Fossil Arthropods of Great Britain

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Chapter 5

The palaeoentomology of Tertiary (Cenozoic) strata in Great Britain

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INTRODUCTION

Of the fossil arthropods considered in this volume, the insects are by far the most important in the Tertiary part of the British stratigraphical record. Inevitably, given the biology of the group, most, but not all, of these fossil forms are continental (terrestrial and freshwater) in habit. As has already been mentioned, the preservation of such organisms depends either upon the formation of geological sediment traps within continental settings that are subsequently preserved as part of the stratigraphical rock record, or their transport into marginal marine and continental shelf settings where they are then recruited to the marine sedimentary rock record. Here the nature of the stratigraphical record of those deposits that host the insect faunas is briefly discussed.

Although the onshore British stratigraphical record of Tertiary deposits is limited to a certain few intervals in the period (see Figure 5.5), fossil insects are quite well represented in their deposits, because many of them were laid down in relatively quiet-water nearshore and transitional marine-freshwater environments with fine-grained deposits, into which insect remains could sometimes be recruited. In addition, early diagenetic rock formation of these sediments also played a major role in the preservation of fossil insects. Of particular importance was the formation of concretions, and also limestone layers within mudstone strata.

The six sites selected for the GCR as representatives of the Tertiary palaeoentomology of Great Britain (Figures 5.1 and 5.2) all lie within the British Palaeogene strata (Palaeogene time comprises the Palaeocene, Eocene and Oligocene epochs, from *c.* 65 to *c.* 23 Ma) and fall into two age groups. The older group ranges from latest Palaeocene in age (Ardtun) to slightly younger but still early Eocene in age (Bognor Regis). The younger group ranges in age from late Eocene (Gurnard) to early Oligocene (Bouldnor). As explained in the introduction to GCR site selection, no Quaternary sites have been selected especially for arthropods, although it is recognized that fossil and subfossil insects play an important role in the dating and palaeoenvironmental interpretation of many 'Ice Age' sites. Indeed, the role of beetles (coleopterans) in the interpretation of Quaternary environments in Wales is discussed by Campbell and Bowen (1989, p.158ff.).

The Palaeogene fossil insect assemblages of the six selected British sites tend to be intimately associated with ancient floras and are often but not always terrestrial elements introduced into otherwise brackish or marine environments of deposition, most of which are nearshore. The insect evidence tends to supplement that of the fossil plants especially in terms of palaeoenvironmental and palaeoclimatic interpretation.

PALAEOCLIMATES AND PALAEO-ENVIRONMENTS

Global climates changed significantly through Tertiary times (for a full discussion see the GCR volume on *British Tertiary Stratigraphy*, Daley and Balson, 1999).

Initially, temperatures rose to a peak in Eocene times and then progressively cooled with the first ice sheet appearing in Antarctica in early Oligocene times although permanent glaciation did not appear until mid-Miocene times when glaciers may have formed in Greenland. In addition there were shorter-term variations superimposed upon these overall trends.

The Palaeocene–Eocene transition in the early Palaeogene, around 56 Ma, was a phase of warm global climates and generally high sea-levels with polar broad-leaved deciduous forests extending high into the Arctic Circle (Basinger *et al.*, 1994). Nevertheless, the fossil plant records show variation in vegetation throughout the interval in response both to climate change and latitudinal position. During the latest Palaeocene times, around 55.1 Ma there was a very short-lived phase of warming followed by a marked cooling around 54.2 Ma.

There has been speculation (Dickens *et al.*, 2003) that the warm phase was a consequence of the greenhouse effect caused by a catastrophic release of gas hydrates from within ocean-floor sediments, perhaps initiated by contemporary volcanism. Southern Britain supported freshwater mires and relatively low diversity, patchy forest-woodland populated with warmth-loving deciduous flowering plants. Farther north, at Ardtun, similar flowering plants were associated with more conifers and ferns. By contrast the floras of the earliest Eocene (as recorded by fossils from the Oldhaven beds and lowest strata of the London Clay) indicate the early development of a frost-free paratropical rain

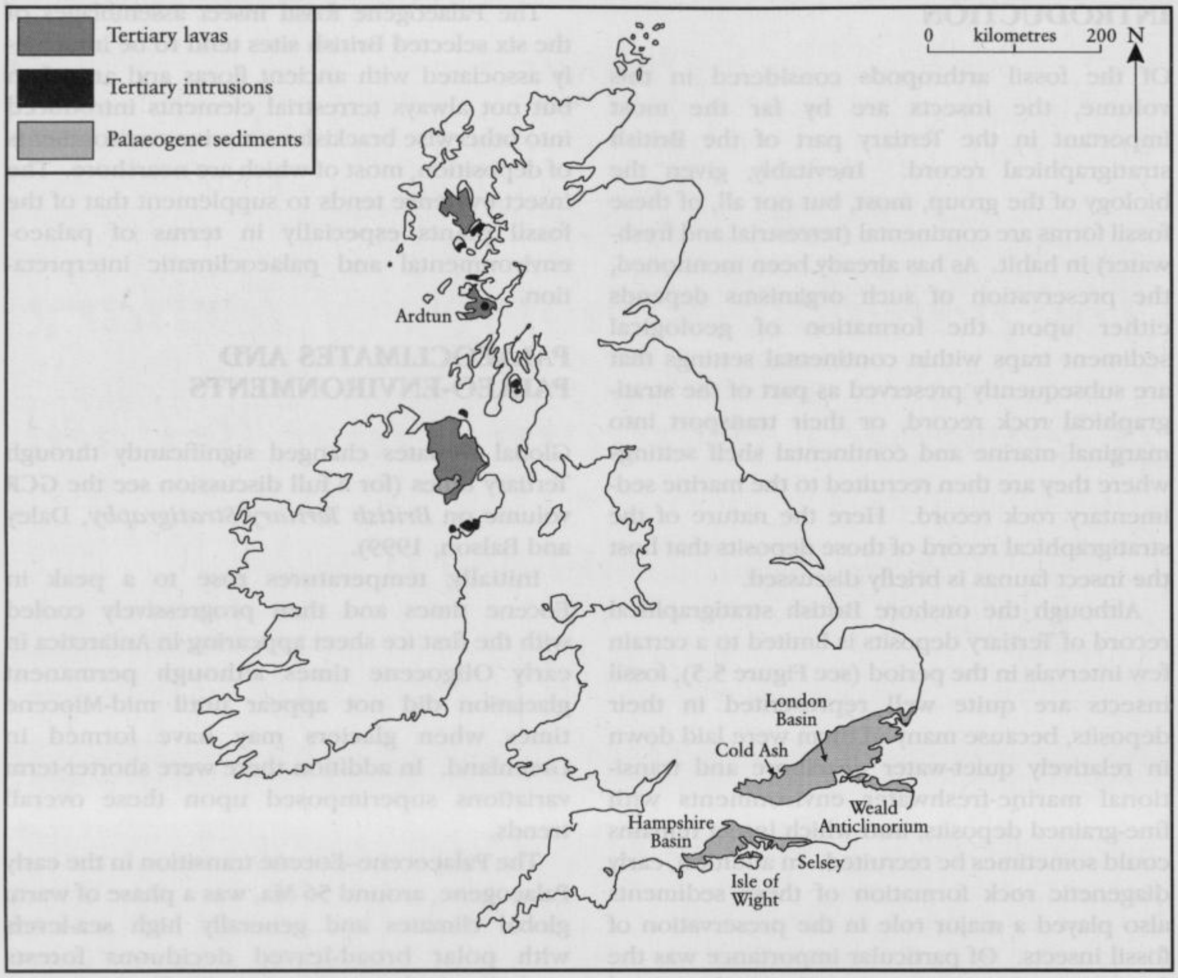


Figure 5.1 Distribution map for Tertiary rocks. (After Benton *et al.*, 2005.)

forest-type vegetation very similar in structure to that of the present day paratropical rain forest. Inevitably these climatic and vegetational developments impacted upon the entomofauna.

PALAEOGEOGRAPHICAL SETTING

There were significant differences between the palaeogeography of Tertiary times and those of today, including a northward plate-movement of Britain over some 8 degrees of latitude. Also important in the Northern Hemisphere context was the persistence of a land connection between Europe and North America that allowed continued biotic interchange (Figure 5.3). However, by late Palaeocene times increasing igneous activity related to the rise of the North Atlantic mantle-plume beneath the continental crust of East Greenland (Figure 5.4) led to the development of the Brito-Arctic Igneous Province (also known as the 'North Atlantic Tertiary Igneous Province') with extensive extrusive vulcanicity and associated intrusion of a variety of igneous bodies. Elevation of the continental crust in mid-late Palaeocene times led to the development of a landmass that encompassed much of present day Scotland and what is now the largely submerged Orkney–Shetland platform (Figure 5.5). The uplift and erosion of this landmass led to large-scale deposition of eroded sediment in the adjacent basins of the North Sea and Faroe–Shetland regions (Figure 5.5) where Tertiary sediment reached maximum thicknesses of 3 km and 4 km respectively.

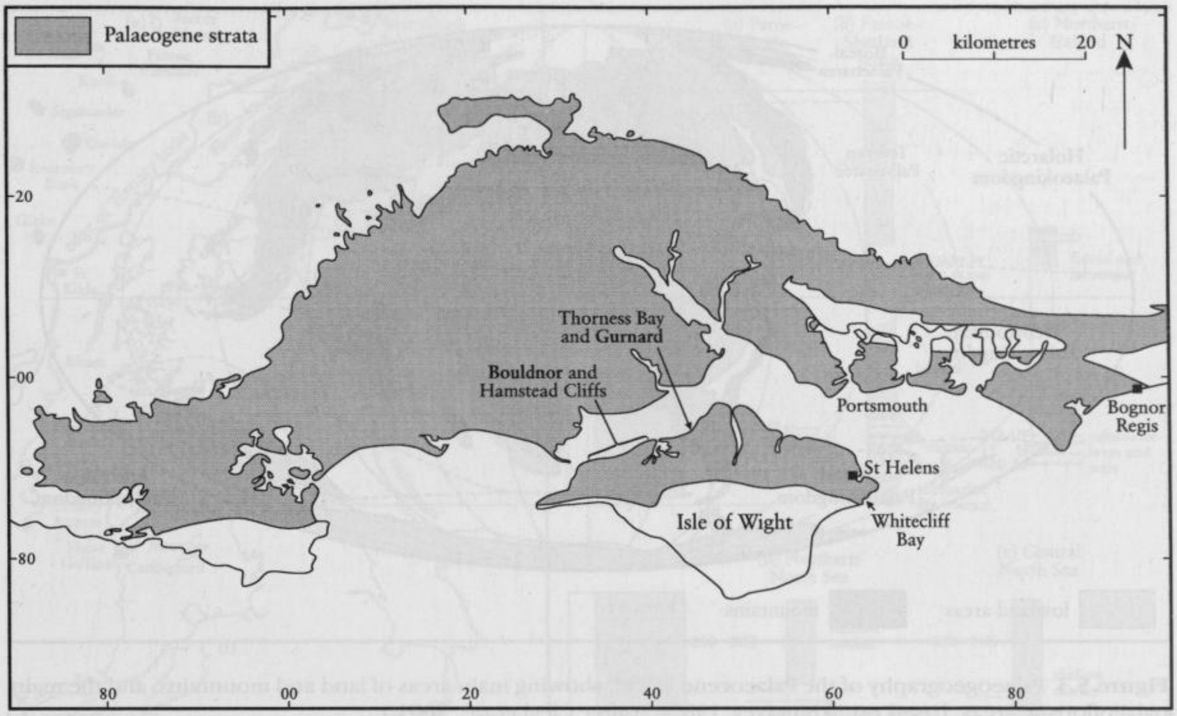


Figure 5.2 Map showing the location of the arthropod GCR sites in the Hampshire Basin.

There is no doubt that the Tertiary- and especially Palaeogene-age deposits were formerly more extensive over Britain. It is thought that the 'clay with flints' which blankets much of the Chalk is made up of the weathered residues of these deposits. However, it is also clear that there were phases during Tertiary times during which Britain was uplifted and eroded. During early- and the beginning of late-Palaeocene times (the first 7 Ma or so years of the Tertiary period) there appear to be no onshore sediments.

Study of borehole data and seismic profiles of this sediment infill has provided important information about the intimate relationship between igneous, tectonic and depositional activity and palaeogeographical evolution of the British Isles throughout much of Tertiary time. Most important from the depositional point of view has been the recognition of eight major depositional cycles within these offshore basins from the Palaeocene through to the Pliocene epochs.

Re-activation of Mesozoic structural, fault-bounded, basins (graben) in north-west Europe was associated with crustal attenuation and widespread vulcanicity (seen in the Ardtun GCR site on the Inner Hebridean island of Mull). These processes eventually led to extensive rifting both to the north-west and north-east of the British Isles. And, in turn this led to progressive opening, beginning around 55 Ma, of the North Atlantic Ocean, as new ocean crust was formed. The new ocean extended northwards from the Central Atlantic area and finally severed the land connection between Europe and North America and isolated Greenland.

In the west of Scotland and north-east of Ireland, the magmatism associated with this phase of intense volcanic activity formed widespread flood basalt sequences associated with lava shields, shallow intrusive centres and spanned the interval from around 60.5–55 Ma. The igneous activity was intermittent with periods of rapid growth of the lava fields and intrusion of a variety of igneous bodies followed by significant hiatuses during which weathering and erosion allowed the development of relatively mature vegetated landscapes whose deposits and fossil remains are to be found within the plateau basalts (see Figure 5.10). Evidence of this Palaeogene volcanism is also present in the south of England where airborne pyroclastic material has been preserved as ash layers in the basal strata of the London Clay.

In comparison, southern Britain was less elevated and two structural basins, known as the 'London Basin' and 'Hampshire Basin', were

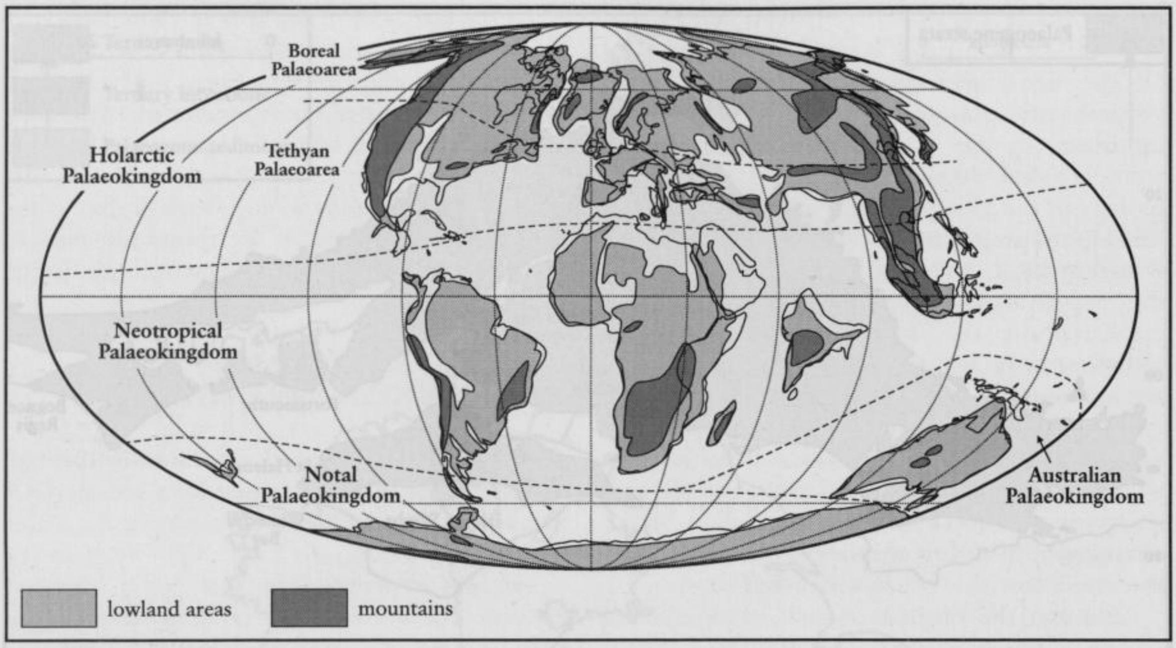


Figure 5.3 Palaeogeography of the Palaeocene world, showing main areas of land and mountains, and the main palaeofloristic areas, based on Akhmetyev, 1987). (After Cleal *et al.*, 2001.)

