbeck Limestone Group are based on those described by Clements (1993, see Figure 4.47). Because of the long history of quarrying and early investigation (Austen, 1852; Bristow and Fisher, 1857), many horizons acquired local names that became entrenched in the literature. When the stratigraphy was re-appraised by Clements and others, these names were retained on an informal basis whereas the overall succession of the Purbeck beds was formally united as the Purbeck Limestone Group.

It is generally considered that the Purbeck Limestone Group spans the Jurassic–Cretaceous (Tithonian–Berriasian) boundary. The biostratigraphy is based on palynomorphs, ostracods and gastropods rather than ammonites, and consequently the actual position of the boundary in the succession has been disputed (Birkelund *et al.*, 1978). But an integrated approach to correlation has made it possible to determine the base of the Berriasian within the Soft Cockle Member (W. A. Wimbledon, pers. comm.).

Details of the fossil distribution throughout the Group are given by Benton and Spencer (1995, pp. 207–8). Of particular interest in the context of the present volume are the Middle Purbeck Corbula Beds (DB 154–89, Clements, 1993, see Figure 4.47). These Beds lie above the marine Scallop Beds and are a relatively thick unit (7.6m). The fossils of the Corbula Beds include dinosaur footprints (West and El-Shahat, 1985) turtles, fishes and insects.

Fauna

All of the Purbeck insect orders, and over half the families, are extant. However, several important Holocene insect groups, such as the Lepidoptera (butterflies and moths) and social Hymenoptera (e.g. bees and ants) are absent and do not become widespread until the radiation of flowering plants after Purbeck times.

The overall character of the terrestrial insect fauna suggests a wooded habitat including, for example, cupedid beetles, a group that feeds on wood today. Other Purbeck insect lifestyles would have included sap-sucking (bugs), foliage-chewing (orthopteran 'grasshoppers'), predation (dragonflies), scavenging (cockroaches), blood-sucking (horse flies) and parasitism (the larvae of some wasps).

Ther major fossil insect groups (orders) from Durlston Bay are:

Odonata (dragonflies)
Blattodea (cockroaches, see Figure 4.48)
Orthoptera ('grasshoppers' and crickets)
Phasmatodea (stick insects)
Hemiptera (bugs)
Neuroptera (lacewings)
Coleoptera (beetles)
Diptera (true flies, see Figure 4.49)
Trichoptera (caddisflies)
Hymenoptera (wasps)
Thysanoptera (thrips)
Raphidioptera (snake flies)
Mecoptera (scorpionflies)
Dermaptera (earwigs) – the latest
  protodiplatedid
Psocoptera (barklice)
Grylloblattida (rock crawlers) – an
  undescribed geinitziid
Ephemeroptera (mayflies)

In 2005, Grimaldi and Engel noted that *Dianafranksia* and *Opetiala* from Durlston Bay are significant earliest records of their dipteran lineages (basal empidoids and advanced Diptera [Cyclorrhapha] respectively).

Most of the terrestrial insect remains are disarticulated; less common intact specimens probably represent either flying insects (usually small) which were blown directly into the lagoons in which they were preserved, or were scavenging insects (e.g. cockroaches) which lived on the lagoon margins rather than in the more distant woodland (Coram, 2005). Remains of aquatic insects are abundant and often well-preserved. Near-freshwater bodies would have supported a high diversity of insects, including beetles, water bugs, the larvae of dragonflies and caddisflies and, more rarely mayflies. More saline (brackish) lagoons had a much more restricted insect fauna dominated by a few species of hardy water bugs and chironomid fly larvae (Coram and Jarzembowski, 1998).

The mid-Purbeck moistening of the climate was reflected by relatively subtle changes in the insect fauna. For example, there is a proportional increase in some moisture-favouring

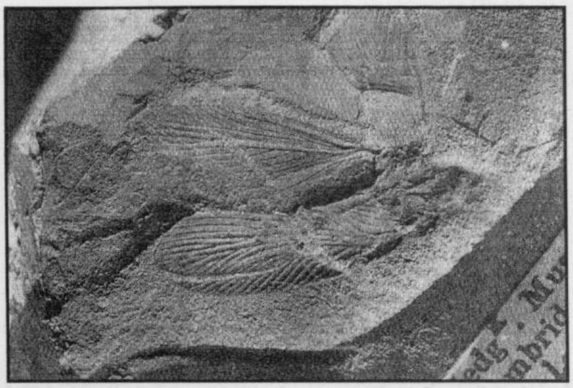


Figure 4.48 'Polyneopteran': *Elisama* sp. (Hexapoda: Blattodea) from the Lower Purbeck Beds of Durlston Bay, Dorset. Sedgwick Museum registration no. X24676a. Length 14 mm. (From Jarzembowski and Ross, 1996.)

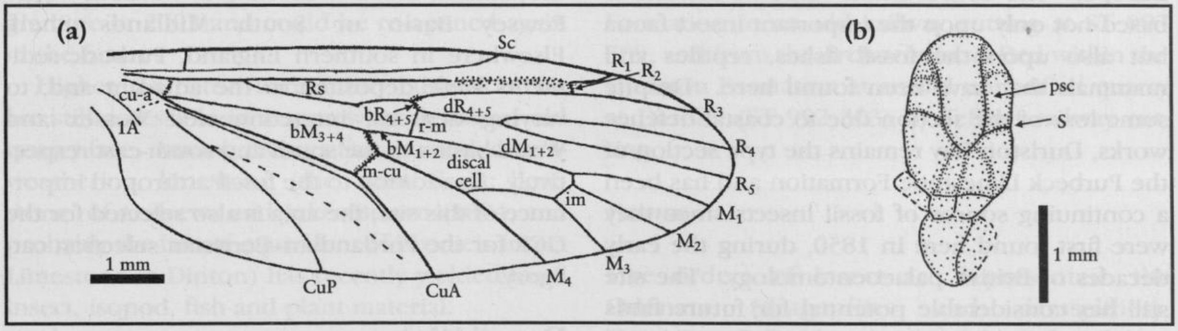


Figure 4.49 (a,b) *Eoptychoptera longifurcata* Lukashevitch, Coram and Jarzembowki, 1998, holotype MNEMG 1998.18, (a) wing; (b) thorax from Durlston Bay, Dorset, Lower Berriasian; (c) *Ptychoptera handlirschi*, thorax,. Scale bars 1.0 mm. (From Lukashevich *et al.*, 2001.)

terrestrial taxa (e.g. empidid dance flies), and a Middle Purbeck increase in caddisfly diversity probably resulted from the greater availability of fresher water for their larval development.

Interpretation

Although both Lower and Middle Purbeck insect-bearing horizons are within micrites, they represent slightly different environments of deposition. The soft white micrites of the Lower Purbeck were deposited under arid conditions whereas those blue-grey micrites of the Middle Purbeck formed under a wetter, Mediterranean-type climate.

Comparison with other localities

Lithological comparison between limestones producing insect fossils at Durlston Bay (Corbula Beds) and similar but younger (Eocene) age limestones in the Isle of Wight resulted in the discovery of a rich new insect-bearing locality near Cowes (see GCR site report for Thorness Bay).

Conclusions

The Purbeck beds of latest Jurassic–earliest Cretaceous (Tithonian–Berriasian age, *c.* 145 Ma) age in Durlston Bay, Dorset have provided Britain's richest Jurassic–Cretaceous insect fauna. The entomofauna includes around 200 described insect species and another around 1000 yet to be described, belonging to 17 orders ranging from beetles to mayflies. This is also the most productive site for insects of this age in Europe. The conservation value of the site is based not only upon the important insect fauna but also upon the fossil fishes, reptiles and mammals that have been found here. Despite some loss of the section due to coastal defence works, Durlston Bay remains the type section of the Purbeck Limestone Formation and has been a continuing source of fossil insects since they were first found here in 1850, during the early decades of British palaeoentomology. The site still has considerable potential for future finds and lithological comparison with late Eocene limestones in the Isle of Wight resulted in the discovery of a rich Tertiary insect fauna near Cowes (see GCR site report for Thorness Bay.

TEFFONT EVIAS, WILTSHIRE (ST 990 311 AND ST 994 309)

Introduction

Teffont Evias and the adjacent Vale of Wardour site of Dinton are both key sites in the history of British palaeoentomology. Lying on the north bank of the River Nadder, west of Salisbury, Teffont Evias (Figure 4.50), like the Dinton site, was originally excavated for limestone from the Purbeck beds in the early part of the 19th century. This Lower Cretaceous (Berriasian, *c.* 144 Ma) stone in the quarry has yielded several new insect species to that pioneer of the study of British fossil insects, the Reverend P.B. Brodie, who described them in his groundbreaking book (Brodie, 1845b). Since then, fossil insects have also been recovered from some nearby outcrops of the Purbeck limestone that also have potential for future finds.

Geological setting

In southern England the beginning of Purbeck times (corresponding approximately to the end of the Jurassic Period (see above), was marked by a regression in which the marine conditions that had dominated the region for most of the Jurassic Period were replaced by marginal marine (lagoonal), or non-marine, environments which persisted until the return of fully marine conditions in early Aptian times. The region comprised a complex of massifs bordered by the steadily widening Proto-Atlantic Ocean to the west, the Boreal Sea to the north-east and the Tethys Ocean to the south. Sediment was deposited in variably inundated basins between the massifs, those of the Vale of Wardour in the Pewsey Basin or South Midlands Shelf. Elsewhere in southern England, Purbeck sediments were deposited in the adjacent and, to varying degrees, interconnected Wessex and Weald basins to the south and south-east respectively. In addition to the fossil arthropod importance of this site, the area is also selected for the GCR for the Portlandian–Berrisian selection category.

Description

The insects found by Brodie occur in Lower–Middle Purbeck (Lulworth Formation)

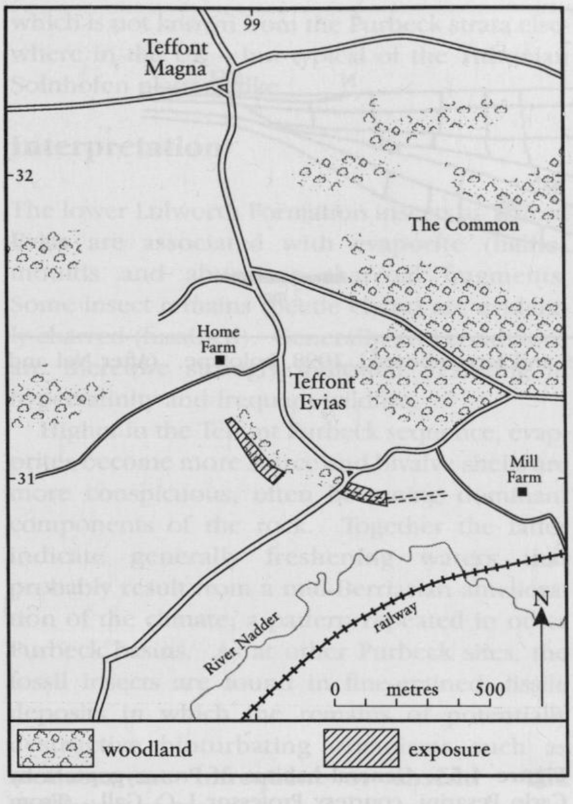


Figure 4.50 Location sketch map for the Teffont Evias GCR site.