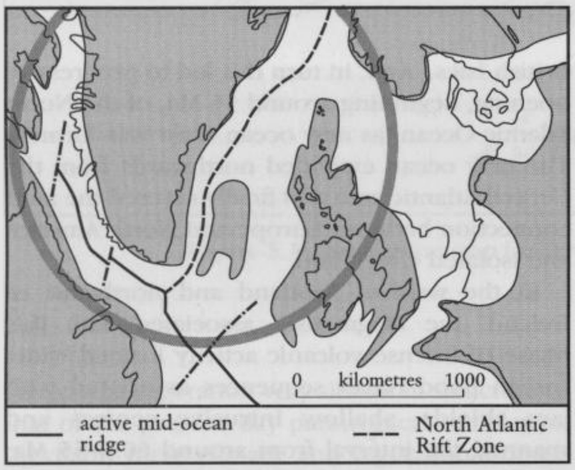


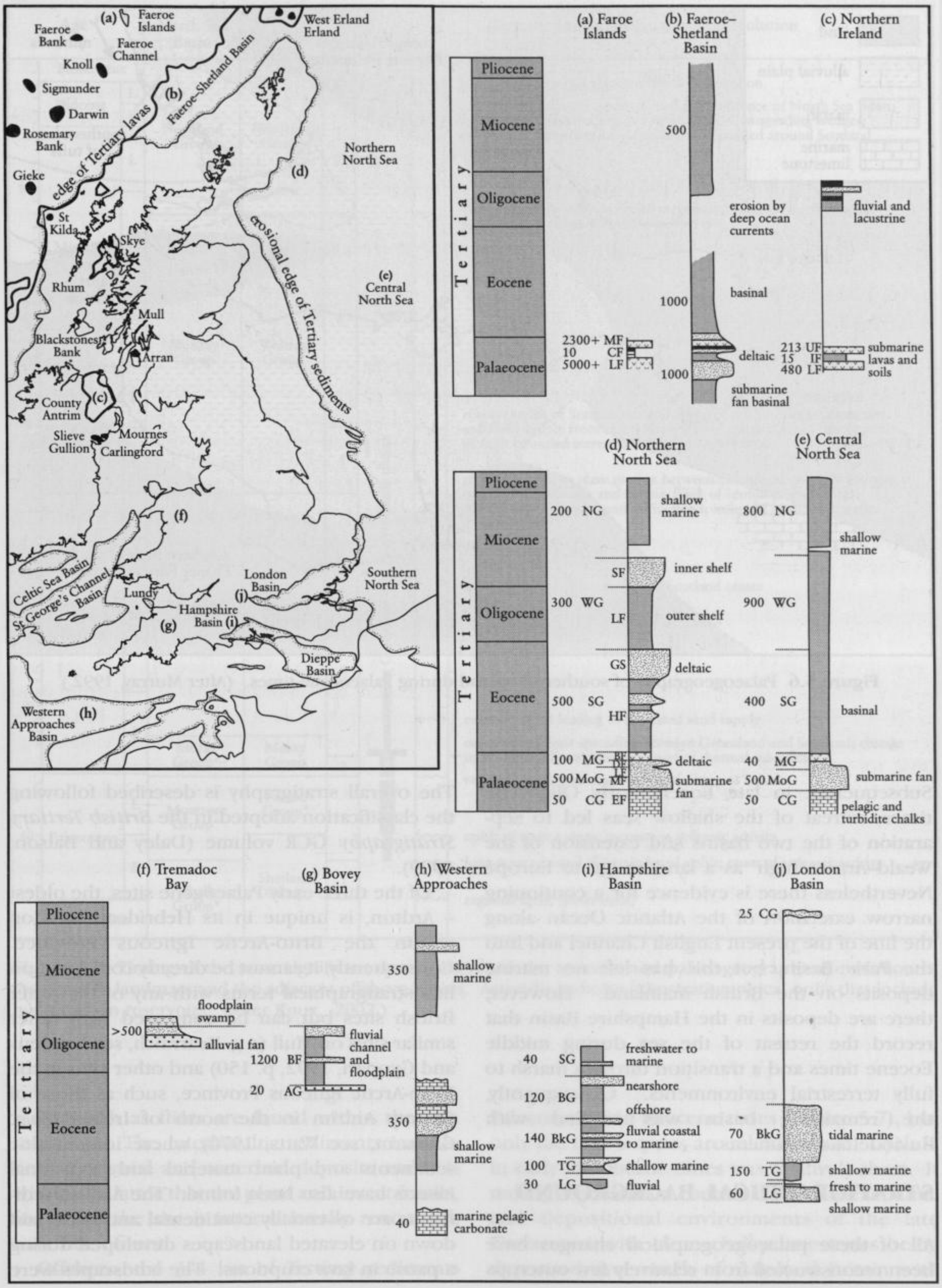
Figure 5.4 Regional tectonic setting prior to the opening of the north-east Atlantic Ocean, between Greenland and Scotland. Inferred land areas are shaded in grey. The circle represents the approximate extent of the proto-Icelandic mantle plume. (After Knox, 2002.)

formed from a single structural 'low' which originally covered much of today's North Sea region, the Low-countries of Belgium, north-east France and south-east England. The formation of the Weald–Artois 'high', which extended just into south-east England from Europe, split the original structural basin in two (Figure 5.6). Global high sea levels resulted in these structural lows also being sites of shallow water deposition with extensive alluvial plains and marshes and brackish to freshwaters dominated by fine-grained mud deposits. Open marine conditions lay to the north-east in the North Sea region and to the south-west in the Western Channel.

By latest Palaeocene to early Eocene times the shallow seas had extended over much of southern England interconnecting the London and Hampshire Basins (see Bognor Regis GCR site report) and flooding over the Low-countries.

Figure 5.5 *(overleaf)* Distribution of Tertiary sediments, lavas and igneous complexes around the British Isles. MF: Middle and Upper Formations; CF Coal-Bearing Formation; LF Lower Formation; LG Lough Neagh Group; UF: Upper Formation; IF: interbasaltic Formation; NG: Nordland Group; WG: Westray Group; SG: Stronsay Group; MG: Moray Group; MoG: Montrose Group; CG Chalk Group; SF: Skade Formation; LF: Lark Formation; GS: Grit Sandstone Member; HF: Horda formation; BF Balder Formation; DF: Dornoch Formation; SF: Sele Formation; LF: Lista Formation; MF: Maureen Formation; EF: Ekofisk Formation; BF: Bover Formation; AG: Aller Gravels; SG: Soloent Group; BG: Barton Group; BkG Bracklesham Group; TG: Thames Group; LG: Lambeth Group; CC Coralline Crag.

Palaeogeographical setting



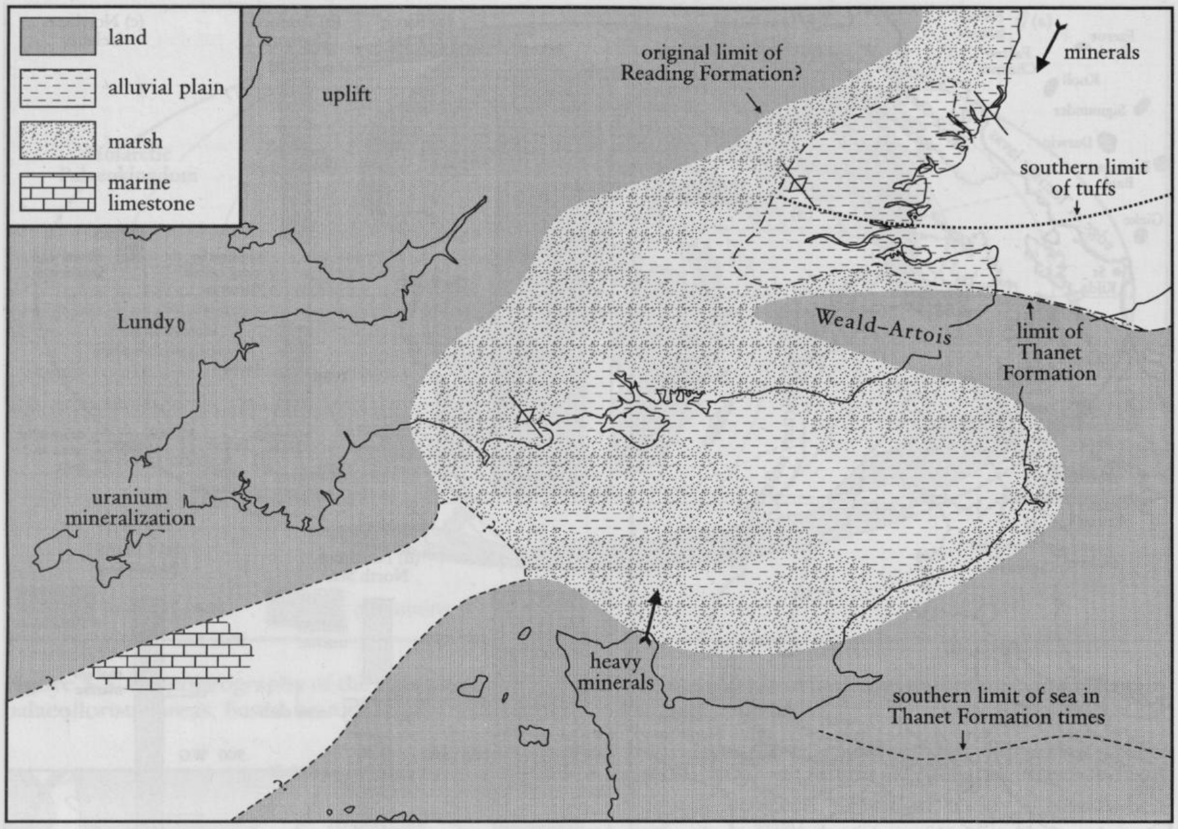


Figure 5.6 Palaeogeography of southern England during Palaeocene times. (After Murray, 1992.)

Subsequently, in late Eocene–early Oligocene times, retreat of the shallow seas led to separation of the two basins and extension of the Weald–Artois 'high' as a land-bridge to Europe Nevertheless there is evidence for a continuing narrow extension of the Atlantic Ocean along the line of the present English Channel and into the Paris Basin, but this has left no marine deposits on the British mainland. However, there are deposits in the Hampshire Basin that record the retreat of the sea during middle Eocene times and a transition through marsh to fully terrestrial environments. Consequently, the remaining basin was infilled with fluviodeltaic sediments.

STRATIGRAPHICAL BACKGROUND

All of these palaeogeographical changes have been reconstructed from relatively few outcrops in the south of England but these onshore outcrops have now been supplemented by a large volume of information from offshore boreholes. The overall stratigraphy is described following the classification adopted in the *British Tertiary Stratigraphy* GCR volume (Daley and Balson, 1999).

Of the three early Palaeogene sites, the oldest – Ardtun, is unique in its Hebridean location within the Brito-Arctic Igneous Province. Consequently, it cannot be directly correlated on lithostratigraphical terms with any of the other British sites but can be compared with other similar sites on Mull (e.g. Bearraich, see Emeleus and Gyopari, 1992, p. 150) and other sites in the Brito-Arctic Igneous Province, such as those of County Antrim in the north of Ireland (e.g. Glenarm, see Watts, 1970) where interbasaltic sediments and plant material and occasional insects have also been found. The Ardtun sediments are essentially continental and were laid down on elevated landscapes developed during a pause in lava eruptions. The landscapes were originally covered either wholly or, in part, by late Cretaceous sediments, patches of which are preserved below the lavas and reworked ele-

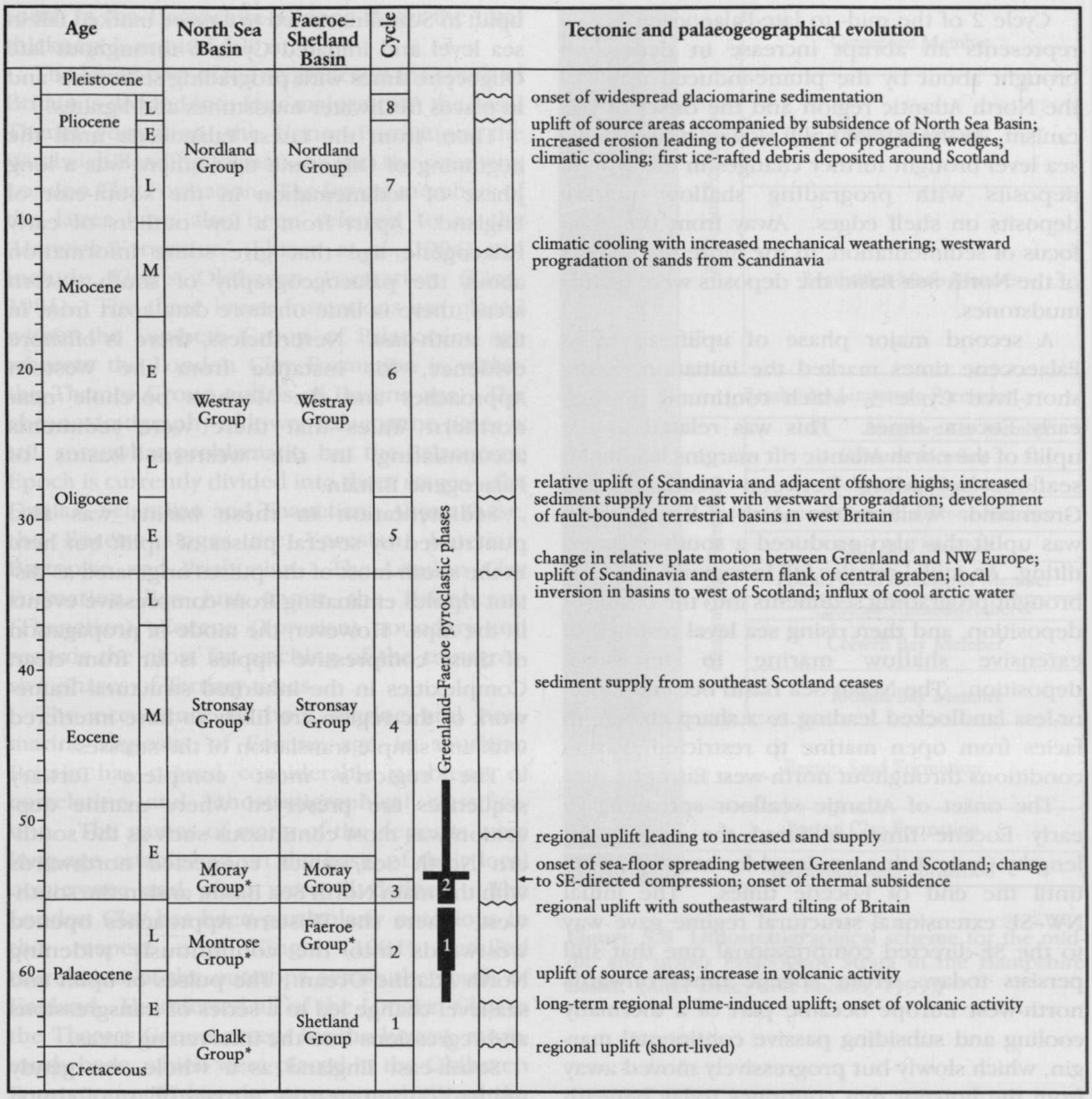


Figure 5.7 Timing of the most significant developments in the tectonic and palaeogeographical evolution of the Scottish landmass and the adjacent offshore basins. Asterisks indicate lithostratigraphical units that include hydrocarbon reservoirs. (After Knox, 2002.)

ments such as flints are found within the lava sequence. The interbasaltic sediments include both terrestrial and waterlain deposits and it is within the latter that the plant and insect fossils, for which the site is internationally renowned, have been found.