Middle Purbeck (4.4 metres)	Soil	
	Rubble of white limestone	0.30
	Marly shale with a layer of 'beef' and lenticular seams of chert, crowded with silicified shells of *Cyclas*	0.30
	Rough, greyish, sandy limestone (Cinder Bed) with *Ostrea distorta*, *Trigonia gibbosa* and a spine of *Cidaris purbeckensis*	0.46
	Yellowish, calcareous, sandy shale	0.23
	Hard, grey, shelly limestone in three courses, with shaly partings; turtle bones, *Hybodus* spines, *Estheria subquadrata*, *Cypridea punctata*, *Cyprione bristovii*, *Cyprione* sp. and *Metacypris* sp.	0.84
	Dry, buff-coloured, sandy and calcareous shales (Scale) full of small *Modiola*; Pycnodont teeth	0.46
	Buff-coloured, marly clay	0.20
	Hard, compact, grey marlstone (White Lias), jointed vertically, no fossils found	0.61
	Dark grey or black shale with *Mesodon macropterus*, *Estheria andrewsii*, *Cypridea fasciculata* and *C. punctata*	0.05
	Hard, grey, shelly limestone showing ripple marks and sun cracks, splitting into slabs which are used as flagstones; *Cypridea fasciculata*, *Cyclas*, fish vertebrae and scales (Tilestone or Flagstone)	0.46
	Yellowish laminated shale with layers of crushed shells	0.18
	Brown and black, shaly clay contains *Cypris purbeckensis* plentifully, *C. fasciculata* (less common), *Estheria andrewsii?*, *Cyclas* and scales of *Lepidotus*	0.30
Lower Purbeck (5.1 metres)	Very hard, compact, grey marlstone (Lias No. 2); fish remains: *Leptolepis*, *Coccolepis* and *Pleuropholis*, with *Archaeoniscus* and wing cases of Coleoptera	1.07
	Brown clay	0.15
	Soft, yellowish, marly sand	0.46
	Hard grey marlstone, very heavy (Lias No. 3), with *Cypris purbeckensis*, *Pleuropholis*, insect remains (Coleoptera and *Libellula*) and plants (*Palaeocyparis*)	1.07
	Brown clay (generally the floor of the quarry)	0.10
	Yellowish sandy marl with oolitic grains and a thin layer of compact marlstone near the top; contains Cyprids (*purbeckensis*) and crocodile scales	0.76
	Grey marly limestone	0.15
	Soft yellowish marl	0.20
	Grey marlstone (or Lias), with vertical jointing	0.38
	Soft sandy marl	0.15
	Hard grey and brown marlstone, compact and heavy, with ochreous patches and markings	0.61+

Figure 4.51 Section of Teffont Evias quarry metricated. (After Andrews and Jukes-Brown, 1894.)

limestones, originally called 'Lias' by quarrymen in the early 19th century; the insects are associated with the biozonal ostracod *Cypridea granulose* (Figure 4.51). The insect-bearing 'Lias' beds are no longer permanently exposed, although they were temporarily re-exposed by English Nature as part of a their 'Facelift' programme in 2002 and could be re-opened again in the future.

Higher (Durlston Formation) Purbeck strata are still accessible in a somewhat degraded old quarry face. Among these, a fine-grained, cream-weathering, limestone (the 'white-fissile limestone' of Andrews and Jukes-Brown (1894, and probably the lateral equivalent of Brodie's Insect Limestone at Dinton) has recently yielded fossil insect, isopod, fish and plant material.

Also, in recent years, new fossil insects, including the narrow-winged, protozygopteran 'dragonfly' *Saxomyrmeleon keatingei* Nel and Jarzemboski, 1998 (Figures 4.52 and 4.53) have been recovered from relatively soft creamy-grey micrites in the lower part of the Lulworth Formation in an old railway cutting at ST 993 309, and from the *Archaeoniscus* Bed within the Durlston Formation at an old unnotified quarry at Dashlet (ST 992 303) by Teffont railway cutting.

Fauna

Five orders of insect are represented: the Odonata (dragonflies and damselflies), Hemiptera (plant bugs), Neuroptera (lacewings) (Figure 4.54), Diptera (true flies) and Coleoptera (beetles). Several taxa (e.g. the lacewing family Kalligrammatidae, Figure 4.54)

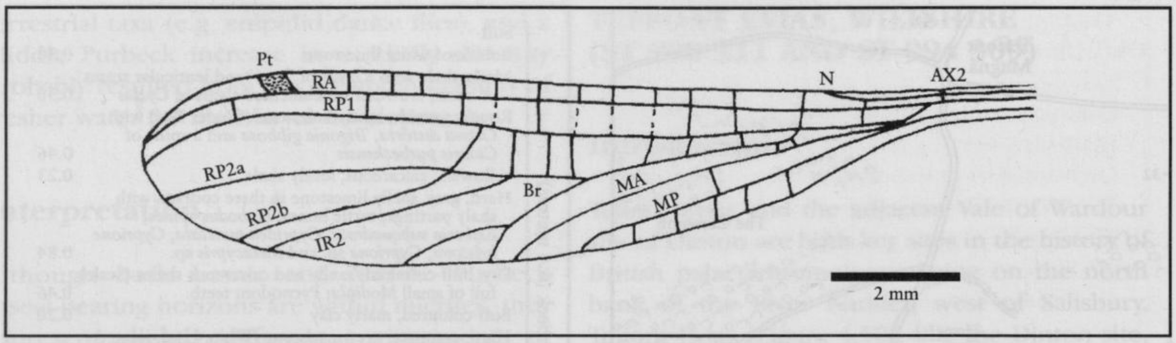


Figure 4.52 Venation of *Saxomyrmeleon keatingei* Nel and Jarzembowski, 1998, holotype. (After Nel and Jarzembowski, 1998.)

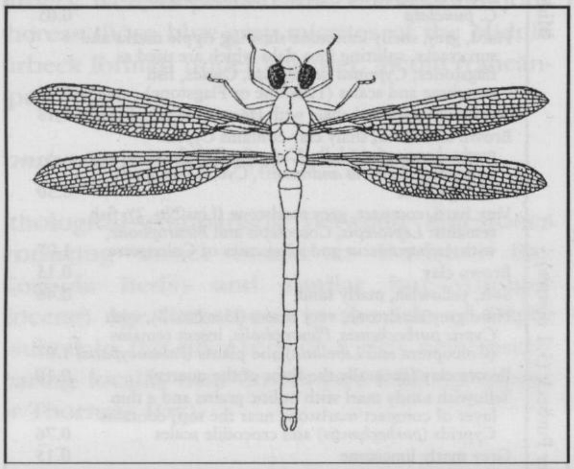


Figure 4.53 General habitus of Protozygoptera by Carlo Pesarini, courtesy Professor J.-C. Gall. (From Nel and Jarzembowski, 1998.)

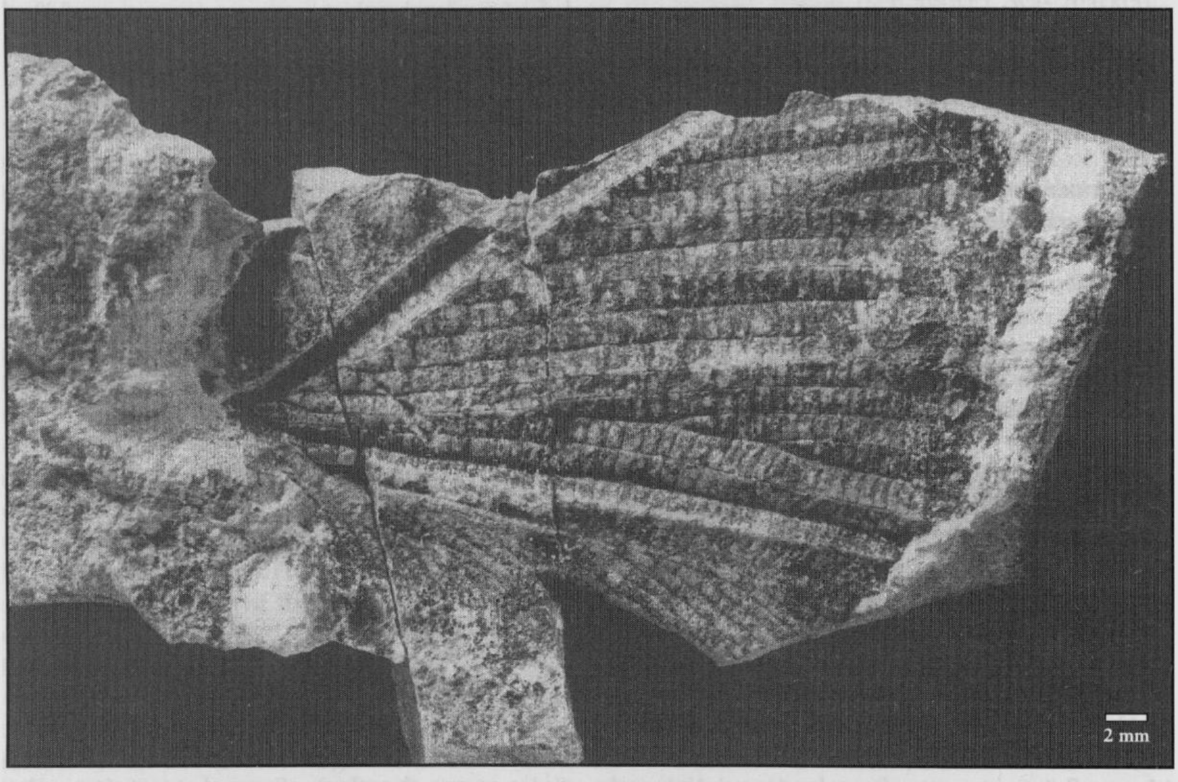


Figure 4.54 Undescribed kalligrammatid lacewing from the Lulworth Formation of Teffont Evias. (From Ross and Jarzembowski, 1996.)

which is not known from the Purbeck strata elsewhere in the UK – but typical of the Tithonian Solnhofen plattenkalke.

Interpretation

The lower Lulworth Formation insects at Teffont Evias are associated with evaporite (halite) moulds and abundant charcoal fragments. Some insect remains (beetle elytra) are evidently charred (fusained). Generally, arid conditions are therefore strongly indicated, resulting in hypersalinity and frequent wildfire.

Higher in the Teffont Purbeck sequence, evaporites become more scarce and bivalve shells are more conspicuous, often becoming dominant components of the rock. Together the latter indicate generally freshening waters that probably result from a mid-Berriasian amelioration of the climate; a pattern repeated in other Purbeck basins. As at other Purbeck sites, the fossil insects are found in fine-grained, fissile deposits in which the remains of potentially destructive bioturbating organisms such as molluscs are infrequent or absent. The restriction of molluscs in the lower part of the Purbeck sequence can probably be best explained by hypersalinity: in higher insect beds by factors such as isolation, salinity fluctuations or water impermanence. For example, the cypridiid ostracods associated with the 'Lias' insects may indicate relatively fresh, but impermanent, water conditions.

Conclusion

Although at the time of writing largely obscured, the original Lower Cretaceous site of Teffont Evias (*c.* 140–145 Ma) is a key one in the history of British palaeoentomology. Its conservation value is largely derived from the diverse fauna of fossil insects obtained from here in the past and described in the first major study of British fossil insects by the Rev. P. B. Brodie. However, the recovery of new fossil insects from both this and adjacent outcrops in recent years shows that there is still considerable potential for future finds. The historical and scientific importance of the insects from here, combined with the stratigraphical and wider palaeontological interest in the site and adjacent outcrops, makes this one of the most important Purbeck localities outside the typical area of Dorset.