Offshore, the 3–4 km of Tertiary sediments that accumulated in the Faeroe–Shetland Basin and North Sea Basin provide evidence that there were eight major depositional cycles between Palaeocene and Pliocene times (Figure 5.7), but only the first 6 cycles are relevant here. Cycle 1 in early Palaeocene times was relatively short. It mostly represents a continuation of the tectonic and depositional environments of the late Cretaceous with clean chalky limestones being deposited over much of mainland Britain with only a thin sequence of clastic materials following on top of Cretaceous sediments in the offshore basins.

Cycle 2 of the mid- to late-Palaeocene Epoch represents an abrupt increase in deposition brought about by the plume-induced uplift of the North Atlantic region and the onset of volcanism. As the rate of uplift slowed down, rising sea level brought further changes in the type of deposits with prograding shallow marine deposits on shelf edges. Away from the main focus of sedimentation, in the more distal parts of the North Sea Basin the deposits were mainly mudstones.

A second major phase of uplift in latest Palaeocene times marked the initiation of the short-lived Cycle 3, which continued through early Eocene times. This was related to the uplift of the north Atlantic rift margins leading to seafloor spreading between Scotland and Greenland. While in the north of Britain there was uplift this also produced a south-eastward tilting. An initial relative fall in regional sea level brought prograding sediments into the basins of deposition, and then rising sea level resulted in extensive shallow marine to terrestrial deposition. The North Sea Basin became more-or-less landlocked leading to a sharp change in facies from open marine to restricted marine conditions throughout north-west Europe.

The onset of Atlantic seafloor spreading in early Eocene times initiated the major and lengthy Cycle 4 that persisted for around 21 Ma until the end of Eocene times. The initial NW–SE extensional structural regime gave way to the SE-directed compressional one that still persists today. From Eocene times onwards north-west Europe became part of a thermally cooling and subsiding passive continental margin, which slowly but progressively moved away from the hotspot that continues today beneath Iceland. There was a rise in sea level and widespread flooding of the shelf areas. Offshore sedimentation was dominated by the deposition of muds, restricted circulation and stratified water columns.

Latest Eocene times were marked by another profound change in tectonic and sedimentary regimes and initiated Cycle 5 that lasted through early Oligocene times. Changes in plate motion in the northern Atlantic Ocean resulted in a shift in the direction of movement of north-west Europe from a south-easterly to a more ESE direction. The focus of uplift moved away from Scotland to Scandinavia produced more uniform patterns of sedimentation and rapid global cooling lowered sea level. The onset of renewed uplift in Scandinavia led to a more marked fall in sea level and initiated Cycle 6 throughout late Oligocene times with prograding sediments and in places freshwater mudstones and lignites.

Then, from the latest Palaeocene until the beginning of Oligocene times there was a long phase of sedimentation in the south-east of England. Apart from a few outliers of early Palaeogene age that give some information about the palaeogeography of south-western areas, there is little onshore data apart from in the south-east. Nevertheless, there is offshore evidence, for instance from the Western Approaches and the Mochras borehole near northern Wales that there were sediments accumulating in the westerns basins of Palaeogene Britain.

Sedimentation in these basins was also punctuated by several pulses of uplift but here in the south most of the pulses originated as distant ripples emanating from compressive events in the Alps. However, the mode of propagation of these compressive ripples is far from clear. Complexities in the inherited structural framework of the region are likely to have interfered with any simple translation of the stresses.

The region's most complete Tertiary sequences are preserved where marine deposition was most continuous such as the southern North Sea, which connected northwards with the main North Sea Basin, and in the south-west, where the Western Approaches opened westwards into the continuously widening North Atlantic Ocean. The pulses of uplift and sea-level change led to a series of transgressions and regressions into the intervening areas.

South-east England as a whole was gently uplifted during an early Tertiary phase of Alpine compression with the result that deposits of lowest Tertiary age are missing and it is late Palaeocene sediments that onlap onto eroded Chalk surfaces. The source for these sediments was the low-relief land surface of central England and parts of northern France, with the intervening depositional basins being infilled with shallow-water, marginal marine and fluviatile, fine-grained sediments. In detail, Palaeogene sequences were influenced by local tectonic movements and eustatic changes in sea level. The total thickness of Tertiary (Palaeogene and Neogene) deposits in southern Britain is much thinner than in the offshore basins to the north. Even so, some 2 km accumulated in the southern part of the North Sea Basin but farther south in the Hampshire–Dieppe Basin the total thickness is around 500 m.

The lower part of the sequence in the south of Britain is divided into four major units: the basal Thanet Formation, the Upnor Formation, the Woolwich/Reading formations and the overlying London Clay Formation. The lowest members of the latter have also been referred to as the 'Harwich Formation' (Ellison *et al.*, 1994) and include King's Oldhaven Formation (King, 1981). The three lower formations are placed within the Lambeth Group of Palaeocene age whereas the London Clay Formation is within the Thames Group and is of Eocene age. The chronostratigraphy of lower Palaeogene times is still somewhat problematic, but the Palaeocene Epoch is currently divided into three stages – the Danian, Selandian and Thanetian. Above these, the Eocene stages are Ypresian, Lutetian, Bartonian and Priabonian. The London Clay Formation lies just above the Palaeocene (Thanetian) –Eocene (Ypresian) boundary and records the most far reaching of the transgressive phases of Tertiary times.

The occurrence of both marine and non-marine deposits of Eocene age in southern Britain has caused considerable problems of correlation and lithostratigraphical classification. The names of many of the deposits were long-ago established on the basis of their local occurrence and often were ill defined. The London Clay has been particularly notorious in this respect until King's (1981) detailed correlation of the outcrops across the south of England. He referred all of the London Clay to the Thames Group except for the lowest, more-sandy beds, which were placed in the Oldhaven Formation. Within the remaining bulk of the London Clay, King recognized five informal divisions ('A' to 'E') separated by discontinuities and perhaps representing cyclic depositional events. More recently, King's Oldhaven Formation and A1 subdivision have been amalgamated by Ellison *et al.* (1994) to form the Harwich Formation.

The only younger strata of concern here are the post-Lutetian deposits of the Solent Group in the Hampshire Basin, especially those of late Priabonian–Rupelian age (late Eocene–Oligocene). Again, lateral variation in facies has resulted in considerable confusion with the lithostratigraphical nomenclature. Following the scheme of the Tertiary stratigraphy GCR volume (Daley and Balson, 1999), the post-Lutetian

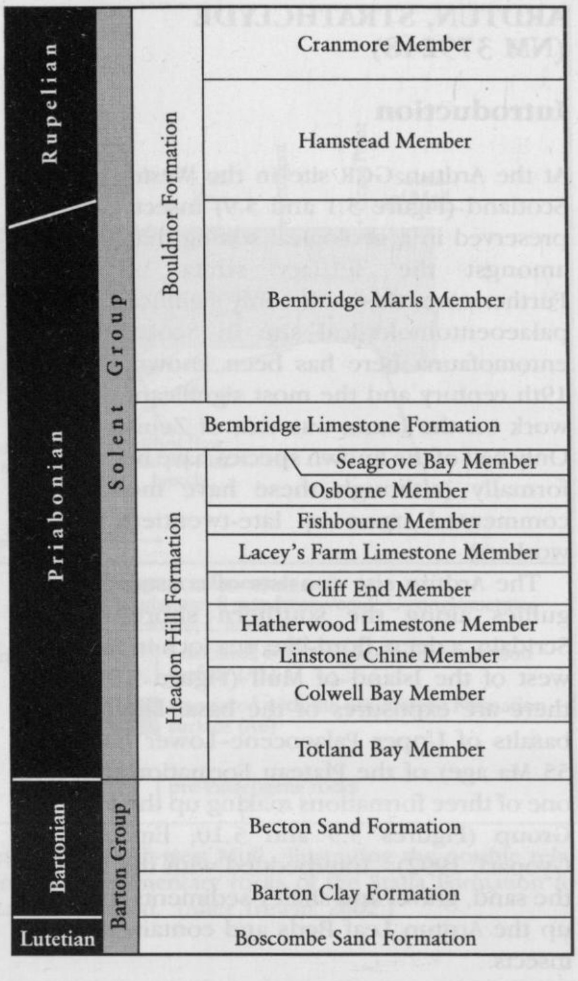


Figure 5.8 Lithostratigraphical scheme for the middle and upper Palaeogene strata in the Hampshire Basin. (After Daley and Balson, 1999.)

deposits are divided into a shallow to marginal marine Barton Group and a brackish to non-marine Solent Group, both of which are divided into a number of formations (Figure 5.8). The Barton Group is middle Eocene in age, and the younger Solent Group, which is of more concern here, is of late Eocene to early Oligocene age. Recognition of the Eocene–Oligocene boundary has been particularly difficult as it is defined by the extinction of certain marine foraminifera and the deposits of the Hampshire Basin had become non-marine by this time (for a detailed discussion see Collinson and Cleal, p. 231–2, in Cleal *et al.*, 2001).

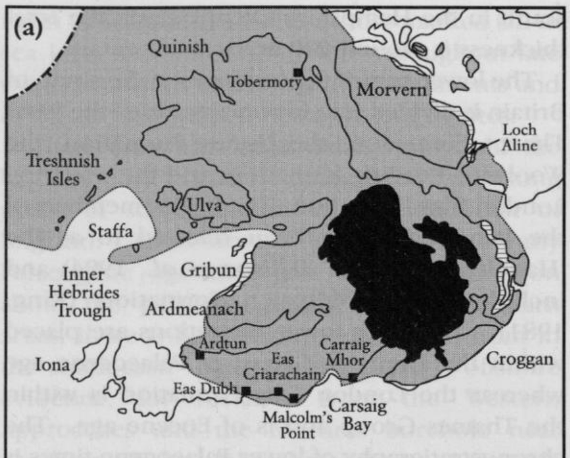
ARDTUN, STRATHCLYDE (NM 379248)

Introduction

At the Ardtun GCR site in the Western Isles of Scotland (Figure 5.1 and 5.9) insect fossils are preserved in a geological setting that is unique amongst the Tertiary strata of Britain. Furthermore, this is the only significant Tertiary palaeoentomological site in Scotland. The entomofauna here has been known since the 19th century and the most significant collective work on the fauna was that of Zeuner (1941). Only half of the known species have been named formally (although these have mostly been commented upon by late-twentieth century workers).

The Ardtun site consists of coastal cliffs and gullies along the southern shore of Loch Scridain, a deep, fjord-like, sea loch in the south-west of the Island of Mull (Figure 5.9). Here there are exposures of the basal lavas (olivine basalts of Upper Palaeocene–Lower Eocene, *c.* 55 Ma age) of the Plateau Formation that form one of three formations making up the Mull Lava Group (Figures 5.9 and 5.10; Emeleus and Gyopari, 1992). Interbedded with the lavas are the sand, gravel and shaley sediments that make up the Ardtun Leaf Beds and contain the fossil insects.

The sediments were originally discovered in the early 19th century by a local man from the nearby village of Bunessan. They were first fully investigated by the then Duke of Argyll, who was well known for his interest in the natural sciences. However, the subsequent description of the sediments and their contained fossils was made by Forbes (1851). For the history of palaeobotanical investigation see Cleal *et al.* (2001, p.181). The find was of major significance in the study of the geology of the Tertiary volcanic rocks of the region because the rich fossil flora allowed the sequence to be given a relative age (early Tertiary) for the first time. This has since been confirmed by radiometric dating of the lavas (Mussett, 1986) at *c.* 58 Ma. In addition to the fossil arthropod importance of this site, the area is also selected for the GCR for the Tertiary Igneous and Tertiary Palaeobotany selection categories (Emeleus and Gyopari, 1992, and Cleal *et al.*, 2001).



Mull Lava Group (Central, Plateau and Staffa formations)
Mesozoic rocks (Triassic–Cretaceous)
pre-Mesozoic rocks (Carboniferous, Devonian and Precambrian)
Central Intrusive Complex
fault, tick on downthrow side

Figure 5.9 Geological map of Mull with the Ardtun locality. (After Trewin, 2002.)

Description

Geological setting

In early Paleogene times, lithospheric thinning of the crust between Greenland and northern Britain led to intense volcanic activity along the continental margin of north-western Europe and ultimately the formation of new ocean crust around 55 Ma. Vestiges of this volcanism are preserved along the west coast of Scotland and especially on the island of Mull. Intermittent igneous activity led to the development of a lava field and interbedded sediments within the North Atlantic Tertiary Igneous Province, a belt of Palaeogene igneous rocks and intra-basaltic sediments that stretch from Rockall to Spitsbergen, ranging in age from 58.5–55 Ma.