DINTON, WILTSHIRE (SU 006 307)

Introduction

Dinton and the adjacent Teffont Evias are two insect-bearing GCR sites in the Purbeck strata (Berriasian, basal Cretaceous age, *c.* 143 Ma) just west of Salisbury in the Vale of Wardour. The Dinton site is a former stone quarry which lies just north of the River Nadder (Figures 4.55 and 4.56) and is of considerable historical importance. It is the main source of the 'Wealden' (Purbeck) insects described in the first book on fossil insects in the English language (Brodie, 1845b). Brodie's pioneering text 'opened up a new aspect of palaeontology' (Cleevely, 1983). Over 70 insect species and an isopod are known from the locality, all occurring in fine-grained limestone. The original quarry was already abandoned and neglected in the 1830s when visited by the Reverend Brodie and subsequently the exact location became lost. The land was inaccessible for a long time as it was taken over by the Ministry of Defence. However, it has now been made available for public use and Brodie's site was re-discovered by an excavation team from the Nature Conservancy Council in 1983 and the 'Insect Limestone' revealed in subsequent site management work as part of the former English Nature's 'Facelift' programme in

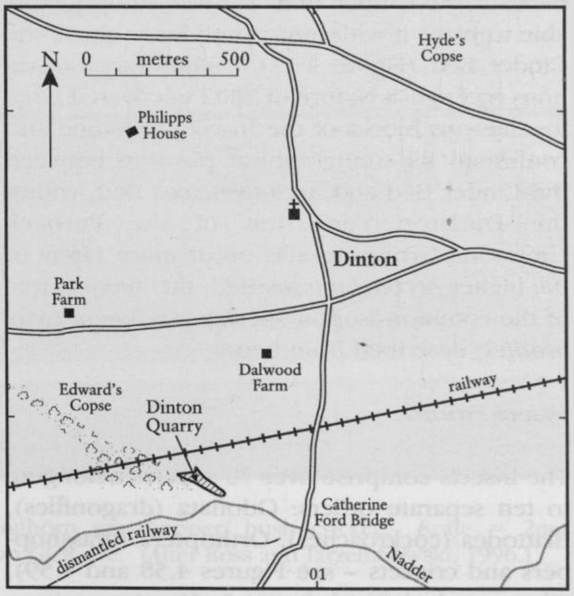


Figure 4.55 Location of the Dinton Quarry GCR site.

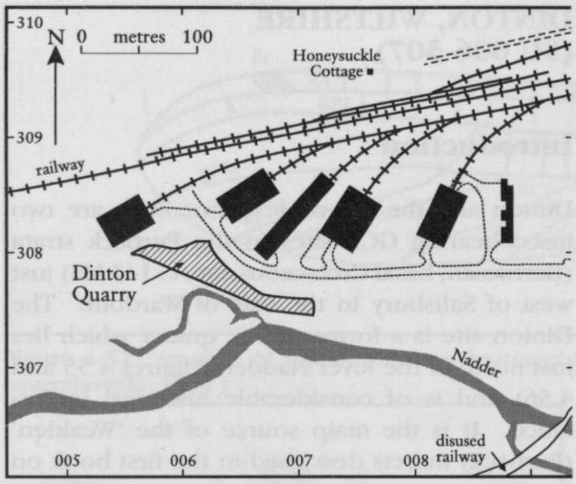


Figure 4.56 Detailed location map of the Dinton Quarry GCR site.

	metres
1. Clay forming the surface a few centimetres	
2. White limestone	0.08
3. Clay	0.05–0.08
4. White limestone, similar to No. 2, containing shells (chiefly Cyclas), a few Unios and Cypris	0.08–0.10
5. Crystalline grit with *Cyclas major*	0.05
6. Clay	0.08
7. Clay with layers of grit	0.08
8. Clay	0.05–0.08
9. Light brown sandstone full of small *Cypris* and *Cyclas*, consisting in the lower part of comminuted shells	0.46
10. Blue and brown clay with innumerable fragments of shells	0.08–0.10
11. Thin-bedded grit	0.05
12. Fibrous carbonate of lime	0.15
13. Grit	
14. Fibrous carbonate of lime	
15. Soft shelly sandstone	0.05
16. Light brown and blue limestone abounding in the Isopod Crustacean (*Archaeoniscus*), in the lower part laminated with numerous *Cyclas* and oysters	0.15–0.20
17. Blue compact grit full of impressions of *Cyclas* and oysters	0.05–0.08
18. White laminated crystalline limestone, very different from Nos. 2 and 4 – probably	0.61
Total	2.24

Figure 4.57 The section through Purbeck strata exposed at Dinton as measured by Brodie (1845b) but metricated.

2002. In addition to the fossil arthropod importance of this site, the area is also selected for the GCR for the Portlandian–Berrisian and Wealden selection categories.

Description

The great majority of Brodie's (1845b) insects came from the 'Insect Limestone', which is a *c.* 30 cm thick, blue-grey micrite when fresh and weathering to white. It also has a gritty basal lag of shell and fish debris. Brodie was unable to examine this bed *in situ* and surmised that it lay beneath the Cinder Bed. He was subsequently able to place it with more confidence above the Cinder Bed (Figure 4.57). Temporary excavations by English Nature in 2002 uncovered large fossiliferous blocks of the Insect Limestone and confirmed its stratigraphical position between the Cinder Bed and *Archaeoniscus* Bed, within the Durlston Formation of the Purbeck Limestone Group. Insects occur more rarely in the higher *Archaeomiscus* Bed, the main source of the common isopod species (*Archaeomiscus brodiei*) described from here.

Insect Fauna

The insects comprise over 70 species belonging to ten separate orders: Odonata (dragonflies), Blattodea (cockroaches), Orthoptera (grasshoppers and crickets – see Figures 4.58 and 4.59), 'Phasmatodea' ('stick insects'), Hemiptera (true bugs), Coleoptera (beetles), Mecoptera (scorpionflies), Diptera (true flies – see Figure 4.60), Trichoptera (caddisflies) and Hymenoptera (wasps) (Ross and Jarzembowski, 1996; Rasnitsyn *et al.*, 1998). The majority of described insect species are unique to this site, although this no doubt simply reflects the incomplete sampling of hyperdiverse Purbeck insect faunas.

Interpretation

The Insect Limestone may well correlate with the lithologically and faunistically simiar 'white fissile limestone' recorded by Andrews and Jukes-Brown (1894) right across the Wardour outcrop of Middle Purbeck limestones, in which case it would have been deposited in a water body at least 5 km across. A degree of marine connection is suggested by the probable presence of glauconite and perhaps the relatively frequent leptolepiform fish, which, in some cases at least, occur in mass-mortality accumulations (Coram, 2005).

However, the presence of *Cypridea* [*Cypris* auct.] ostracods suggests that water conditions were also fairly fresh at times, and the apparent absence of the remains of immature aquatic insects may be explained by stressful salinity fluctuations between fresh- and near-marine

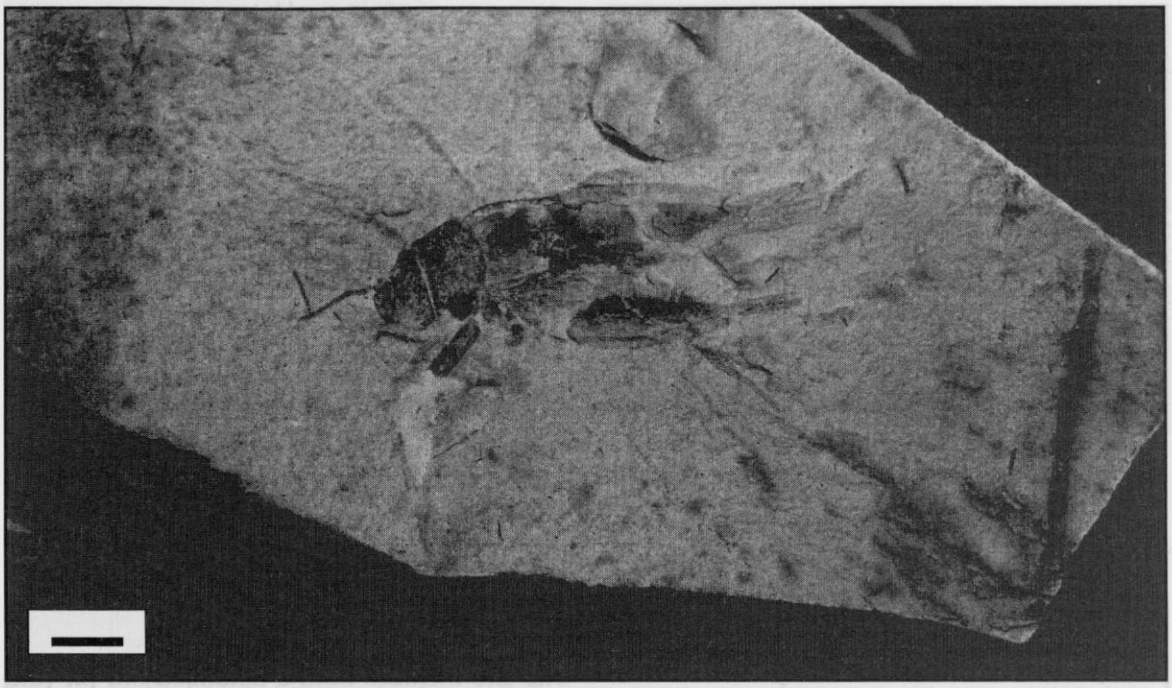


Figure 4.58 *Protogryllus segwickei* (Brodie), a cricket Scale = 2mm. *Archaeoniscus* Bed (Isopod Limestone) from the Dinton GCR site. (From Ross and Jarzembowski, 1996.)

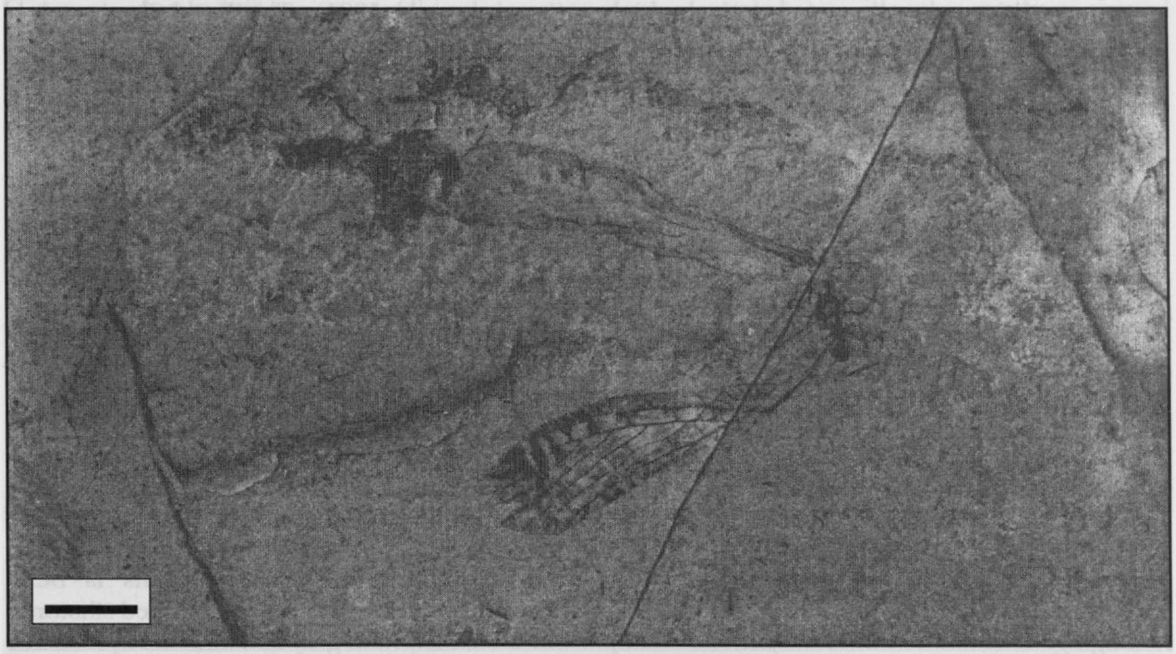


Figure 4.59 *Panorpidium dubium* (Giebel), a longhorn grasshopper/ bush cricket. Scale = 2mm. *Archaeoniscus* Bed (Isopod Limestone) from the Dinton GCR site. (After Ross and Jarzembowski, 1996.)