The lavas at Ardtun belong to the Mull Plateau Lava Formation, the middle of three formations that comprise the overall architecture of the Mull Lava Field that has an overall thickness of

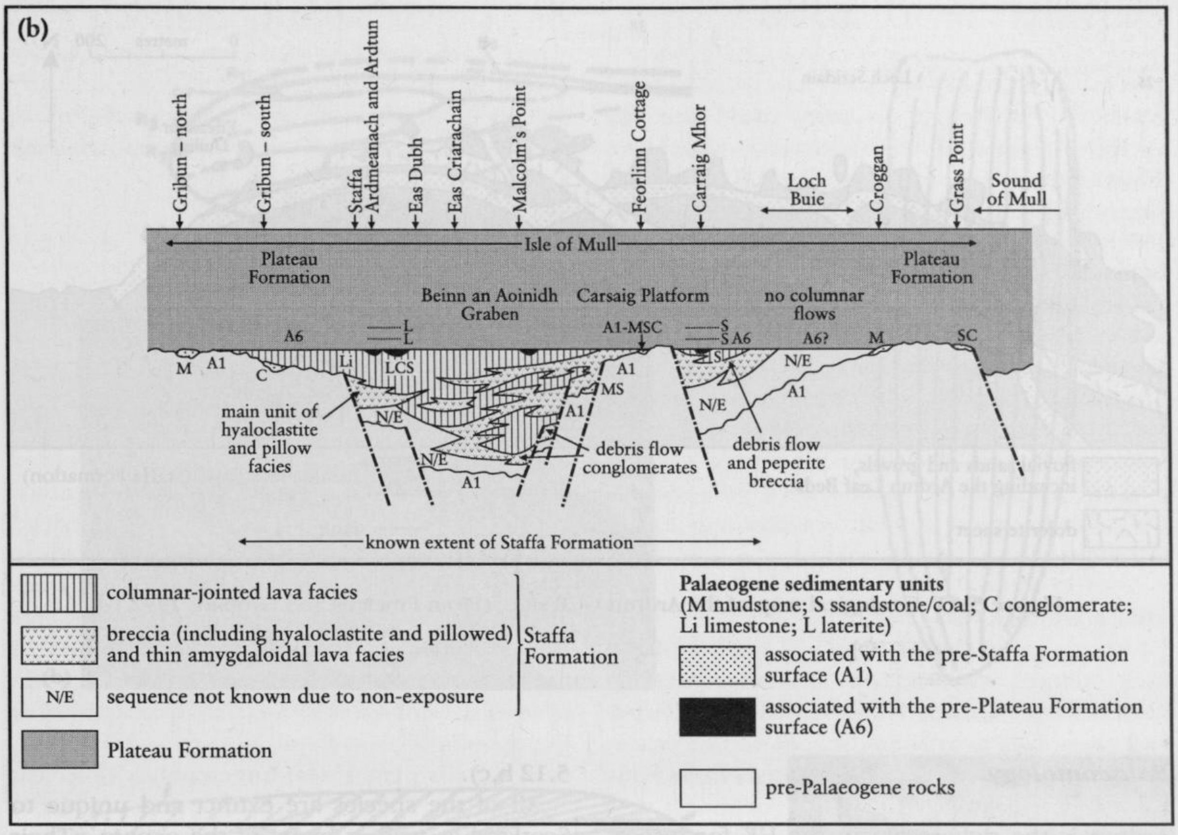


Figure 5.10 Schematic cross section of the lava succession in south-west Mull, illustrating the posible relationships between the various volcanic facies and intercalated sedimentary rocks of the Staffa Formation to 'basement' structures and the succeeding Mull Plateau Lava Formation. (After Trewin, 2002.)

about 1800 m. The stratiform flow sequences were dominated by subaerial lava facies, ranging in composition from alkaline olivine basalts to trachytes with some tholeiites. Eruption was from fissure systems now represented by dyke swarms and from some central vents now represented by deeply eroded central igneous complexes. Between the lavas there are a variety of pyroclastic, epiclastic and volcaniclastic deposits, including tuffs and lahars, along with fluviatile and lacustrine sediments. These were deposited in quiescent phases within the eruptive sequence during which there was weathering, erosion and landscape development with the formation of soils, vegetation and extensive drainage systems (Figure 5.10).

Stratigraphy

The sedimentary succession at Ardtun varies in thickness between 4 and 15 m and was deposited upon the upper slaggy amygdaloidal zone of a thick columnar lava flow and is covered by a second major flow. Both flows show well-developed columnar cooling joints and the lavas are olivine basalts of the Staffa magma Type (Thompson *et al.*, 1986).

The best section through the sediments is seen in the ravine at Slochd an Uruisge and has been described in detail by Skelhorn (1969). The sediments are predominantly flint-bearing conglomerates and grits (*c.* 6 m thick) of the Ardtun Conglomerate Member that represent the first major hiatus in the volcanism of the region. The sedimentary sequence represents an alluvial debris fan deposit with three interbedded finer-grained horizons (Upper, Middle and Lower) of silty sandstone and clay that form the Ardtun Leaf Beds. These finer-grained beds have been interpreted as fluviatile and lacustrine units (Jolley, 1997) and contain an abundant fossil flora and rare fossil insects.

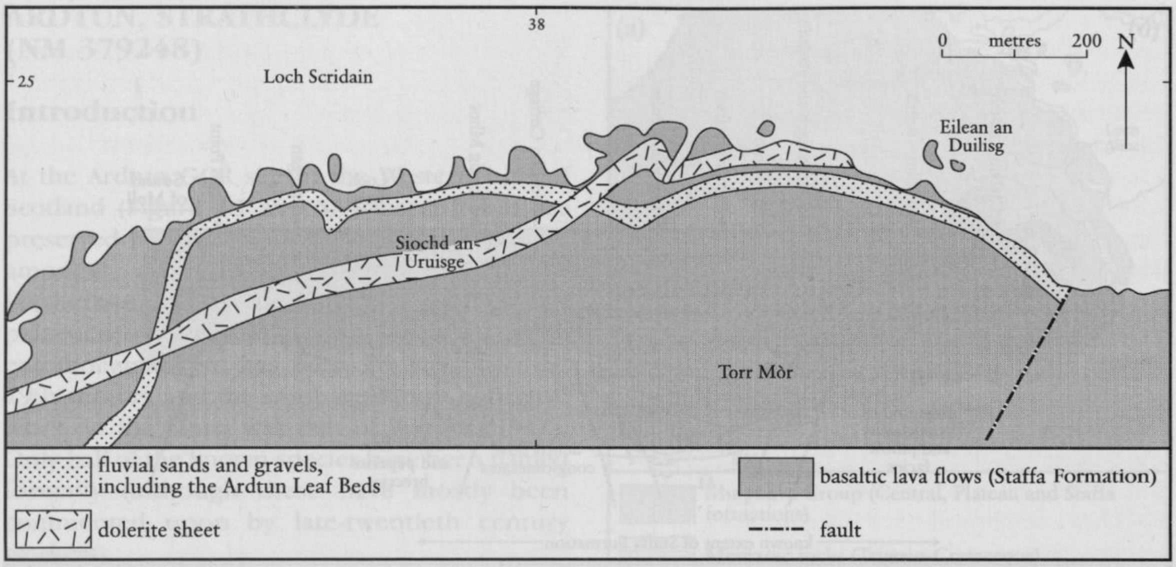


Figure 5.11 Geological map of the Ardtun GCR site. (From Emeleus and Gyopari, 1992.)

Palaeontology

Ardtun is the richest site in the UK for insects representing the Brito-Arctic Igneous Province (BIP) with over 16 species in at least six orders (in contrast, only solitary finds are known from the BIP in Northern Ireland). The entomofauna provides insight into the early Tertiary fauna of high northern latitudes (in contrast to the entomofauna found further south in the UK and continental Europe). Dating from the late Palaeocene at 58 Ma, the entomofauna (Figure 5.12), is found associated with a rich and significant fossil flora including the leaves of maidenhair tree (*Ginkgo*) and tree-forming angiosperms such as plane (*Platanus*), hazel (*Corylus*) and oak (*Quercus*). The plant remains are exceptionally well preserved, some being more than 30 cm in length (Cleal *et al.*, 2001).

The insects are mainly disarticulated remains found in interbasaltic, fine-grained siliciclastic sediments (Ardtun Leaf Beds). The fauna includes aquatic and terrestrial forms comprising beetles (Coleoptera, Figure 5.12c), flies (Diptera: 'March' and Crane-flies, Krzemiński, Figure 5.12a), a long-horned grasshopper or bush cricket (Orthoptera), a dragonfly (Odonata), a caddisfly (Trichoptera, Figure 5.12f) and several kinds of bugs (Homoptera: a cicada, spittlebug and leafhopper, Figure 5.12 b,c).

All of the species are extinct and unique to Scotland as well as many of the genera. Their affinities are mainly (but not exclusively) with modern non-European fauna, for example the cicada *Eotettigarcta scotica* (Whalley, 1983; Figure 5.12b) has upland south-east Asian affinities. Cicadas no longer range as far north as Scotland. Some species are the earliest representatives of their groups, for example the anostostomatid orthopteran *Zeuneroptera scotica* (Gorochov, 1995; Figure 5.12d) is the earliest representative of stenopelmatoids.

An accompanying sparse fauna includes molluscs (Cooper, 1979). The lowest leaf bed is underlain by a thin coal seam below, which is a 0.15–0.20 m whitish concretionary seat-earth clay containing root traces. The Ardtun flora also differs from the Reading Formation plant fossils of southern England in being dominated by deciduous species of both conifers and hamamelidids. The reason for this may partly be due to the more northerly latitudes of the site. However, despite its high latitude, the flora does not represent cold-climate vegetation, but temperate or even warm-temperate conditions that prevailed in very early Tertiary times. Also the location within a highly active volcanic region of disturbed habitats, poor soils and acid rain no doubt also played a role.

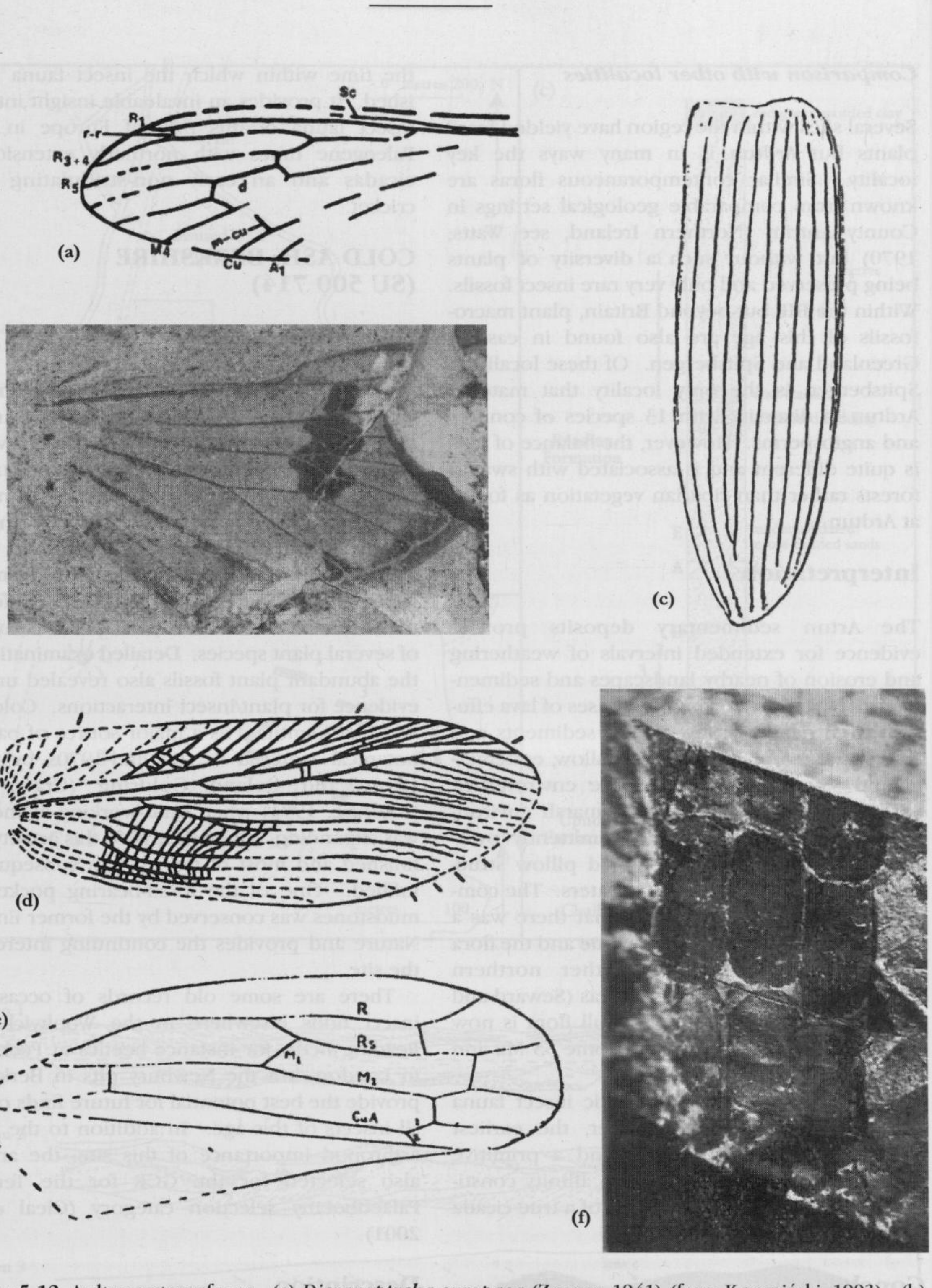


Figure 5.12 Ardtun entomofauna. (a) *Dicranoptycha europaea* (Zeuner, 1941) (from Krzemiński, 1993). (b) *Eotettigarcta scotica* (Zeuner, 1944) (from Whalley, 1983). (c) *Carabites scoticus*, Cockerell, 1921, elytron, × 17 (from Zeuner, 1941). (d) *Zeuneroptera scotica* (Zeuner, 1939) (Anostostomatidae) male (?) forewing, wing fragment 27 mm long (from Gorochov in Rasnitsyn and Quicke, 2002). (e) *Maleojassus primitivus* Zeuner, 1941, tegmen, × 10.3 (from Zeuner, 1941). (f) *Folindusia zeuneri* Vyalov and Sukacheva, 1976 (loc. cit.). a, c, d, e forewings; b, hindwing; f, caddiscase. The key to venation annotations can be found in Figure 4.23.

Comparison with other localities

Several sites within the region have yielded fossil plants but Ardtun is in many ways the key locality. Similar contemporaneous floras are known from comparable geological settings in County Antrim (Northern Ireland, see Watts, 1970) but without such a diversity of plants being preserved and only very rare insect fossils. Within the BIP but beyond Britain, plant macrofossils of this age are also found in eastern Greenland and Spitsbergen. Of these localities, Spitsbergen is the only locality that matches Ardtun in diversity with 13 species of conifers and angiosperms. However, the balance of taxa is quite different and is associated with swamp forests rather than riparian vegetation as found at Ardtun.

Interpretation

The Artun sedimentary deposits provide evidence for extended intervals of weathering and erosion of nearby landscapes and sedimentation in lake basins between phases of lava effusion from nearby fissures. The sediments and flora indicate deposition in a shallow, ephemeral and stagnant fluvio-lacustrine environment with shallow lake, swamp and marsh environments, all of which were intermittently overflowed by lavas which generated pillow structures on contact with the lake waters. The composition of the flora indicates that there was a warm temperate climate at the time and the flora has been correlated with other northern European early Tertiary fossil floras (Seward and Holtum, 1924), although the Mull flora is now considered to be the oldest at some 55 Ma and of Paleocene age.

The varied terrestrial and aquatic insect fauna includes a primitive leafhopper, the earliest stenopelmatoid bush cricket, and a primitive cicada with south-east Australian affinity constituting the most northerly record of a true cicada in the British Isles (Figure 5.12).

Conclusions

Situated in an active volcanic province of early Tertiary age (late Paleocene, around 55 Ma), this is a unique location in Britain and has a wider European significance. Its plant fossils are internationally famous and provide important evidence for the environments and climates of the time within which the insect fauna flourished. It provides an invaluable insight into the insect fauna of this part of Europe in early Paleogene times with northerly extension of cicadas and an early non-stridulating bush cricket.

COLD ASH, BERKSHIRE (SU 500 714)

Introduction

Sediments in the Reading Formation (Lambeth Group) at Cold Ash Pit near Newbury in Berkshire have yielded insect fossils along with a diverse flora from the Palaeocene–Eocene transition of early Paleogene age (*c.* 55 Ma); indeed Cold Ash is an important GCR fossil plant site (Cleal *et al.*, 2001) whose unusually well-preserved flora includes various plant elements (foliage, fruit and seeds). The combination of these elements allows the partial reconstruction of several plant species. Detailed examination of the abundant plant fossils also revealed unique evidence for plant/insect interactions. Cold Ash was first identified as a major source of palaeobotanical material in the mid-1970s by Peter Crane and Roland Goldring (Crane and Goldring, 1991) when sand-working at the site was expanding, but by the 1980s this activity had finished and most of the pit was subsequently infilled. One of the fossil-bearing pockets of mudstones was conserved by the former English Nature and provides the continuing interest in the site.

There are some old records of occasional insect finds elsewhere in the Woolwich and Reading Beds, for instance beetles at Peckham, in London, but the Newbury pits in Berkshire provide the best potential for future finds of fossil insects of this age. In addition to the fossil arthropod importance of this site, the area is also selected for the GCR for the Tertiary Palaeobotany selection category (Cleal *et al* 2001).

Description

Sedimentary succession

The stratigraphy of the old quarry site, as exposed at its previous maximum extent, revealed a sedimentary succession dominated by unconsolidated and poorly consolidated cross-

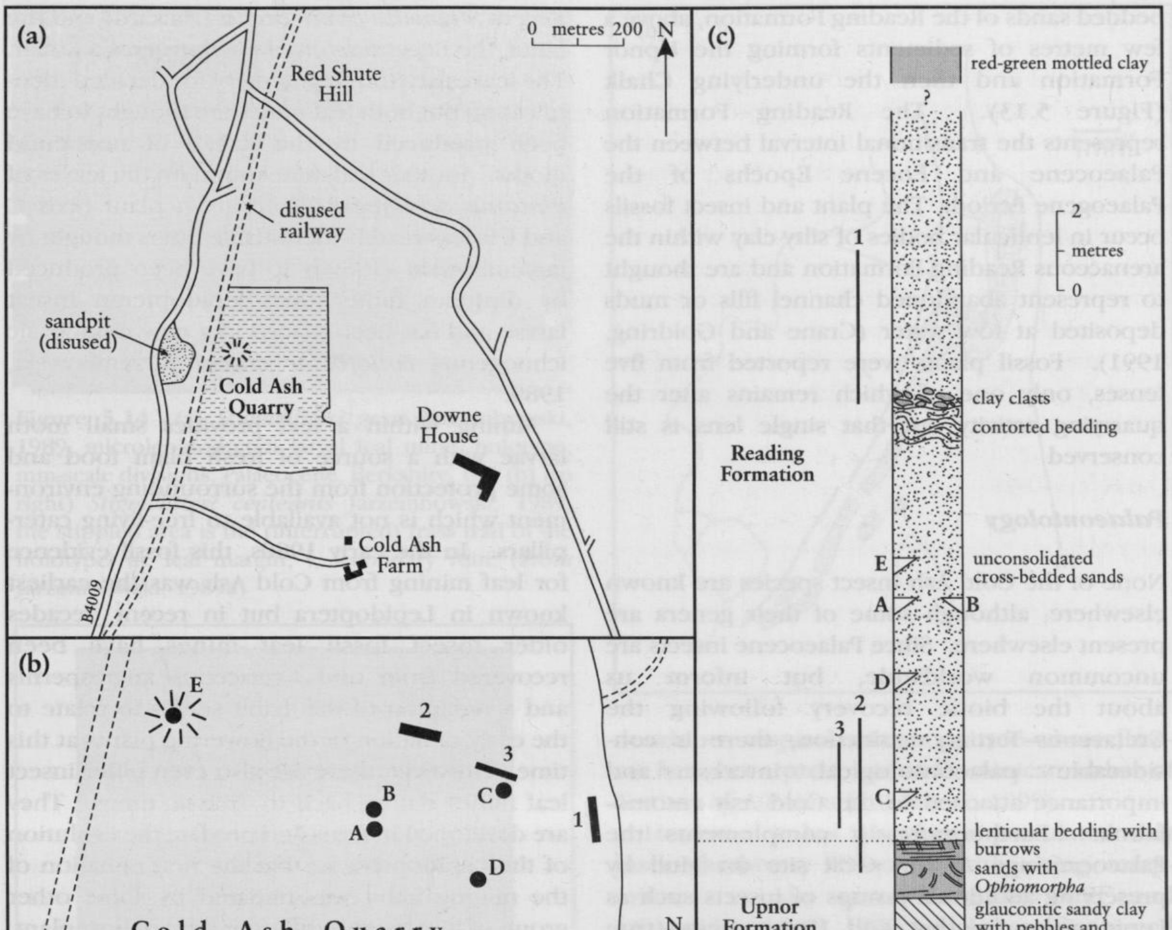


Figure 5.13 Cold Ash Quarry in the early 1980s; (a) and (b) show plans of the site and include the location of the sections represented in (d). Also shown are the locations of the main plant-bearing lenses (A to E) on the composite stratigraphical section (c). (After Crane and Goldring, 1991.)

bedded sands of the Reading Formation, above a few metres of sediments forming the Upnor Formation and then the underlying Chalk (Figure 5.13). The Reading Formation represents the transitional interval between the Palaeocene and Eocene Epochs of the Palaeogene Period. The plant and insect fossils occur in lenticular bodies of silty clay within the arenaceous Reading Formation and are thought to represent abandoned channel fills or muds deposited at low water (Crane and Goldring, 1991). Fossil plants were reported from five lenses, only one of which remains after the quarrying activity but that single lens is still conserved.

Palaeontology

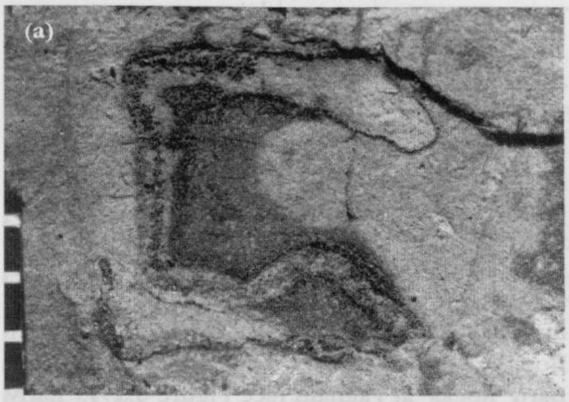
None of the Cold Ash insect species are known elsewhere, although some of their genera are present elsewhere. Since Palaeocene insects are uncommon worldwide, but inform us about the biotic recovery following the Cretaceous–Tertiary extinction, there is considerable palaeontological interest and importance attached to the Cold Ash entomofauna. Furthermore, it complements the Palaeocene-age Ardtun GCR site on Mull by preserving additional groups of insects such as Lepidoptera (moths) and Heteroptera (true bugs). These are preserved as trace and body fossils at Cold Ash.

Jarzembowski (1989a) has described the unique preservation of the leaf mines produced by both Lepidoptera and Diptera from the fossil flora of Cold Ash. Other pits at a similar stratigraphical horizon in the area have provided further unpublished information about leaf galling and possible beetle borings in wood of *Entandrophragminium lewisii* Crawley, 2001 (Meliaceae). Leaf mines and galls have also been described from the mid-Eocene age Branksome Sand Formation at Bournemouth Cliffs (Lang *et al.*, 1995): these were based purely on museum collections and the sites have been lost due to the building of amenity and sea-defence structures. The Cold Ash leaf mines are better preserved than those found at Bournemouth which are decarbonized.

The leaf mines from Cold Ash have been named by Jarzembowski (1989a) as a new species of the ichnogenus *Stigmellites*, *S.? gossi* Jarzembowski, 1989 and *S.? centennis*, both from plant bed E. The former resembles the Recent *Stigmella pomivorella* (Packard) and the latter, the Recent *Nepticula hemargyrella* Kollar. The leaves are too fragmentary for detailed identification but both leaf mines are thought to have been produced by the larvae of nepticulid moths. Another leaf mine found on the leaves of *Platanus schimperi* (Heer) from plant beds C and E is less readily identifiable but is thought by Jarzembowski (1989a) to have been produced by dipteran rather than lepidopteran insect larvae and has been placed in a new monobasic ichnogenus *Foliofossor cranei* Jarzembowski, 1989.

Mining within a leaf provides small moth larvae with a source of fresh plant food and some protection from the surrounding environment which is not available to free-living caterpillars. In the early 1980s, this fossil evidence for leaf mining from Cold Ash was the earliest known in Lepidoptera but in recent decades older insect fossil leaf mines have been recovered from mid Cretaceous angiosperms and a radiation of this habit seems to relate to the early radiation of the flowering plants at this time. However, there are also even older insect leaf mines dating back to Triassic times. They are developed in ferns and predate the evolution of the Lepidoptera so that the first radiation of the mining habit was initiated by some other group of insects on a different kind of host plant. Lepidoptera appeared in Jurassic times as small species before the angiosperms so there may have been some host transfer involved. Leaf mining has arisen independently in different insect groups as shown by the fossils from Cold Ash.

The somewhat younger *c.* 34 Ma (latest Eocene), and even more abundant and diverse fossil plants from Florissant in Colorado in the USA, record an even bigger range of plant–insect interactions, such as leaf margin feeding, hole feeding, skeletal feeding, galls, leaf cutting and leaf mining. A quantitative study of insect damage on Florissant fossil leaves (Smith, 2000a,b; Meyer, 2003) shows that 23 % of the fossil leaves had insect damage, with 1.4 % of the total leaf area, of all leaves examined, having been removed by insect herbivory. Interestingly, this is much less than found in a sample of six modern forests, where 72–90 % of the leaves had been damaged and 4–10 % of the leaf area has been removed. The rare leaf mines at Florissant were excavated in leaves of the souca or piocha (*Trichilia*, a meliacean (Figure 5.15) an extant



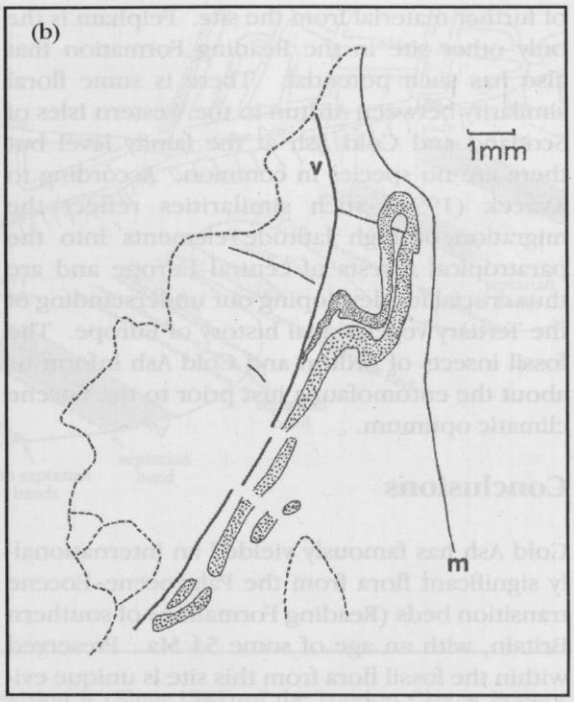


Figure 5.14 (a) *Stigmellites? gossi* Jarzembowski, 1989, microlepidopteran larval leaf mine, holotype, mm-scale divisions, Palaeocene, Berkshire, UK. (b) (to right) *Stigmellites? centennis* Jarzembowski, 1989, the stippled area is the (interrupted) frass trail of the holotype; m, leaf margin; v, secondary vein. (From Jarzembowski, 1989a)

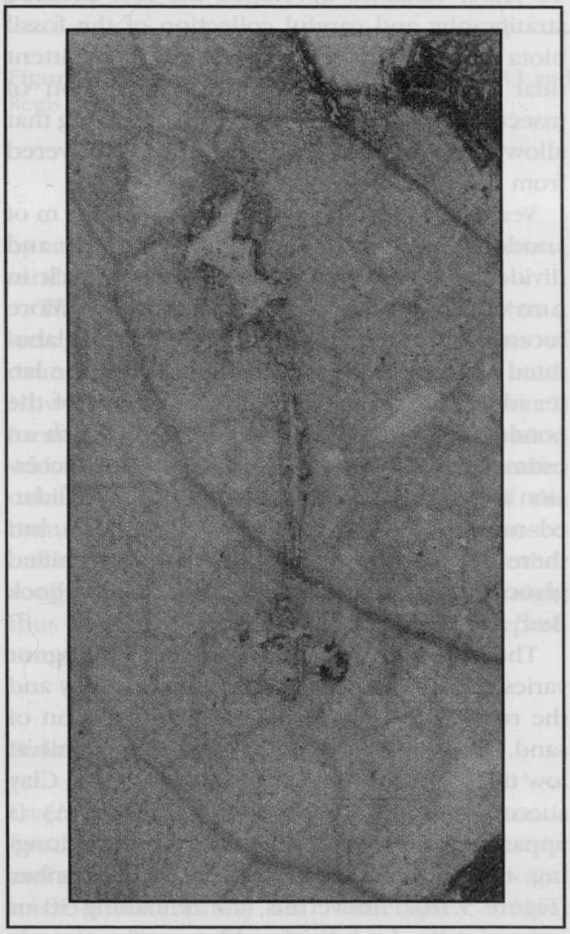


Figure 5.15 *Trichilia* leaf from Florissant, Colorado, demonstrating leaf mining activity (× 6). The egg was laid at the base; the larva then tunnelled through leaf tissue, eventually making a pupation chamber - seen as the hole at the top. (From Meyer, 2003.)

deciduous tropical subcanopy tree whose flowers have been preserved in Dominican amber of Tertiary age (Poinar and Poinar, 1999).

However, it has also been postulated that insect herbivory increases with rising temperature at any given latitude (Wilf and Labandeira, 1999). Wilf and Labandeira tested the idea using abundant fossil data from late Palaeocene–early Eocene deposits of south-western Wyoming in the USA (e.g. the Green River Basin, their, fig. 2) and did indeed find that global warming at that time was reflected by an increase in more types of insect damage (such as leaf mining) per host species and higher attack frequencies.

The diverse flora, recovered from Cold Ash, is dominated by fossils derived from angiosperm trees of the plane, katsura and walnut families. The Cold Ash flora contains type material upon which some important aspects of global palaeobiogeography have been built. It includes the only recorded example of Palaeogene *Rhododendron* from anywhere in the world and the earliest known member of the tribe Coryleae, which subsequently became specialized for animal dispersal (Collinson, 1999a,b).

Interpretation

Much of the Cold Ash flora remains to be documented and there is potential for the collection of further material from the site. Felpham is the only other site in the Reading Formation that also has such potential. There is some floral similarity between Ardtun in the Western Isles of Scotland and Cold Ash at the family level but there are no species in common. According to Kvacek (1994) such similarities reflect the migration of high latitude elements into the paratropical forests of central Europe and are thus crucial for developing our understanding of the Tertiary vegetational history of Europe. The fossil insects of Ardtun and Cold Ash inform us about the entomofauna just prior to the Eocene climatic optimum.