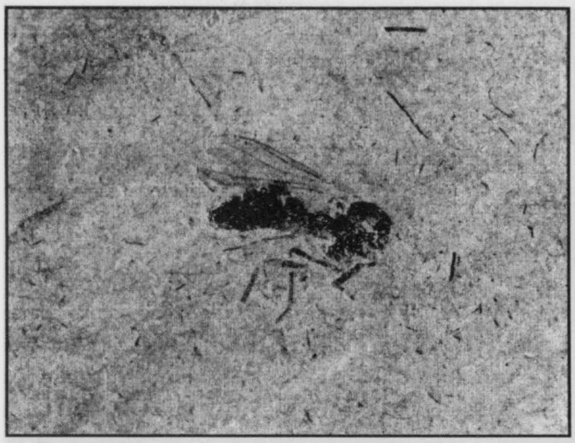


Figure 4.60 *Olbiogaster fittoni* (Brodie), a true fly, × 6. From the Insect Limestone of the Dinton GCR site. (From Ross and Jarzembowski, 1996.)

waters. Conditions probably never became strongly hypersaline since there is no evidence of evaporites.

The remains of adult insects such as dragonflies and caddisflies, which have aquatic larvae, indicates that there were also more-stable freshwater conditions locally. A relatively high proportion of intact terrestrial insect fossils, along with common plant remains and abundant quartz grains, suggest that there was emergent land fairly close by (probably to the south).

Conclusion

The Dinton GCR site is a locality of international importance from which a rich diversity of fossil insects has been obtained. The insects were found within the Purbeck limestones of the Durlston Formation. The conservation value of the site lies in its historic importance and the potential for further excavation of the site.

This historically important basal Cretaceous site in Middle Purbeck limestones (*c.* 143 Ma) has provided some 70 fossil insects including the type specimens of a number of species belonging to some 10 different orders. They were the main source of the early Cretaceous insects described by Brodie in 1845, in the earliest book on fossil insects in the English language.

CLOCKHOUSE BRICKWORKS, SURREY
(TQ 176 383)

Introduction

This early Cretaceous site is part of a network of GCR sites (see also GCR site reports for Smokejacks and Auclaye brickworks) in the Weald Clay (*c.* 130 Ma) of southern England. It has produced an abundant (several thousand fossils), and diverse (13 orders known at present) insect fauna, including one of the earliest described social insects, a termite, along with other important faunal elements such as *Iguanodon* dinosaur remains.

Description

The site includes both a landfilled old pit (the 'Clockhouse' of the British Geological Survey reports) south of the brickworks, and new pits on the east. Some 35 m of gently dipping (1.5°N) Lower Weald Clay are exposed beneath BGS bed numbers 3a and 3 (Okehurst and Clockhouse Sands respectively, Figure 4.61) (Jarzembowski, 1991). The Weald Clay is mainly non-marine, but a stratigraphically significant brackish/quasi-marine or 'Cassiope' band occurs near the base of the pit and is intermittently exposed here.

Fauna

The Clockhouse Brickworks site has yielded the largest number of insect remains in the Wealden deposits (several thousand specimens) and is the main fossil insect site in the Weald. The fossil insects invariably occur in lenticles and basin casts of calcareous siltstone that are usually well cemented with cross-bedded lamination internally, and fine sole markings on the underside of the beds. This is an unusual type of preservation not found elsewhere in Eurasia. The detail on small insect fossils is best-preserved in a pale yellow, fine-grained siltstone, but a coarser, blue-grey siltstone also preserves some larger specimens. The siltstones occur between Bed 3 and the 'Cassiope' band (Gallois and Worssam, 1993) and are considered to be scour fills from turbidity flows down crevasse splays or new fluvial channels.

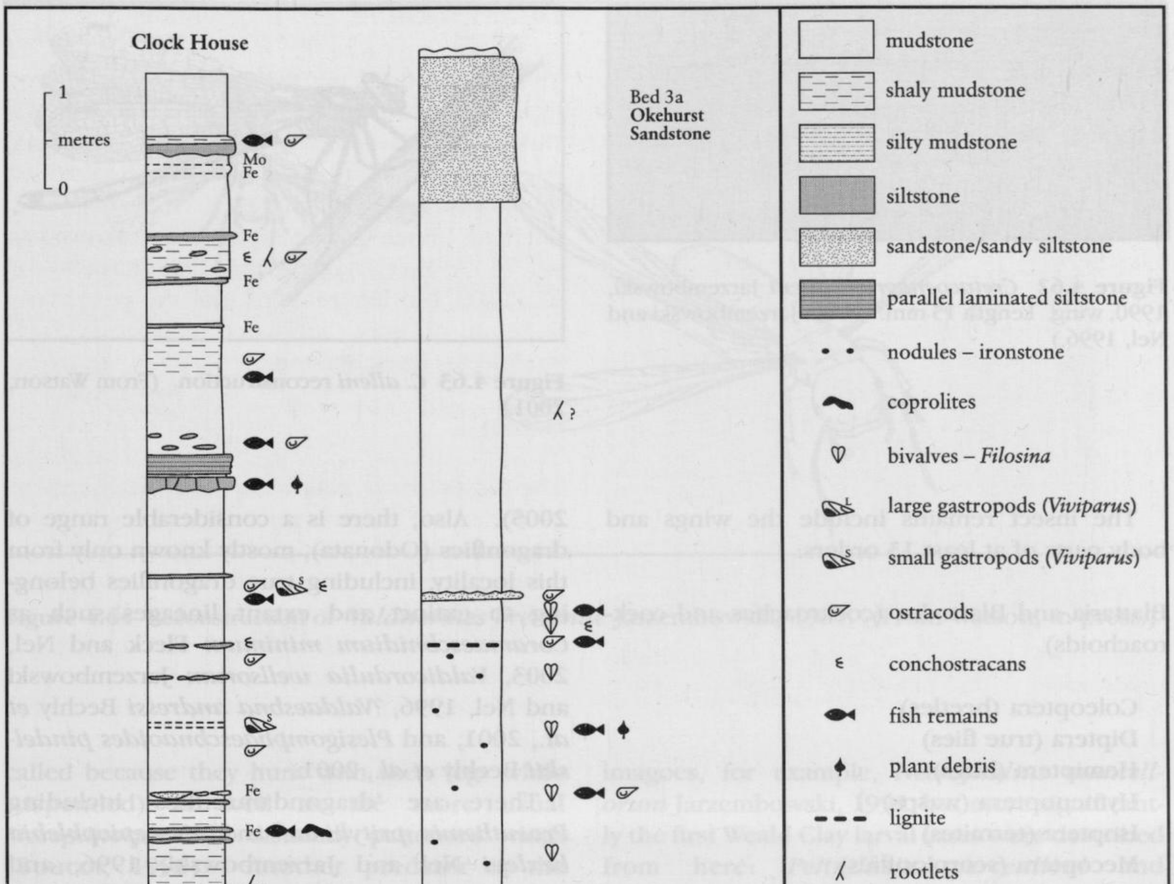


Figure 4.61 Composite lithological log (a, b) of the upper part of the Lower Division of the Weald Clay Formation exposed in the 'new' pit at Clockhouse Brickworks, based on unpublished field notes and Horne (1988, figs 9 and 10). The beds yielding bones other than those of fish, and the colours of the deposits are not shown. Sampling horizons are indicated on the left-hand side of the column. The inset beneath it, shows the stratigraphical location and extent of the section relative to BGS beds 3, 3a, 3c and 5c, and compared to that at Smokejacks Brickworks (S).

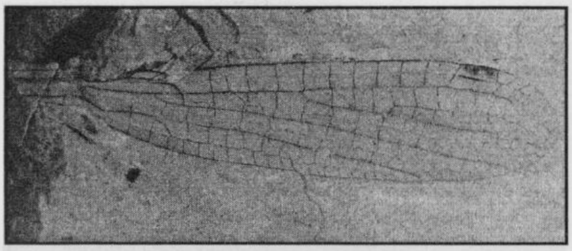


Figure 4.62 *Cretacoenagrion alleni* Jarzembowski, 1990, wing. Length 15 mm. (From Jarzembowski and Nel, 1996.)

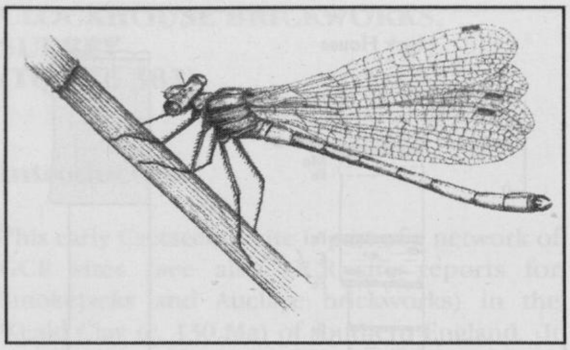


Figure 4.63 *C. alleni* reconstruction. (From Watson, 2001.)

The insect remains include the wings and body parts of at least 13 orders:

Blattaria and Blattodea (cockroaches and cockroachoids)

Coleoptera (beetles)
Diptera (true flies)
Hemiptera (bugs)
Hymenoptera (wasps)
Isoptera (termites)
Mecoptera (scorpionflies)
Neuroptera (lacewings)
Odonata (dragonflies)
Orthoptera (crickets and grasshoppers)
Psocoptera (barklice)
Raphidioptera (snakeflies)
Trichoptera (caddisflies)

The insects are associated with burrows, conchostracan (spinicaudate) carapaces (which are commonly comminuted), ostracods, isopods, amphipod- and astacuran-like crustaceans, coprolites, fish teeth, scales, bones and egg cases, bivalves (*Filosina*, *Unio,* which are often fragmented), occasional gastropods (*Viviparus*) and operculae, and plant remains (wood, comminuted debris, pieces of *Weichselia* and *Bevhalstia* plus rootlets).

The insects are occasionally fusainized (charred) like plants (a few Blattodea and Coleoptera, e.g. *Coleopteron semicrematus* Jarzembowski, 2003). This pit has yielded the critical material of *Valditermes brenanae* Jarzembowski 1981 (Figure 4.64, an internationally important genus and species because it is the most basal fossil termite and one of the earliest-known social insects (Grimaldi and Engel, 2005). Also, there is a considerable range of dragonflies (Odonata), mostly known only from this locality, including true dragonflies belonging to extinct and extant lineages such as *Coramaeschnidium minimum* Fleck and Nel, 2003, *Valdicordulia wellsorum* Jarzembowski and Nel, 1996, *?Valdaeshna andressi* Bechly *et al.*, 2001, and *Plesigomphaeschnaoides pindelskii* Bechly *et al.*, 2001.

There are 'dragondamselflies' including *Proeuthemis pritykinae* and *Mesoepiophlebia bexleyi* Nel and Jarzembowski, 1996, and *Turanophlebia anglicana* Fleck *et al.*, 2004. There are true damselflies including *Cretalestes martinae* Jarzembowski *et al.*, 1998 and *Cretacoenagrion alleni* Jarzembowski,1990 (Figures 4.62 and 4.63) – in its own family Cretacoenagrionidae – and even 'archaic damselflies' (Nel and Jarzembowski, 1998).

In the absence of ants, cockroaches and cockroachoids (Blattaria and Blattodea) are numerically second only to Coleoptera (beetles). Orthoptera are represented by both main subdivisions and new species of crickets and 'grasshoppers' are described by Gorochov *et al.* (2006). Hemiptera described from here include *Penaphis woollardi* Jarzembowski, 1989, an uncommon aphid probably associated with gymnosperms, and three species of Progonocimicidae – a coleorrhynchan family with Southern Hemisphere affinity: *Yuripopovia woottoni* Jarzembowski, 1991, *Ildavia sherbakovi* and *Valdiscytina jarzembowskii* Popov in Klimaszewski and Popov (1993).