Conclusions

Cold Ash has famously yielded an internationally significant flora from the Palaeocene–Eocene transition beds (Reading Formation) of southern Britain, with an age of some 54 Ma. Preserved within the fossil flora from this site is unique evidence of insect plant co-evolution in the form of leaf mines and there is the potential for further investigation of the remaining fossiliferous deposits.

BOGNOR REGIS, WEST SUSSEX (SZ 918 984)

Introduction

Foreshore exposures of the Ypresian London Clay Formation at the coastal resort of Bognor Regis have over several decades provided an abundant and diverse fossil biota, notably of insects. This biota has proven to be of international significance as the most important source of pyritized insects of any age. In addition, these most easterly exposures of the London Clay in the Hampshire Basin have considerable stratigraphical and palaeoenvironmental significance.

The site has also been selected independently as a GCR site on other counts: for its fossil plants (Cleal *et al.*, 2001), fishes (Dineley and Metcalf, 1999), mammals and birds (Benton *et al.*, 2005) and its stratigraphy (Daley and Balson, 1999). In addition to the fossil arthropod importance of this site, the area is also selected for the GCR for the Tertiary Palaeobotany, Mesozoic–Tertiary Fish/Amphibia and Aves selection categories.

Description

Stratigraphy

The intermittent foreshore exposures between Bognor Regis and Pagham to the west comprise silty muds and sands of the lower to middle part of the London Clay Formation, which dip here at a low angle to the south-west (Figure 5.16). The succession is interrupted by two marker horizons – the stratigraphically lower and older Bognor 'Rocks' and the higher and younger Barn 'Rocks' at Pagham (see Figure 5.17). Early research in the 19th century focused largely on the Bognor Rocks (see, for example, Dixon, 1850; Reid, 1897). From the late 1920s, the modern phase of detailed investigation was initiated by a local collector Edmond Martin Venables (1901–1990). Over a period of nearly 40 years, Venables developed the first detailed stratigraphy and careful collection of the fossil biota (see Bone, 2003). Because of intermittent tidal exposure and the low concentration of insects, it was Venables' long-term collecting that allowed so much information to be recovered from this site.

Venables (1929, 1963) recorded some 90 m of London Clay exposed along the foreshore and divided the succession into 'Groups' which in turn were partially subdivided into 'Beds'. More recently, the succession has been further elaborated by Bone (1978) and King (1981). The latter identified a general informal division of the London Clay into A, B and C divisions with an estimated total thickness of 90 m. The succession is comprised mostly of partially consolidated mudrocks (silty clays and clayey silts) but there are also two horizons of more lithified glauconitic sands known as the 'Bognor Rock Bed' and the 'Barn Rock Bed'.

The exposure of the succession at Bognor varies depending upon winter storm activity and the relative local removal and or deposition of sand. Most of the sequence is only accessible at low tide. The lowest part of King's London Clay succession (Subdivision A1 of Division A) is apparently absent with the lowest strata belonging to Subdivision A2, the Walton Member (Figure 5.18). Above this, the remaining 30 or more metres of subdivision A3 comprise a coarsening upwards sequence of sandy clay and finally the glauconitic sandstones of the Bognor Rock Bed (Bognor Member) for which this site is the stratotype. The sediments are partly cemented

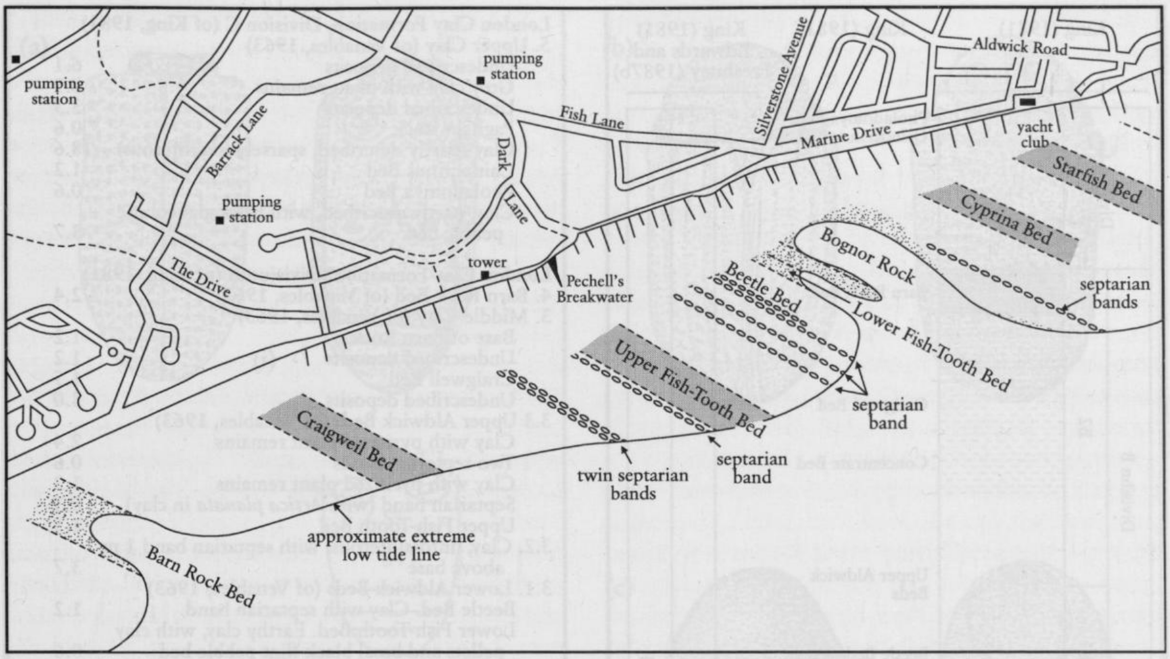


Figure 5.16 Foreshore exposure of Division A3 and Division B (King, 1981) of the London Clay at Bognor Regis. (After Venables, 1962.)

by carbonate to form large nodules of calcareous sandstone.

The base of the succeeding Division B has a base marked by a conglomeratic horizon of rounded black flint pebbles in a sandy mud. However, overall, the succession of Division B forms another coarsening upwards succession which terminates in the second partly cemented calcareous and glauconitic sandstones of the barn Rock Bed. Division C is seldom exposed but is thought to have a base marked by another conglomeratic flint pebble layer, which might thus represent the beginning of a third depositional rhythm.

Palaeontology

Overall, much of the London Clay Formation is fossiliferous with a diverse biota, both terrestrial and marine, of plants, invertebrates (macro- and micro-invertebrates) and vertebrates. Most abundant in species terms are molluscs (altogether some 141 species, of which 75 are gastropods, 65 bivalves and one scaphopod known so far) and plants (some 130 species, mostly angiosperms, forming the most diverse early Eocene fruit and seed flora in Britain). The Bognor flora, mostly from Division B, is important as the main source of information about plants from this level within the London Clay Formation (the Isle of Sheppey outcrop being younger).

However, vertebrates are also common, especially fish, but also a few birds (six species) have been found. The fish records include some 47 species, mostly comprised of the teeth of cartilagenous chondrichthyans, but also the bones and otoliths of some 12 teleosts. The abundance of predatory fish indicates that local waters were highly productive. However, the distribution of individual groups within the overall biota is very variable with particular assemblages being dominant at specific horizons. Historically these have been identified by the name of one especially common or obvious kind of fossil, for example the Astarte bed (at the base of subdivision A3), named after the bivalve *Astarte subrugata*, which is abundant within this horizon.

Most important in the present context is the faunal succession at the base of Subdivision B1 above the Bognor Member. Much of the B1 silty clays are characterized by an abundant micro-

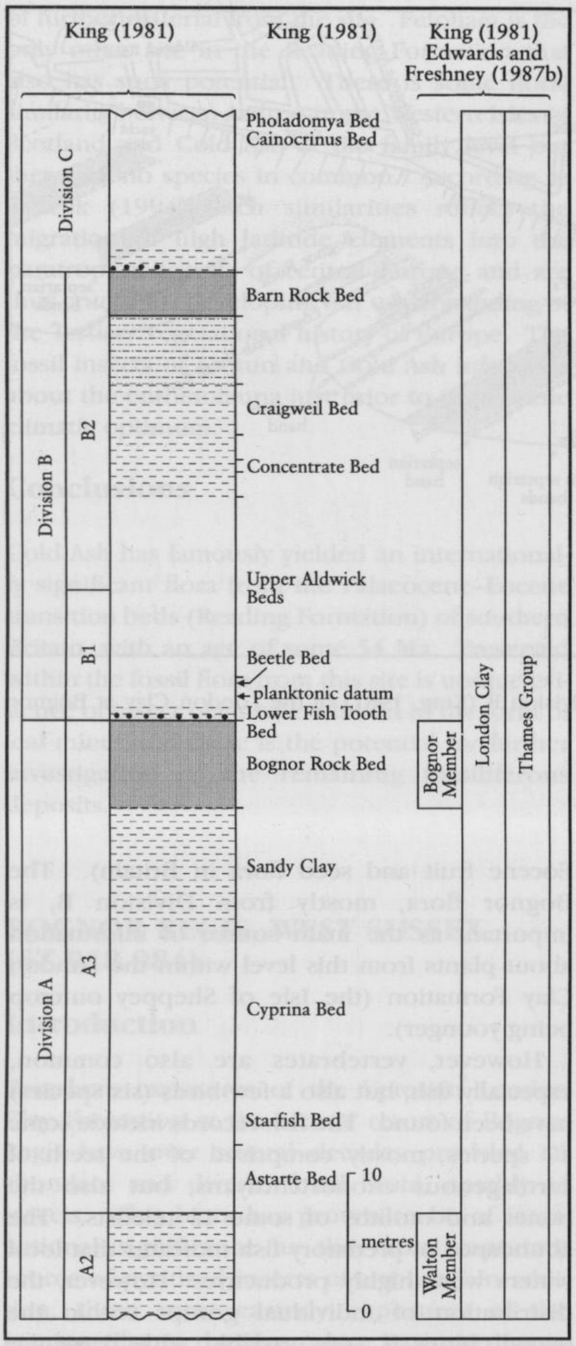


Figure 5.17 London Clay succession at Bognor Regis, West Sussex. (After King, 1981.)

London Clay Formation, Division C (of King, 1981)	
5. Upper Clay (of Venables, 1963)	
Undescribed deposits	6.1
Grey clay with plant remains	0.9
Undescribed deposits	3.5
Pagham Rock	0.6
Clay (partly described, sparsely fossiliferous)	18.6
Cainocrinus Bed	1.2
Pholadomya Bed	0.6
Clay, partly described, with basal glauconitic pebble bed	3.7
London Clay Formation, Division B (of King, 1981)	
4. Barn Rock Bed (of Venables, 1963)	2.4
3. Middle Clay (of Venables, 1963)	
Base of Barn Rock	1.2
Undescribed deposits	1.2
Craigwell Bed	1.5
Undescribed deposits	3.0
3.3 Upper Aldwick Beds (of Venables, 1963)	
Clay with pyritized plant remains	2.4
Two septarian bands	0.6
Clay with pyritized plant remains	1.2
Septarian band (with *Artica planata* in clay)	0.3
Upper Fish-Tooth Bed	1.5
3.2. Clay, unfossiliferous, with septarian band 1 m above base	3.7
3.1. Lower Aldwick Beds (of Venables, 1963)	
Beetle Bed. Clay with septarian band	1.2
Lower Fish-Tooth Bed. Earthy clay, with clay pellets and basal black flint pebble bed	0.6
London Clay Formation, Division A3, Bognor Member (of King, 1981)	
2. Bognor Rock Group (of Venables, 1963)	
Bognor Rock Bed. Interbedded unconsolidated grey sand and partially cemented, fine glauconitic sandstone	6.7
Sandy clay, and soft sandstone	3.0
London Clay Formation, Division A2, Walton Member (of King, 1981)	
1. Lower Clay (of Venables, 1963)	
Septarian band, with white clay, iron stained	0.6
'Cyprina' Bed	5.5
Starfish Bed	1.8
Clay	1.2
Astarte Bed	2.4
Friable clay	2.7
Clay with occasional pyritized plant remains	2.7
Sandy layer	0.3
Clay, partly described	4.6
Septarian band, with white clay, iron stained	0.3
Dark grey, silty clay	0.6
Deposits obscured by alluvium	3.0

Figure 5.18 The succession at Bognor Regis. (From Dineley and Metcalf, 1999).

fauna containing elements of the nodosariid-rich (planktonic foraminiferid) datum of the London Basin. The sediment is enriched with secondary pyrite ranging from small grains to nodules and a common pyritization of the fossil fauna.

The insects

Of especial interest here are the remains of numerous pyritized beetles (Coleoptera) and a hemipteran, mostly adult stages (imagines) all of

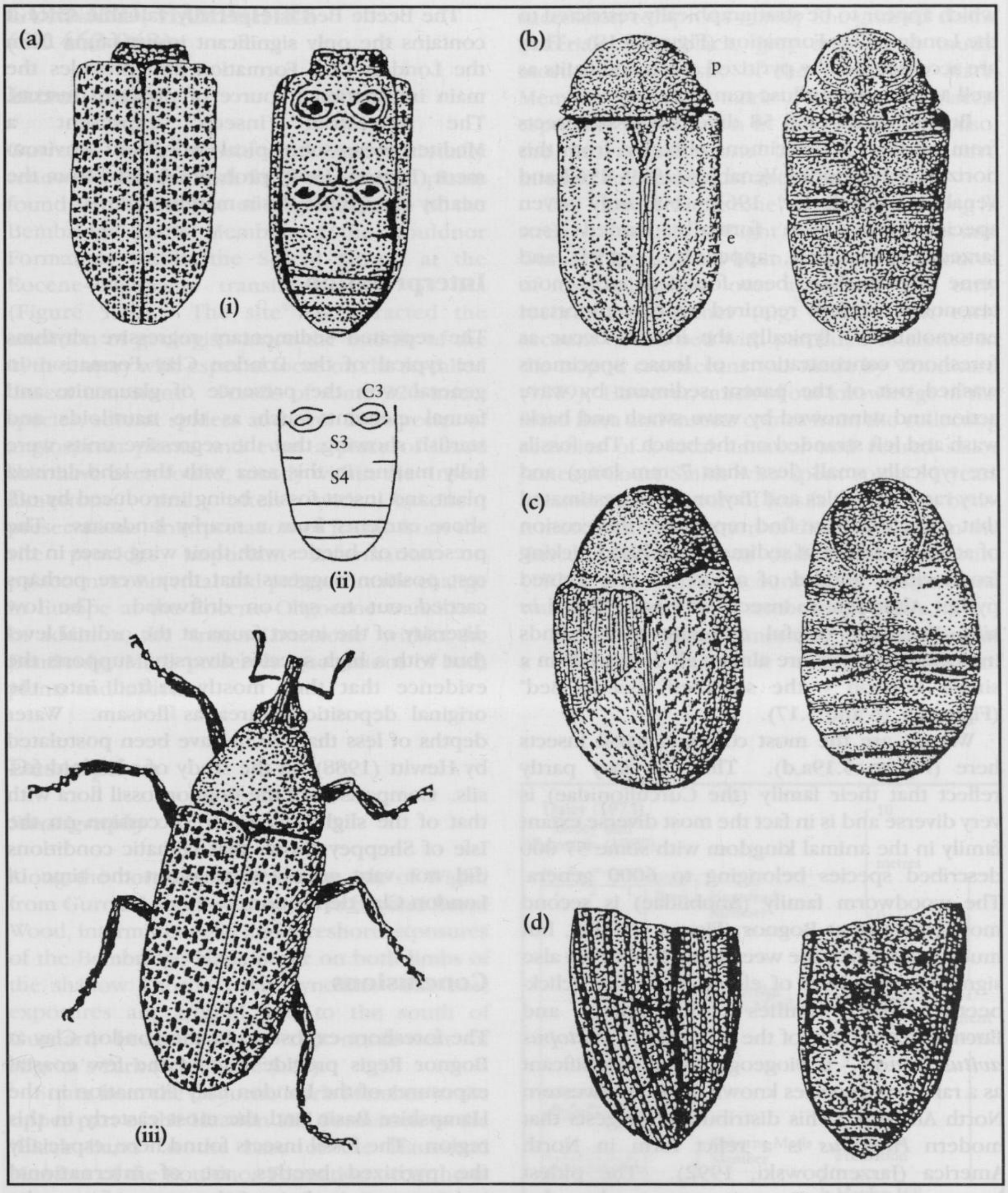


Figure 5.19 (a) *Pissodites argillosus* Britton (Curculionidae: Hylobiinae), Beetle Bed, Bognor Regis, Sussex. (i) Hindbody, dorsal and ventral views, length 3 mm. [Holotype in NHM, In. 49325], (ii) hindbody showing diagnostic curculionid characters (S3, S4, basal abdominal stemites; C3, hind coxa); (iii) reconstruction. (b)–(d) Coleoptera in Tony and Bett Parker collection, NHM, from the Beetle Bed, Bognor Regis, dorsal and ventral views. (b) Anobiid gen. et. sp. nov., length 2mm, In. 64733; p, pronotum, e, elytron,; (c) *Venablesia* sp. nov. (Anobiidae). Length 5mm, In. 64732. (d) Curculionid with cuticle preserved, ?In. 64734, (After Venables' work and as figured in Jarzembowski, 1992.)

which appear to be stratigraphically restricted to the London Clay Formation (Figure 5.19). They are accompanied by pyritized seeds and fruits as well as fish and mollusc remains.