Mecoptera from here include *Antiquanabittacus nanus* Petrulevičius and Jarzembowski, 2004, a rare representative of the now exotic family Bittacidae (hangingflies – so-

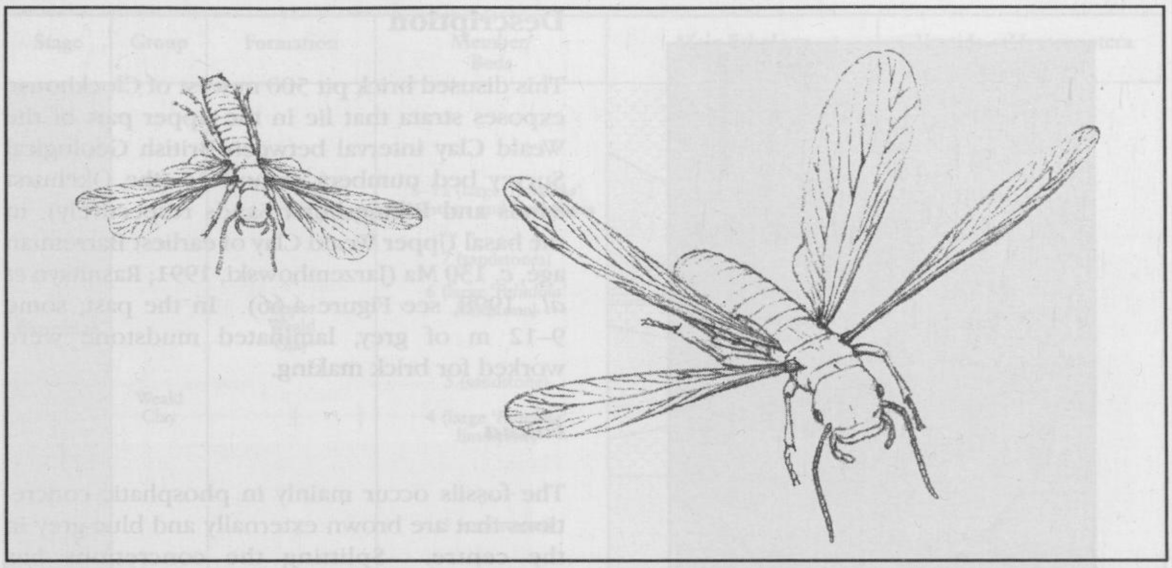


Figure 4.64 Reconstruction of *Valditermes brenanae* Jarzembowski, 1981. (From Watson, in press.)

called because they hunt with their legs while suspended) as well as the more usual *Mesopanorpa* with distinctly patterned wings (Boucot, 1990). Another predator is the snakefly *Proraphidia hopkinsi* Jepson and Jarzembowski, 2008 which would have hunted insects such as *Penaphis* (above) in a snake-like manner by analogy with Holocene species. Fragile Diptera are surprisingly common and include crane-flies ('*Architipula*' *austeni* and ?*Gynoplistia mitchelli* Jarzembowski, 1991) and false craneflies (*Eoptychopterina camura* and *Zhiganka woolgari* Lukashevitch, Coram and Jarzembowski, 2001) as well as a snipe-fly (*Ptiolinites raypearcei* Mostovski *et al*. 2000) and biting snipe-fly (*Athericites finchi* Mostovski, Jarzembowski and Coram, 2003). Another basal brachyceran, *Sinonemestrius akirai* Jarzembowski and Mostovski, 2000, has Chinese affinities. A non-biting mosquito (chaoborid) was figured by Coram and Jarzembowski (1998).

Hymenoptera described from here include a probable parasitoid of cockroaches (*Cretevania concordia*) plus various digger wasps (*Archisphex proximus*, *Angarosphex consensus*, *A. bleachi*, ?*Baissodes* sp., ?*Pompilopterus worssami*, ?*P. leei* Rasnitsyn & Jarzembowski in Rasnitsyn, Jarzembowski and Ross (1998). Trichoptera include two species based on imagoes, for example, *Necrotaulius mantellorum* Jarzembowski, 1991, but more significantly the first Weald Clay larval cases were described from here: *Pelindusia percealleni* and *Piscindusia sukachevae* Jarzembowski, 1995 (Figure 4.65); the latter ichnogenus is uniquely Wealden (Grimaldi and Engel, 2005).

Interpretation

The sedimentological setting in which the insects occur suggests that the remains were naturally concentrated in fills within a fluviatile environment of deposition. The insects occur in siltstone concretions whose structure indicates that they are indeed lithified current scour fills.

Due to its unique sedimentary environment, this locality has yielded the greatest diversity and abundance of fossil insects in the Weald Clay. The entomofauna represents a complex terrestrial community living' on the wooded edge of a muddy wetland with some more remote fresh water elements (Jarzembowski, 1995). The insects lived in and on growing and rotting marginal vegetation, accompanied by their predators, parasites and scavengers.

Valditermes and other insects support the interpretation of the climate as a humid 'Mediterranean' one (Coram and Jarzembowski, 2002; Ross *et al*., 2000).

Figure 4.65 Caddis case: holotype of *Piscindusia sukachevae* Jarzembowski, 1995. (From Jarzembowski, 1995.)

Conclusion

The Lower Weald Clay of Clockhouse Brickworks near Capel, Surrey is the most productive strata for fossil insects of Early Cretaceous age in southern England. The conservation value of the site lies in the abundance, diversity and scientific value of its insect fauna which includes one of the earliest records of a social insect, the termite *Valditermes brenanae*. Potential for future finds is good as the site is actively worked for brick making, and insect-bearing siltstones are regularly exhumed.

AUCLAYE, SURREY
(TQ 168 388)

Introduction

Part of a network of Weald Clay arthropod GCR sites (see also GCR site reports for Smokejacks Pit and Clockhouse Brickworks), this early Cretaceous site (earliest Barremian, *c*. 130 Ma) in the Mole Valley, Surrey, has produced a diverse fauna of insects belonging to eight different orders.

Description

This disused brick pit 500 m west of Clockhouse exposes strata that lie in the upper part of the Weald Clay interval between British Geological Survey bed numbers 3a and 3c (the Okehurst Sands and Billingshurst Sands respectively), in the basal Upper Weald Clay of earliest Barremian age, *c*. 130 Ma (Jarzembowski, 1991; Rasnitsyn *et al*., 1998, see Figure 4.66). In the past, some 9–12 m of grey, laminated mudstone were worked for brick making.

Fauna

The fossils occur mainly in phosphatic concretions that are brown externally and blue-grey in the centre. Splitting the concretions has revealed various insect fossils, some small plant remains including charcoal (fusain) and wood, occasional fish scales, bones and egg cases, coprolites and isopod remains. Carapaces of a conchostracan (clam shrimp) are locally abundant, but lamellibranchs and ostracods are rare, suggesting ecological opportunism on a variable-salinity mudplain.

Trace fossils in the form of thin burrows of the worm *Cochlichnus* also occur and are sometimes associated with insect remains. Other vertical, pyritized, tubular trace fossils probably record the past presence of wetland plants.

The phosphatic preservation of the Wealden insects shows the greatest amount of detail known for fossil insects with the exception of preservation in amber. Thus the best-preserved Wealden dragonfly (odonatan) known, *Valdaeshna surreyensis* Jarzembowski, 1988, was found here (see Figure 4.69, from Jarzembowski and Nel, 1996b). Its preservation has allowed reconstruction of an insect unlikely ever to be found fossilized in amber. This extinct hawker enjoys its own subfamily Valdaeshninae (Bechly *et al*., 2001). Other true dragonflies found here include a new species of the late Mesozoic family Aeschnidiidae (Fleck and Nel, 2003) and the widespread (i.e. found at the other Wealden localities) small darter *Cretaneophya strevensi* Jarzembowski and Nel 1996. Damselflies include another widespread species *Cretarchistigma greenwoodi* Jarzembowski *et al*., 1998.

In addition to Odonata, insects recorded – mainly from wings – include:

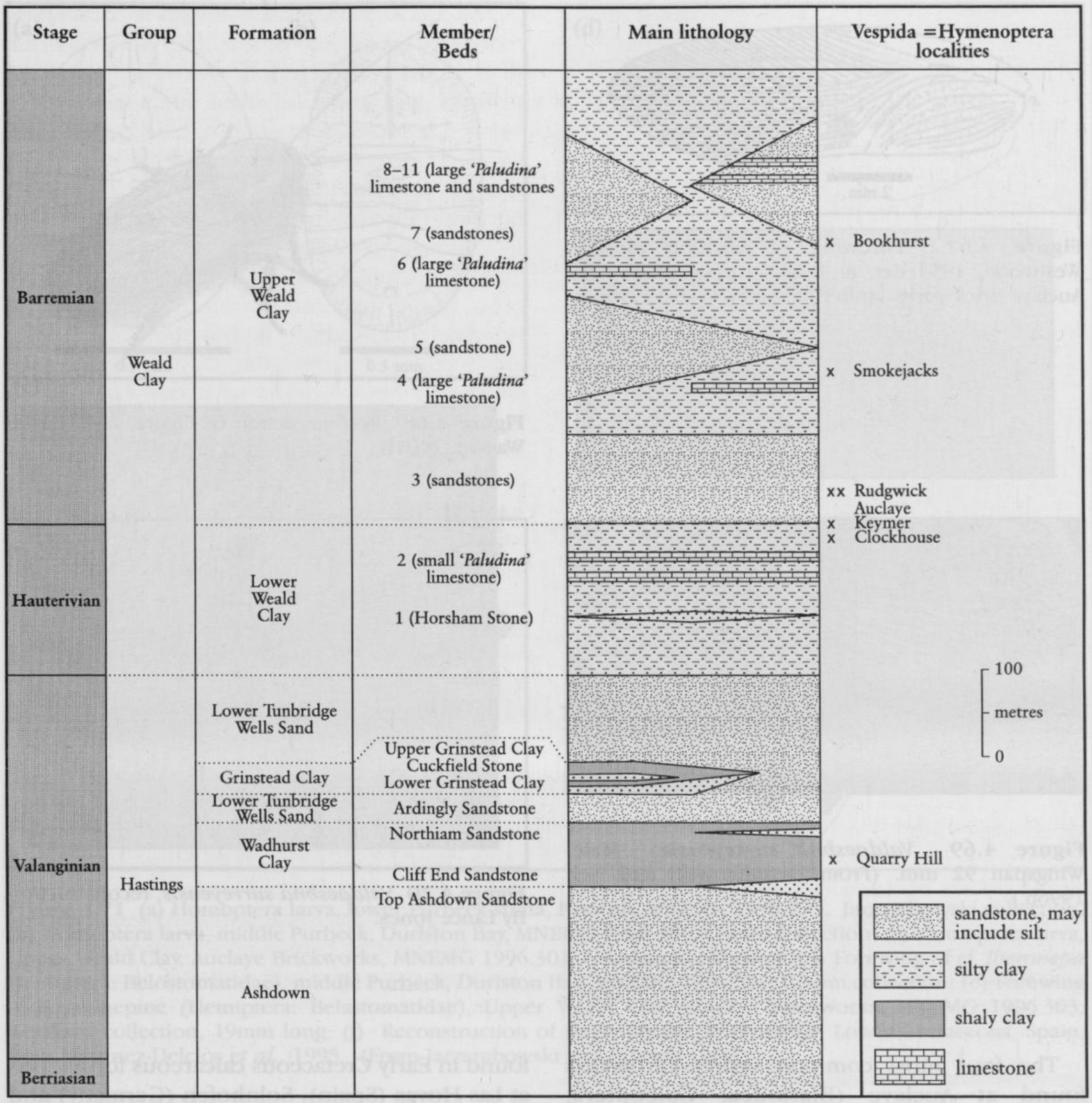


Figure 4.66 The stratigraphy of the Wealden Supergroup of the Weald, showing the localities (pits) where Vespida have been found. (From Rasnitsyn *et al.*, 1998.)

Coleoptera (Beetles)
Blattaria/Blattodea (Cockroaches and cockroachoids)
Hemiptera (Bugs)
Othoptera (Crickets and grasshoppers)
Diptera (True flies)
Hymenoptera (Wasps)
Neuroptera (Lacewings)
Mecoptera (Scorpionflies)
Trichoptera (Caddisflies)

Further, unique finds of Raphidioptera (snakeflies) and Isoptera (termites) have been recorded since the graph drawn in Jarzembowski (1991). The predominance of Coleoptera and Blattodea over other orders is typical of the Weald Clay (Jarzembowski, 1995). As Isoptera had separated by this time, true cockroaches are present as well as the usual Palaeozoic–Mesozoic cockroachoids (Figures 4.67 and 4.68, the long-ranging blattarian *Elisama molossa* Westwood).

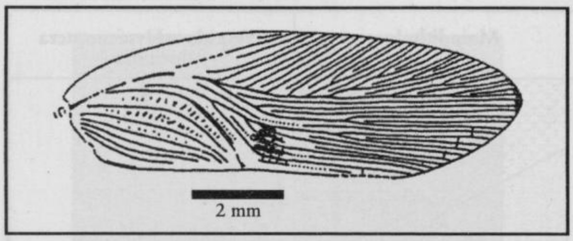


Figure 4.67 Forewing of *Elisama mollosa* Westwood, 1854 det. A. Ross. Upper Weald Clay, Auclaye Brickworks. (After Jarzembowski, 1999b.)

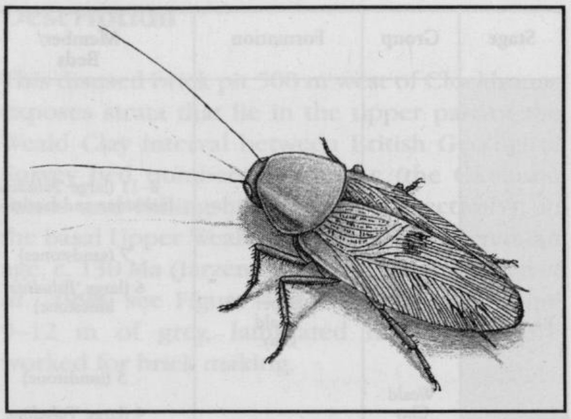


Figure 4.68 Reconstruction of Figure 4.67. (From Watson, 2001.)

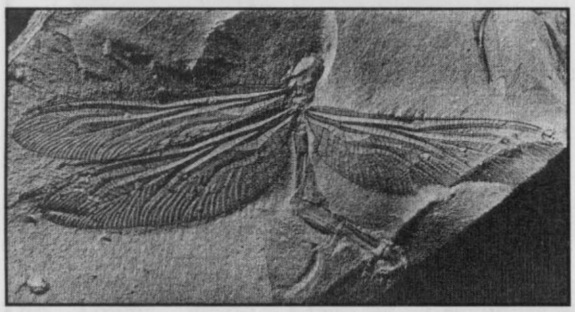


Figure 4.69 *Valdaeshna surreyensis*. Male. Wingspan 92 mm. (From Jarzembowski and Nel, 1996b.)

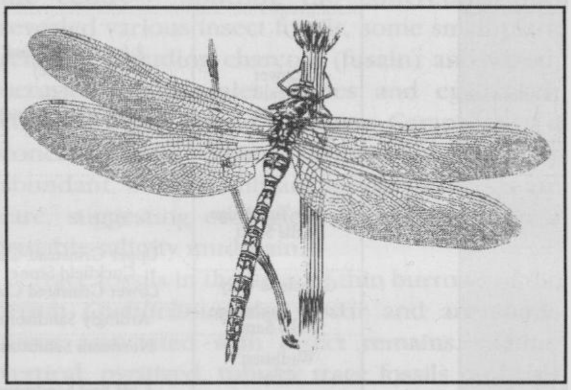


Figure 4.70 *Valdaeshna surreyensis*, reconstruction By Lance Jones.

The four most common orders of insects found at Auclaye (Blattodea, Coleoptera, Hemiptera and Orthoptera) have forewings modified for protection (elytra/tegmina). The Orthoptera include crickets, bush crickets and grasshoppers (although grasses had not yet appeared) and have been monographed recently (Gorochov *et al.*, 2006).

Generally, the aquatic orders (Odonata, Trichoptera) are uncommon in the Weald Clay. Three species of the latter have been described from Auclaye – more imagoes than from the other Weald Clay localities (Sukatsheva and Jarzembowski, 2001). Water bugs are uncommon in the Wealden strata (unlike in the Purbeck strata) and include a rare belostomatid (toe-pincher bug) from Auclaye belonging to an unusual subfamily Stygeonepinae, previously found in Early Cretaceous calcareous formations at Las Hoyas (Spain), Solnhofen (Germany) and in the British Purbecks (Jarzembowski and Coram, 1997: fig 10, see Figure 4.71). Immature stages of insects are also uncommon in the Wealden but a rare bug larva (homopteran) has also been found at Auclaye (Figure 4.71c).

Interpretation

Insect remains are generally less abundant at Auclaye than at Clockhouse Brickworks, but body parts appear to be more common, suggesting less sorting and a quieter water body at Auclaye Brickworks. Many of the body parts remain to be identified hence the long 'indet.' column in Jarzembowski (1991). It is likely, however, that they probably belong to orders

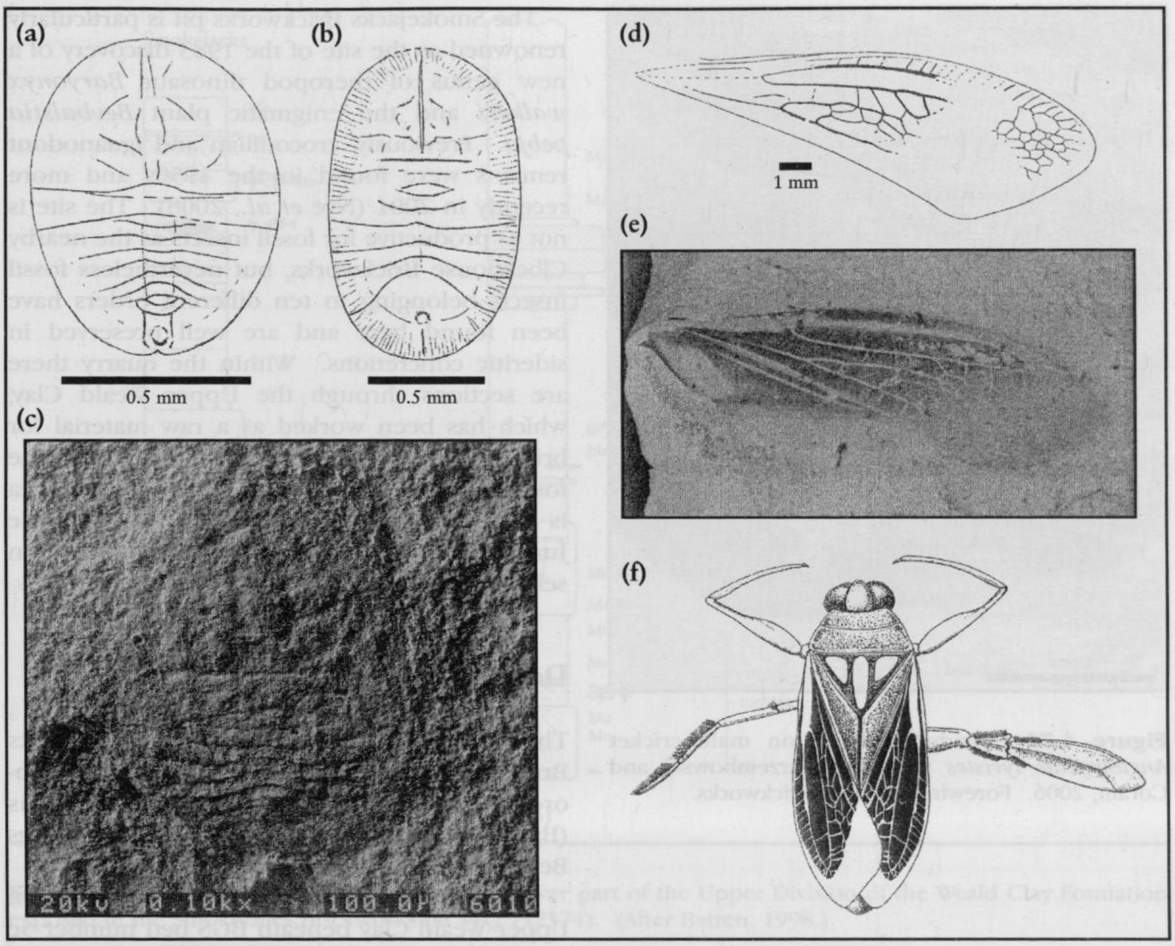


Figure 4.71 (a) Homoptera larva, lower Purbeck strata, Poxwell, MNEMG 1996.299, Jarzembowski collection. (b) Homoptera larva, middle Purbeck, Durlston Bay, MNEMG 1996.300, Coram collection; (c) Homoptera larva, Upper Weald Clay, Auclaye Brickworks, MNEMG 1996.301, Goodman collection; (d) Forewing of cf. *Iberonepa* Hemiptera: Belostomatidae), middle Purbeck, Durlston Bay, MNEMG 1996.302, Coram collection; (e) Forewing of stygeonepine (Hemiptera: Belastomatidae), Upper Weald Clay, Auclaye Brickworks, MNEMG 1996.303, Woollard collection, 19mm long; (f) Reconstruction of stygeonepine (*Iberonepa*), Lower Cretaceous, Spain, from Martínez-Delclòs *et al.*, 1995. (From Jarzembowski and Coram, 1997.)

already recorded from here. Hymenoptera include articulated specimens, for example, the parasitoid *Manlaya capelensis* Rasnitsyn & Jarzembowski and the digger wasp *Archisphex boothi* Jarzembowski. The latter is allied to bees and presages these important pollinators (Jarzembowski, 1991; Rasnitsyn *et al.*, 1998). These species also illustrate the varied geographical affinities of the Wealden fauna, that is *Archisphex* is endemic to the Wealden area, whereas *Manlaya* is typically Asian.