Britton recognized 58 different fossil insects from among 231 specimens obtained from this horizon at Bognor by Venables (1929, 1962 and Venables and Taylor, 1963), but only seven species have been formally named (see Jarzembowski, 1992, appendix 1, p.94) and none of them have been found *in situ*; more taxonomic work is required on this important entomofauna. Typically, the insects occur as foreshore concentrations of loose specimens washed out of the parent sediment by wave action and winnowed by wave swash and backwash and left stranded on the beach. The fossils are typically small (less than 7 mm long) and very rare. Venables and Taylor (1963) estimated that each foreshore find represents the erosion of at least a tonne of sediment and hand picking from within a third of a litre of fine-grained pyrite. Although no insects have been found *in situ*, Venables' careful mapping of his finds indicated that they are almost all derived from a single horizon – the so-called 'Beetle Bed' (Figures 5.16 and 5.17).

Weevils are the most common fossil insects here (Figure 5.19a,d). This fact may partly reflect that their family (the Curculionidae) is very diverse and is in fact the most diverse extant family in the animal kingdom with some 57 000 described species belonging to 6000 genera. The woodworm family (Anobiidae) is second most common at Bognor (Figure 5.19b,c), but much less so than the weevils, and there are also significant numbers of elateroid beetles (click-beetle like families Throscidae and Eucnemidae). One of the elateroids – *Pactopus avitus* Britton – is biogeographically significant as a rare living species known only from western North America. This distribution suggests that modern *Pactopus* is a relict form in North America (Jarzembowski, 1992). The oldest known eucnemid, *Potergite senectus* has also been found at Bognor. In addition, there are occasional shield bugs (Pentatomidae) and members of the Scarabaeidae. Although this latter family are best known as scarabs, their fossil representatives at Bognor are not typical. For example they include a species of *Saprosites* which is an extant genus of wood-boring beetle. Another genus, *Onthophagus*, does however include extant species associated with dung.

The Beetle Bed is especially valuable since it contains the only significant insect fauna from the London Clay Formation and provides the main international source of pyritized insects. The terrestrial insects represent a Mediterranean-subtropical woodland environment (Britton, 1960) probably derived from the nearby Hampshire Basin margin.

Interpretation

The repeated sedimentary regressive rhythms are typical of the London Clay Formation in general with the presence of glauconite and faunal elements such as the nautiloids and starfish showing that the regressive units were fully marine in this area with the land-derived plant and insect fossils being introduced by offshore currents from a nearby landmass. The presence of beetles with their wing cases in the rest position suggests that they were perhaps carried out to sea on driftwood. The low diversity of the insect fauna at the ordinal level (but with a high species diversity) supports the evidence that they mostly drifted into the original depositional area as flotsam. Water depths of less than 70 m have been postulated by Hewitt (1988) on the study of nautiloid fossils. Comparison of the Bognor fossil flora with that of the slightly younger succession on the Isle of Sheppey shows that climatic conditions did not vary greatly throughout the time of London Clay deposition.

Conclusions

The foreshore exposures of the London Clay at Bognor Regis provide one of the few coastal exposures of the London Clay Formation in the Hampshire Basin and the most easterly in this region. The fossil insects found here, especially the pyritized beetles, are of international importance. Analysis of the entomofauna, the accompanying diverse biota and sediments provides important evidence for regional palaeogeographical and palaeoenvironmental interpretation. The site also has considerable potential for future finds with the shallow dip of the strata producing wide outcrops and an unusually good opportunity for the collection and study of the fossil biota.

GURNARD, HAMPSHIRE (SZ 462 943)

Introduction

Gurnard is a classic and internationally renowned site for both fossil insects and plants found within the Isle of Wight outcrop of the Bembridge Marls Member of the Bouldnor Formation within the Solent Group at the Eocene–Oligocene transition some 34 Ma (Figure 5.20). The site has attracted the attention of geologists since the middle of the 19th century with especial focus on the so-called 'Insect Limestone'. Fossils of some 220 insect species, several spiders and over 100 species of angiosperm plants and even a piece of lizard skin have been found, mostly within the 'Insect Limestone' and often with excellent preservation. Interpretation of fossils from the site provides important information on palaeoenvironmental and palaeoclimatic change in Europe at the Eocene–Oligocene transition. In addition, the 'Insect Limestone' within the Bembridge Marls preserves associations of both plants and insects.

Description

Stratigraphy

Along the northern shore of the Isle of Wight, from Gurnard south-westwards to beyond Burnt Wood, intermittent cliff and foreshore exposures of the Bembridge Marls occur on both limbs of the shallow Thorness Bay Syncline. The best exposures are around and to the south of Gurnard Ledge and to the north-west of Pilgrim's Park (see Figure 5.22).

Strata from the Osborne Marls Member in the upper part of the Headon Hill Formation to the 'Black Band' at the base of the Hamstead Member of the Bouldnor Formation occur here. However, the most palaeontologically significant sections are in the Bembridge Limestone Formation and lower part of the Bembridge Marls Member at the base of the Bouldnor Formation. The exposed sequence has a total thickness of less than 30 m. At Gurnard Ledge, the Bembridge Limestone Formation is 6.7 m thick and the overlying Bembridge Marls Member is 21.5 m thick (including the 'Insect Limestone', see section in Figure 5.21). The succession comprises mainly fine-grained clastic materials with black, grey and green muds, mostly characteristic of the Bembridge Marls Member, although marls do occur in places, especially lower down in the succession. Also, the 'Insect Limestone' is a very distinctive micritic limestone, just above the base.

The 'Insect Limestone' is exposed along a stretch of the Isle of Wight coast in Thorness and Gurnard Bay and has been shown to be a source of fossil plants for over a century with early records by Gardner (e.g. 1888). An early account of this bed with particular reference to the isopod crustaceans was made by Woodward (1879). However, much of our knowledge of the fossil flora and insects comes from the collecting activities of a local amateur and retired sailor James A'Court Smith who spent some 30 years amassing a collection of fossils from these beds. A more modern account of the isopods from the 'Insect Limestone' was undertaken by Martini (1972), and a major acount of the insect fauna was undertaken by Jarzembowski (1980a,b).

The name 'Insect Limestone' is something of a misnomer since it really consists of

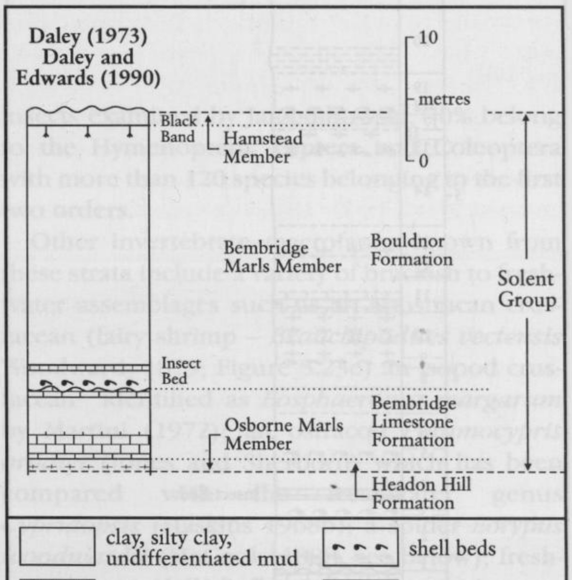


Figure 5.20 Stratigraphical succession at Thorness Bay, Isle of Wight. (After Daley and Balson, 1999, fig. 5.43.)

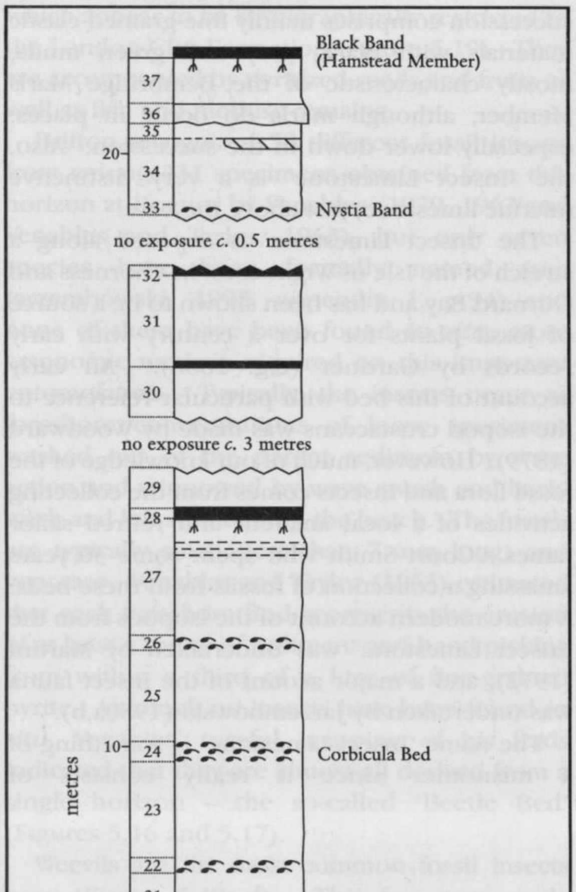


Figure 5.21 Bembridge Marls member (Bouldnor Formation) succession at Gurnard Ledge, Isle of Wight. (After Daley, 1972.)

discontinuous concretionary limestones and hard marls within a predominantly argillaceous unit, although in places they develop into a tabular limestone up to 10+ cm thick. Within the limestones, which resemble some Purbeck micrites in lithology, the preservation of extremely delicate biological tissues and structures is facilitated by the exceptionally fine grain of the sediment. Unusually, the insects and the spiders are also preserved in three dimensions (see Figure 5.24), sometimes with details of their internal anatomy preserved in calcite. They are of taphonomic interest because the cuticle and colour patterns are preserved, the former as an aliphatic compound. It is this type of preservation that has recorded the presence of an unknown lizard in the fauna. A fragment of lizard skin with its characteristic scaly texture has been recently discovered in a private collection.

Palaeontology

Most of the fossils come from exposures immediately south of Gurnard Ledge, although the 'Insect Limestone' is also exposed on the southern side of the Thorness Bay Syncline.

Early references to the insect fossils were made by Smith (1874) but a major modern contribution has been made in recent decades by Jarzembowski (1976, 1980a,b).

The fossil insects (the entomofauna, Figure 5.23) comprise the largest insect fauna in the British Tertiary deposits, with some 15 orders represented, namely:

- Odonata (dragonflies and damselflies, e.g. a damselfly – *Lestes* aff. *regina* Theobald, 1937, Figures 5.23h)
- Plecoptera (stoneflies, e.g. *Leuctra priscula*)
- Blattodea (undescribed cockroaches)
- Isoptera (termites, e.g. *Mastotermes anglicus* von Rosen, 1913, Figure 5.23q)
- Orthoptera (crickets and locusts, e.g. a mole cricket – *Pterotriamescaptor primus* (Cockerell, 1921); Figure 5.23n)
- Psocoptera (barklice, e.g. *Psocus acourti* Cockerell, 1921; Figure 5.23d)
- Thysanoptera (thrips, e.g. *Aeolothrips brodiei* Cockerell, 1917; Figure 5.23k)
- Hemiptera (bugs)
- *Carsidarina hooleyi* Cockerell, 1915; Figure 5.23c (a jumping plant louse)
- Neuroptera (lacewings, e.g. *'Megalomus' tinctus* (Jarzembowski, 1980); Figure 5.23i)

Figure 5.22 The lowest parts of the cliffs at Gurnard, showing, at the base, the Bembridge Limestone muds rich in fruits and seeds. The overlying Bembridge Marls include patches of plant-rich Insect Bed. (Photo: M.E. Collinson.)

Coleoptera (beetles, e.g. *Pterostichus gurnetensis* (Cockerell, 1921) – a ground beetle

Mecoptera (scorpionflies, e.g. *Bittacus veternus* (Cockerell, 1921) – a hanging fly)

Diptera (true flies, e.g. a black fungus gnat – *Sciara lacoei* Cockerell, 1915; Figure 5.23a; a soldier fly – *'Odontomyia' brodiei* Cockerell, 1915; Figure 5.23f)

Trichoptera (caddisflies, e.g. *Beraeodes anglica* Cockerell, 1921; Figure 5.23p)

Lepidoptera (moths and butterflies, e.g. *Paratriaxomasia solentensis* Jarzembowski, 1980; Figure 5.23j)

Hymenoptera (ants and wasps, e.g. a weaver ant – *Oecophylla perdita* Cockerell, 1915; Figure 5.23b,m)

Two more have been found recently – an earwig (Dermaptera) and a praying mantis (Mantodea), bringing the total representation of presently known families to *c.* 167 (Ross, 2005). Of the insects examined by Jarzembowski, 70% belong to the Hymenoptera, Diptera and Coleoptera with more than 120 species belonging to the first two orders.

Other invertebrate macrofauna known from these strata include a variety of brackish to freshwater assemblages such as an anostracan crustacean (fairy shrimp – *Branchipodites vectensis* Woodward, 1879; Figure 5.23e) an isopod crustacean identified as *Eosphaeroma margarum* by Martini (1972); an ostracod *Potamocypris brodiei* (Jones and Sherborn) which has been compared with the freshwater genus *Cypridopsis* (Haskins 1968b); a spider *Eotypus woodwardii* (McCook, 1888, see below); freshwater gastropods *Galba* and the brackish water bivalve *Polymesoda*.