Conclusions

Part of a network of Wealden, early Cretaceous, sites in southern England, Auclaye Brickworks' conservation value lies in the high fidelity of preservation and diversity of fossil insects obtained from the Weald Clay here. Representatives of eight different orders have been found. The Auclaye site lies stratigraphically between the Clockhouse and Smokejacks brickworks GCR sites. Together, the three localities preserve a representative insect fauna

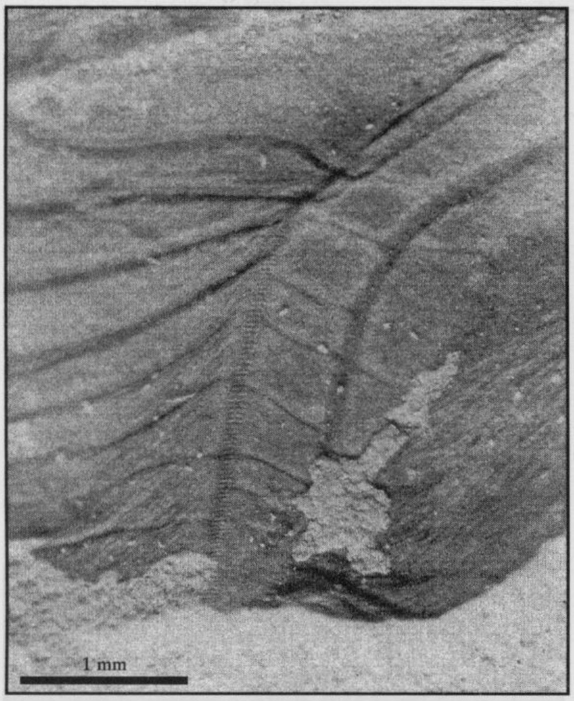


Figure 4.72 Stridulatory file on male cricket *Anglogryllus lyristes* Gorochov, Jarzembowski and Coram, 2006. Forewing, Auclaye Brickworks.

of the Upper Wealden (Hauterivian–Barremian) of the UK. This Wealden insect assemblage is the first intensively studied assemblage of Cretaceous insects and comprises a world-renowned early Cretaceous entomofauna

SMOKEJACKS BRICKWORKS, SURREY,
(TQ 112 374)

Introduction

Smokejacks Brickworks, near Ockley, Surrey (Figure 4.2) is part of a network of early Cretaceous (Wealden) GCR sites in southern England (see also GCR site reports for Clockhouse and Auclaye brickworks). The Early Cretaceous strata here are slightly younger (Barremian Stage, *c.* 128 Ma) than those at Clockhouse Brickworks.

The Smokejacks Brickworks pit is particularly renowned as the site of the 1983 discovery of a new genus of theropod dinosaur *Baryonyx walkeri* and the enigmatic plant *Bevhalstia pebja*. Previously, crocodilian and iguanodont remains were found in the 1950s and more recently in 2001 (Nye *et al.*, 2008). The site is not as productive for fossil insects as the nearby Clockhouse Brickworks, but nevertheless fossil insects belonging to ten different orders have been found here and are well preserved in sideritic concretions. Within the quarry there are sections through the Upper Weald Clay, which has been worked as a raw material for brick making for some time. In addition to the fossil arthropod importance of this site, the area is also selected for the GCR for the Jurassic–Cretaecous Reptilia and Wealden selection categories.

Description

The Weald Clay is exposed in Smokejacks Brickworks as a succession of clays with subordinate sandstone of Early Cretaceous (Barremian age), lying well above the Hastings Beds.

This actively worked pit exposes 23 m of Upper Weald Clay beneath BGS bed number 5c (Alfold Sand Member) of early Barremian age, changing from dark blue-grey below to greenish-grey and reddish-brown above, associated with shoaling (Jarzembowski, 1991). A section is given by Batten (1998, Figure 4.73).

Fauna

This early Barremian site is famous for having yielded the theropod dinosaur *Baryonyx walkeri* ('Claws') as well as herbivorous dinosaurs, crocodile and pterosaur bones. Insect remains commonly occur in silty ironstone (sideritic) concretions. Also found in the ironstone are burrows, plant stem/rootlet casts, clay clasts, fish fragments and egg cases, isopods, conchostracans, bivalve fragments and gastropod operculae, ostracods, plant remains including the fusainized fern *Weichselia*, conifers, and the early aquatic angiosperm *Bevhalstia pebja* (Hill & Jarzembowski, 1996). The insect remains are often concentrated in partings or thin layers and include ten orders:

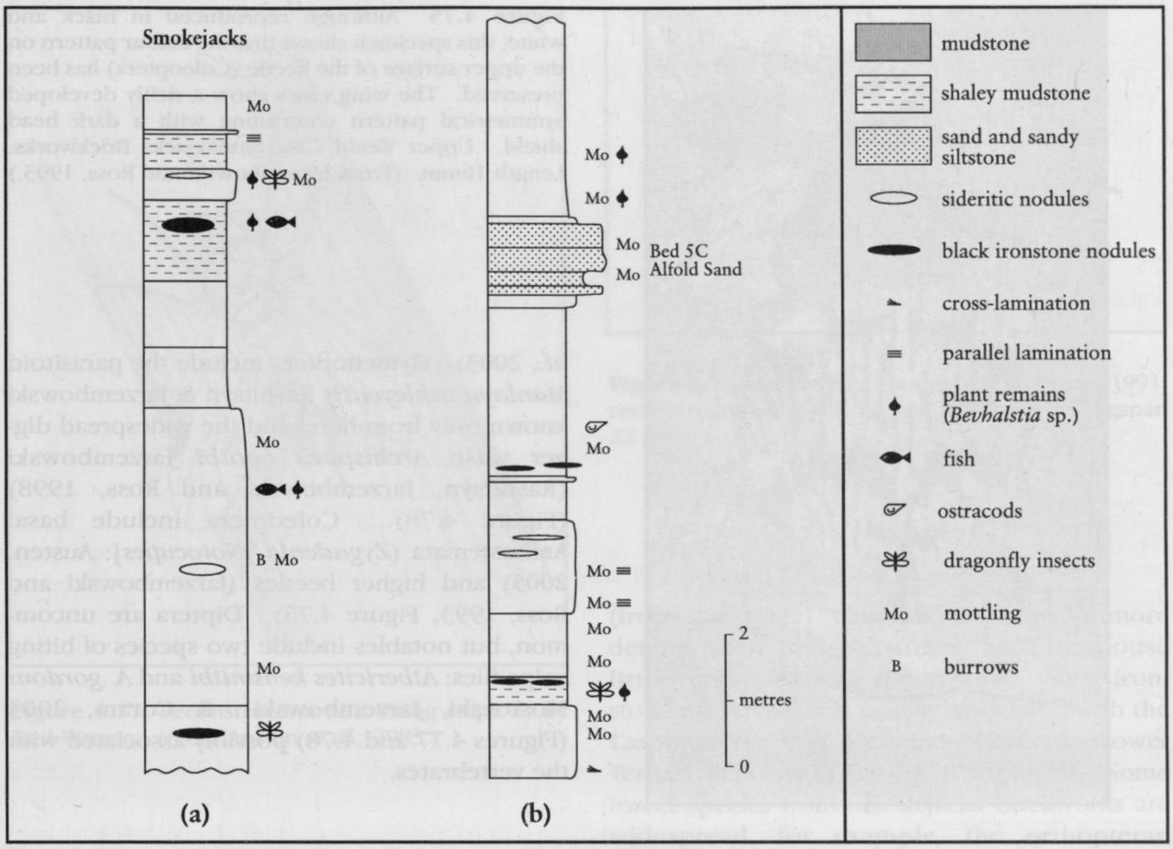


Figure 4.73 Composite lithological log of the lower part of the Upper Division of the Weald Clay Formation exposed in the Smokejacks Brickworks pit (TQ 112374). (After Batten, 1998.)

Blattaria/Blattodea (cockroaches and cockroachoids)
Coleoptera (beetles)
Diptera (true flies)
Hemiptera (bugs)
Hymenoptera (wasps)
Isoptera (termites)
Mecoptera (scorpionflies)
Neuroptera (lacewings)
Odonata (dragonflies)
Orthoptera (crickets and 'grasshoppers')

Aquatic insects include adult Odonata comprising true dragonflies like the aeschnidiid *Lleidoaeschnidium maculatum* Fleck & Nel, 2003 and petaluridan *Pseudocymatophlebia hennigi* Nel *et al.*, 1998 (in its own subfamily Pseudocymatophlebiinae, known only from this pit); darters are represented by the widespread *Cretaneophya strevensi* Jarzembowski & Nel, 1996a,b and damselflies by the equally widespread *Cretarchistigma greenwoodi* Jarzembowski *et al.*, 1998.

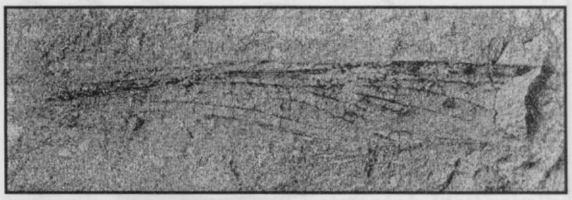


Figure 4.74 Locustopseid forewing, *Mesolocustopsis problematica* Gorochov, Jarzembowski and Coram, 2006. Upper Weald Clay, Smokejacks Brickworks. Length 16 mm. (From Jarzembowski and Coram 1997.)

Blattodea are discussed by Ross (2001) and Orthoptera by Jarzembowski (1999, Figure 4.74). A true cricket, bush cricket and grasshopper are formally described and named by Gorochov *et al.* (2006). Mecoptera include undescribed 'Protomecoptera' and Hemiptera, and an unusual plant hopper (Jarzembowski, 1987). Neuroptera include a psychopsid resembling the typically Purbeck genus *Pterinoblattina* (Ross and Cook, 1995; Austen *et*

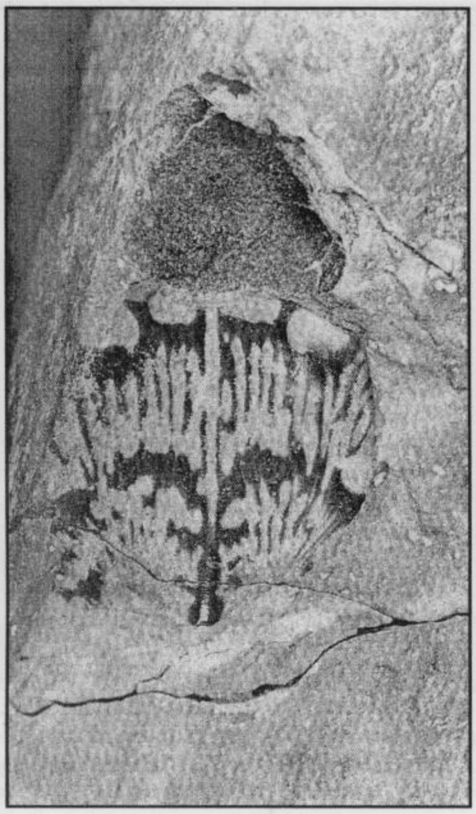


Figure 4.75 Although reproduced in black and white, this specimen shows that the colour pattern on the upper surface of the beetle (Coleoptera) has been preserved. The wing cases show a richly developed symmetrical pattern contrasting with a dark head shield. Upper Weald Clay, Smokejacks Brickworks. Length 16mm. (From Jarzembowski and Ross, 1993.)

al., 2003). Hymenoptera include the parasitoid *Manlaya ockleyensis* Rasnitsyn & Jarzembowski known only from here, and the widespread digger wasp *Archisphex boothi* Jarzembowski (Rasnitsyn, Jarzembowski and Ross, 1998) (Figure 4.78). Coleoptera include basal Archostemata (*Zygadenia* [*Notocupes*]: Austen, 2005) and higher beetles (Jarzembowski and Ross, 1993, Figure 4.75). Diptera are uncommon, but notables include two species of biting snipe flies: *Athericites kensmithi* and *A. gordoni* Mostovski, Jarzembowski & Coram, 2003 (Figures 4.77 and 4.78) possibly associated with the vertebrates.

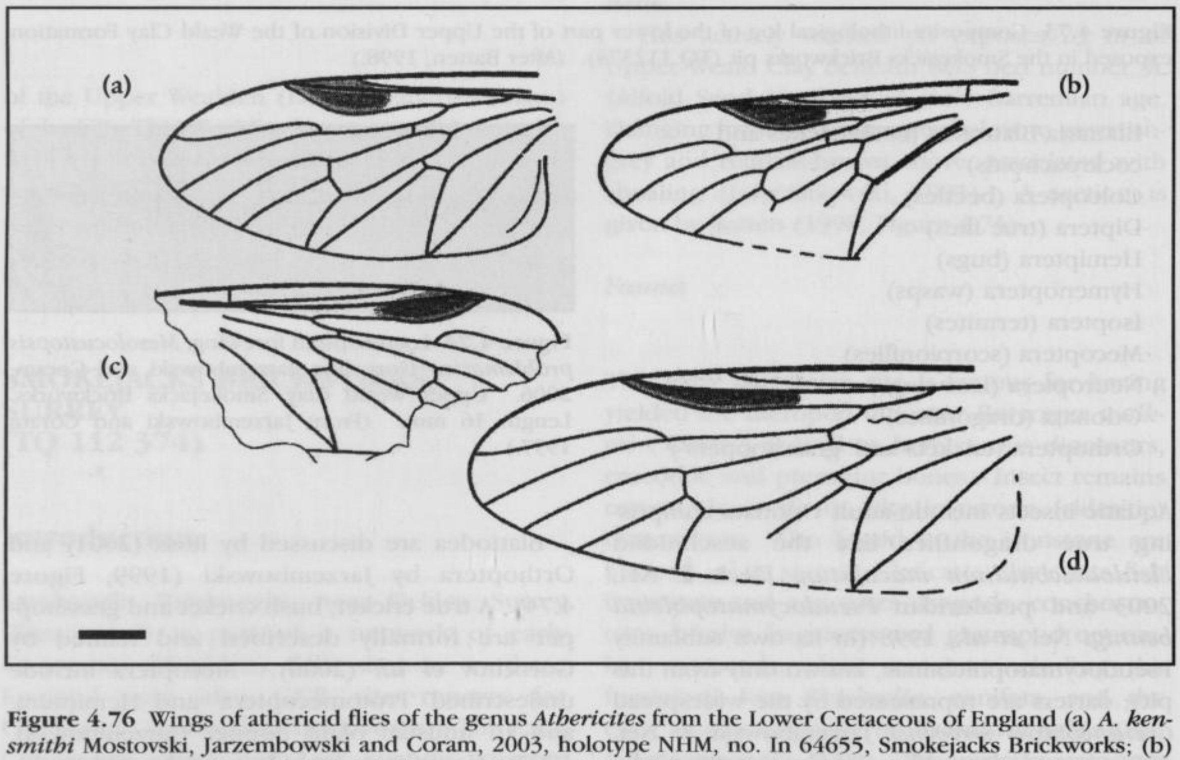


Figure 4.76 Wings of athericid flies of the genus *Athericites* from the Lower Cretaceous of England (a) *A. kensmithi* Mostovski, Jarzembowski and Coram, 2003, holotype NHM, no. In 64655, Smokejacks Brickworks; (b) *A. gordoni* Mostovski *et al.*, 2003, holotype BMB, no. 023835, Smokejacks Brickworks; (c) *A. finchi* Mostovski *et al.*, 2003, holotype BMB, no. 023836, Clockhouse Brickworks; and (d) *A. sellwoodi* Mostovski *et al.*, 2003, holotype MNEMG, no. 2001.47, Durlston Bay. The scale bar is 1 mm. (After Mostovski *et al.*, 2003.)

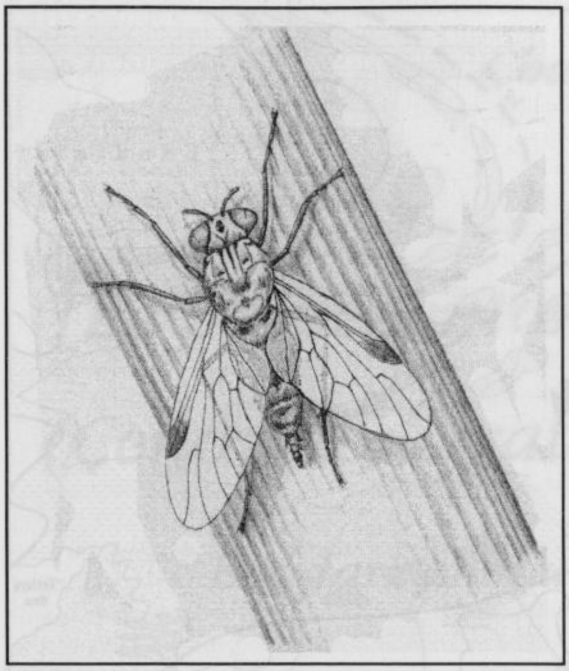


Figure 4.77 Reconstruction of a biting snipe fly by Neil Watson. (From Austen *et al.*, 2003.)

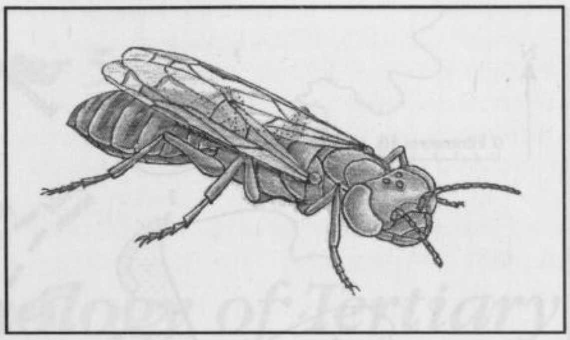


Figure 4.78 *Archisphex boothi* Jarzembowski, 1991, reconstruction by Neil Watson. Estimated wingspan 22 mm.

Interpretation

The sedimentary environment in which the insect remains are preserved has been interpreted as representing to overbank deposits developed during a flood (Benton and Spencer, 1995, p. 234). The overall environment of deposition of the Weald Clay has been reconstructed by Allen (1976, p. 414) as an alluvial floodplain with lagoons and short-lived sand-filled channels (Figure 4.79). With links to the East Anglian Sea to the north-west, salinities varied from nearly marine to freshwater. All sediments were liable to exposure, as reflected by the presence of large dinosaur footprints in the sands, suncracks and mudflake conglomerates, soil beds and horsetail stems in life position.

The fossil biota combines both terrestrial forms (such as the dinosaurs and trees) and aquatic (freshwater–brackish) ones such as crocodilians, fish and molluscs. The insects and other arthropods also include both terrestrial forms (such as the cockroaches and wasps) and freshwater aquatic ones (such as the ostracods and conchostracans).

The insects are typically preserved in sideritic (iron carbonate) concretions showing more details than the siltstones at Clockhouse Brickworks (see GCR site report). Such ironstone preservation is usually associated with the Carboniferous Coal Measures or even the Lower Tertiary deposits in the UK (Chapter 5). Some insect species from Smokejacks Brickworks are widespread, for example, the orthopteran *Panorpidium bimaculatum* Gorochov *et al.*, 2006, whereas others belong to genera only know from this pit, e.g. the cricket *Speculogryllus* Gorochov et al., 2006, and a problematic 'grasshopper' (Baldock, 1999). *Mesochlorogomphus crabbi* Fleck *et al.*, 2008, is a dragonfly from here uniquely in its own family, Mesochlorogomphidae. Also found is the only Weald Clay representative of the extinct neuropteran (lacewing) family Kalligrammatidae, typically know from the Solnhofen Plattenkalke Lagerstaette. Wealden Neuroptera are dominated by Psychopsidae (silky lacewings) unlike the myrmeleontoid (e.g. antlion)-dominated fauna from the arid Brazilian Lower Cretaceous (Jepson pers.comm.). A relatively humid Weald Clay climate is supported by the much more common cockroach (Blattodea) remains.

Conclusion

Part of a network of sites (see also GCR site reports for Clockhouse and Auclaye brickworks) in the Weald Clay, this early Cretaceous site has younger (Barremian, *c.* 128 Ma) strata than Clockhouse Brickworks. Although insects are less common here than at Clockhouse

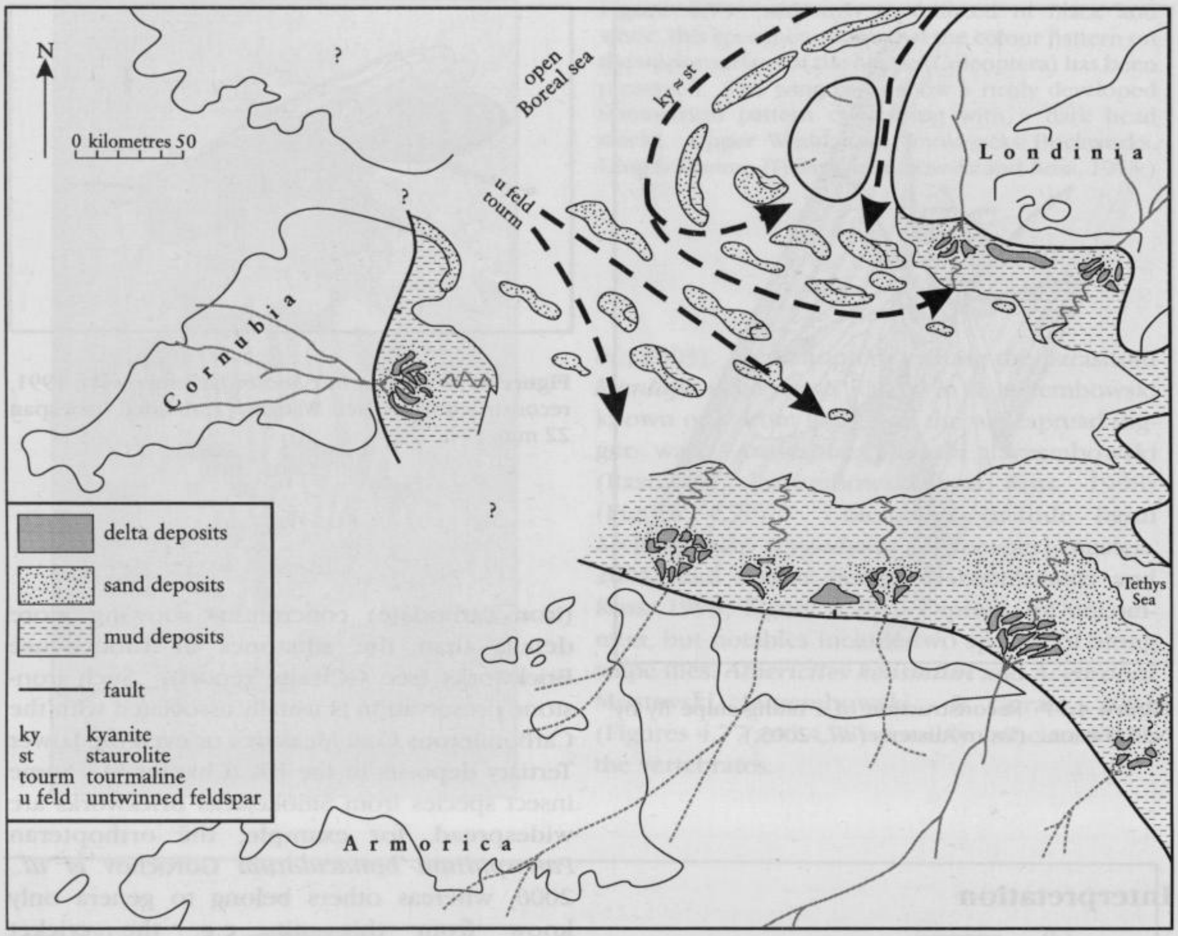


Figure 4.79 Provinicial model for argillaceous Wealden formations in southern England and northern France. (After Allen, 1981.)

Brickworks, nevertheless, fossil representatives of some ten orders of insects have been found in more detailed preservation. The preservational facies – in sideritic ironstones – is more commonly associated with the British Carboniferous and complements the other Wealden insect GCR sites dominated by siltstone or phosphatic concretions. The Smokejacks fossil insects include taxa unique to this pit as well as representations of widespread Lower Cretaceous species. The site is also famous for its reptile remains and was selected separately within the GCR for its fossil reptiles. The extensive excavation offers considerable potential for future finds.