Finally, some rare fossil bird feathers have been found over the years since the 19th century (e.g. Brodie, 1878, Jarzembowski, 1980a,b) as well as the piece of lizard skin mentioned above, plus arthropod eggs and coprolites.

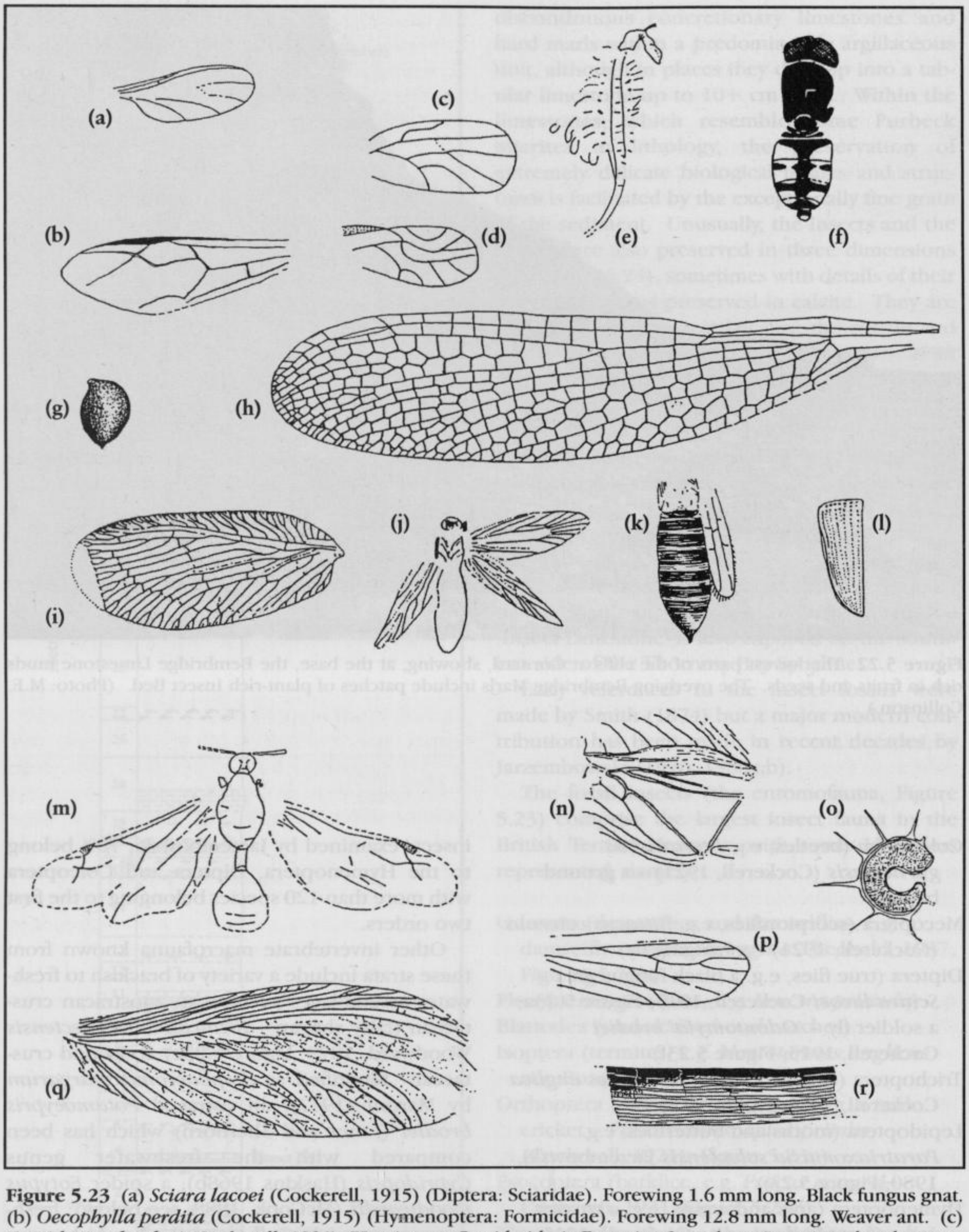


Figure 5.23 (a) *Sciara lacoei* (Cockerell, 1915) (Diptera: Sciaridae). Forewing 1.6 mm long. Black fungus gnat. (b) *Oecophylla perdita* (Cockerell, 1915) (Hymenoptera: Formicidae). Forewing 12.8 mm long. Weaver ant. (c) *Carsidarina hooleyi* (Cockerell, 1921) (Hemiptera: Carsidaridae). Forewing 3mm long. Jumping plant louse or psyllid. (d) *Psocis acourti* (Cockerell, 1921) (Psocoptera: Psocidae). Forewing 3mm long. Bark or book louse. (e) *Branchipodites vectensis* Woodward, 1879 (Anostraca: Branchipodidae?). Length 5mm. Fairy shrimp. (f) *'Odontomyia' brodiei* (Cockerell, 1915) (Diptera: Stratiomyidae). Male, 11.5mm long. Soldier-fly. (g) *Limnocarpus spinosus* (Reid and Chandler, 1926) (Monocyotyledones: Potamogetoneae?). endocarp, 1 mm long. 'Stiff' pondweed. (h) *Lestes* aff. *regina* (Théobald, 1937) (Odonata: Lestidae). Forewing, 22 mm long. Damselfly. (i) *'Megalomus' tinctus* (Jarzembowski, 1980) (Neuroptera: Hemerobiidae). Forewing 5 mm long. Brown lacewing. *(Caption continued on following page)*

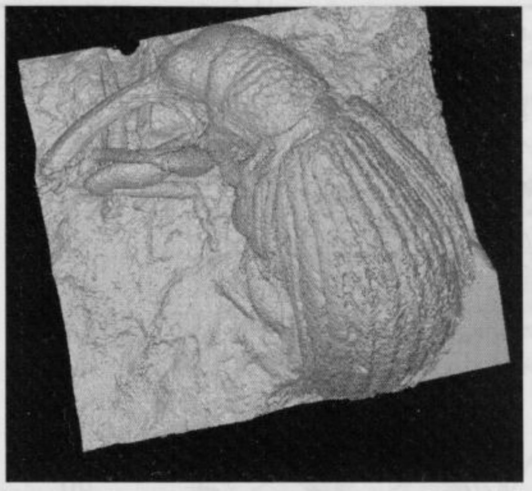


Figure 5.24 XMT of void of apionid weevil. (From Sutton, 2008).

Spiders

Recently, Selden (2001b) has described a new fossil spider, *Vectaranaeus yulei* (Figures 5.25 and 5.26) and re-described the only previously described spider, *Eoatypus woodwardii* McCook, 1888, from the Insect Bed at this locality. Spiders are occasionally found (there are 50 specimens in the collections of the Natural History Museum, London) in this horizon and noted (Jarzembowski, 1976) but are rarely described. Like so many of the insects, the spiders occur in a massive fine-grained limestone resembling the lithology of the main tabular insect-bearing horizon. According to Selden (2001b) one spider-bearing block includes fragments of the reed *Typha*, hymenopterans, dipterans and juvenile araneans which might indicate a mass mortality or surface water aggregation.

The importance of these fossil spiders arises from the extremely fine preservation of their internal structures such as muscle fibres replaced by calcite and delicate structures such as tracheae, book-lung lamellae and spinnerets. Similar mineralization is also found in the fossil insect tissues. Selden's detailed analysis of these structures has shown that the wide, medially positioned, tracheal spiracle and large tracheae which enter the prosoma are adaptations for an amphibious mode of life. Apparently, *Vectaranaeus yulei* does not have specific adaptations for a fully aquatic mode of life. The three-dimensional preservation of such structures indicates that the fossils represent actual cadavers rather than moults.

Such an amphibious mode of life supports the evidence for the local habitat provided by sedimentology and associated biota with both aquatic (lacustrine) and terrestrial (woods, meadows and marshes) elements present. As Selden (2001b, p.721) writes, 'possibly, the Bembridge spider was aquatic and is preserved in its life habitat; however, it is likely that, under normal circumstances, an aquatic spider would be less prone to be killed by drowning than a terrestrial spider'. Nevertheless, the additional presence of other aquatic animals such as salinity-tolerant crustaceans and molluscs in the Insect Bed of the Bembridge Marls suggests that some abnormal conditions, such as change in salinity, was responsible for their death. This suggestion is re-inforced by the presence of a locally abundant fairy shrimp, the extreme scarcity of fish and occasional pseudomorphs after halite in the 'Insect Limestone' and gypsum in the accompanying marls, all of which point to hypersaline conditions.

Plants

In addition, over 113 plant species, dominated by angiosperms, are known to occur here but

(Figure 5.23 *continued caption***).**

(j) *Paratriaxomasia solentensis* Jarzembowski, 1980 (Lepidoptera: Tineidae). Wingspan 8 mm. Moth. (k) *Aeolothrips brodiei* Cockerell, 1917 (Thysanoptera: Aelothripidae). Length 1.3 mm. Thrip. (l) Undescribed weevil (Coleoptera: Curculionoidea). Elytron 5.7 mm long. Hamstead Beds. Beetle. (m) *Oecophylla* cf. *perdita* Cockerell, 1915 (Hymenoptera: Formicidae). Wingspan 27 mm. (n) *Pterotriamescaptor primus* (Cockerell, 1921) (Orthoptera: Gryllotalpidae). Forewing fragment 6.5 mm long. Mole cricket. (o) *Potamogeton pygmaeus* Chandler, 1925 (Monocotyledones: Potamogetonaceae). Fruit, maximum diameter 2 mm. Pond weed. (p) *Beraeodes anglica* Cockerell, 1921 (Trichoptera: Beraeidae). Forewing 4.5 mm long. Caddisfly. (q) *Mastotermes anglicus* von Rosen, 1913 (Isoptera: Mastotermitidae). Forewing 22 mm long. Termite. (r) *Typha latissima* Al. Braun, 1851 (Monocotyledones: Typhaceae). Leaf fragment 45 mm long. Bulrush (Cattail U.S.A.). (From Jarzembowski, 1999a.)

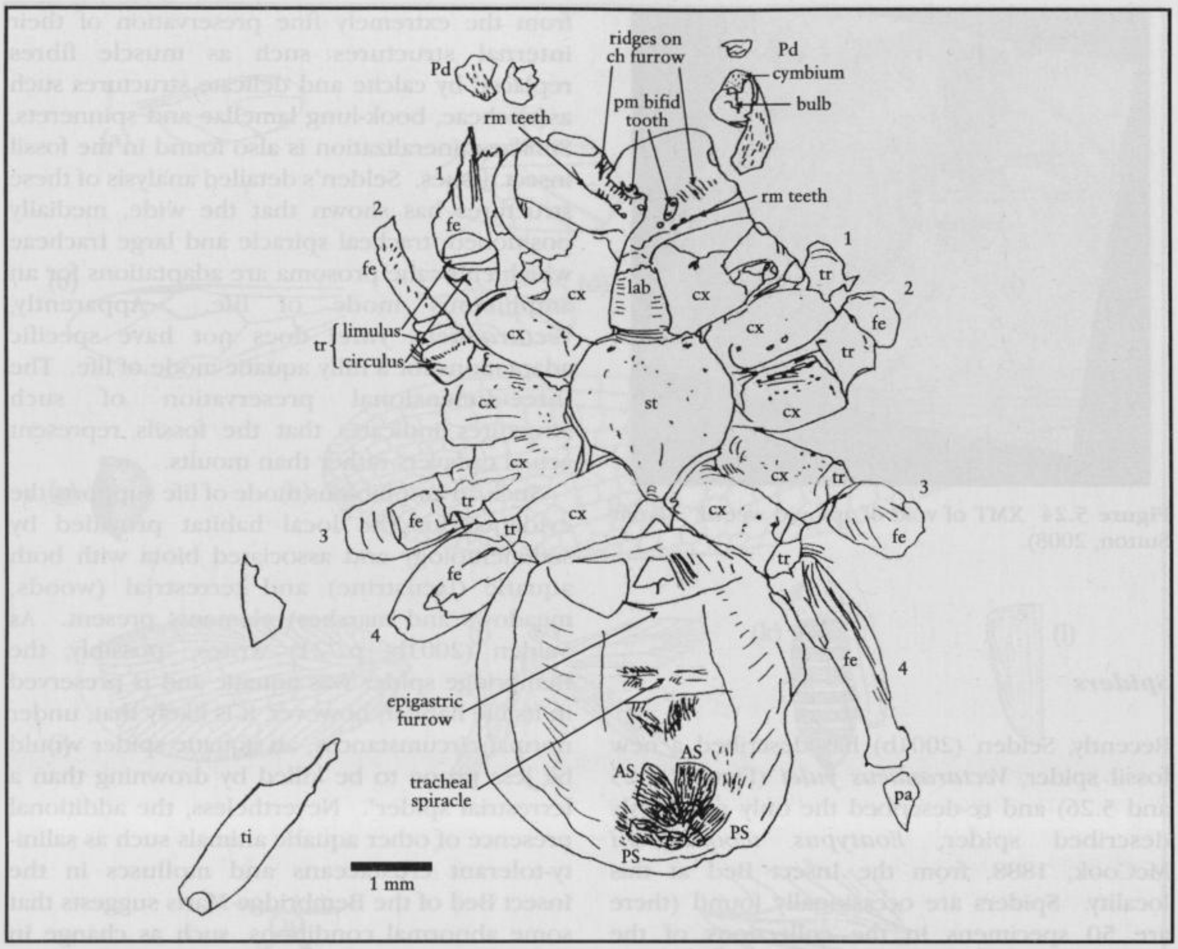


Figure 5.25 *Vectaraneus yulei* gen. et sp. nov., upper Eocene, Bembridge Marls, Isle of Wight. Drawing of paratype, IWCMS 1999.6. cx: coxa; tr: tochanter; pa: patella; fe: femur; ti: tibia; rm: retromarginal; pd: pedipalp; ch: chelicera; pm: promarginal; lab: labium; st: sternum; ti: tibia; pa: patella; AS/PS anterior/posterior spinneret. (From Selden, 2001b.)

not all have been described. Most of the macroplant fossils described by Reid and Chandler (1926) also originate from the 'Insect Limestone' with the majority coming from A'Court Smith's collection. The fossil flora accumulated in the 'Insect Limestone' has preferentially preserved wind-transported fruits and seeds with delicate wings or plumes. The remarkable preservation includes three-dimensional seeds of the free-floating aquatic plant *Stratiotes* some of which have been found with rodent gnaw marks on the tough seed coat in adjacent formations. The plants include aquatic species (such as the pond weeds – *Potamogeton pygmaeus* Chandler, 1925 and *Limnocarpus spinosus* Reid and Chandler, 1926; a bulrush – *Typha latissima* Al. Braun, 1851) along with climbers, herbs and rare remains of trees from the neighbouring forests and fresh-water charophytes (Figure 5.23).

Detailed analysis of the flora by Collinson *et al.* (1993) showed that the Bembridge Limestone was formed in carbonate-rich ponds or lakes within relatively arid surrounding landscapes. By contrast, the Bembridge Marls represent marshlands with more immediately adjacent woodlands which may have resulted from temperature fluctuation during deposition. The assemblage shows marked changes in both aquatic and forest floral components from earlier British Tertiary records. The decline in the tropical–subtropical elements of the

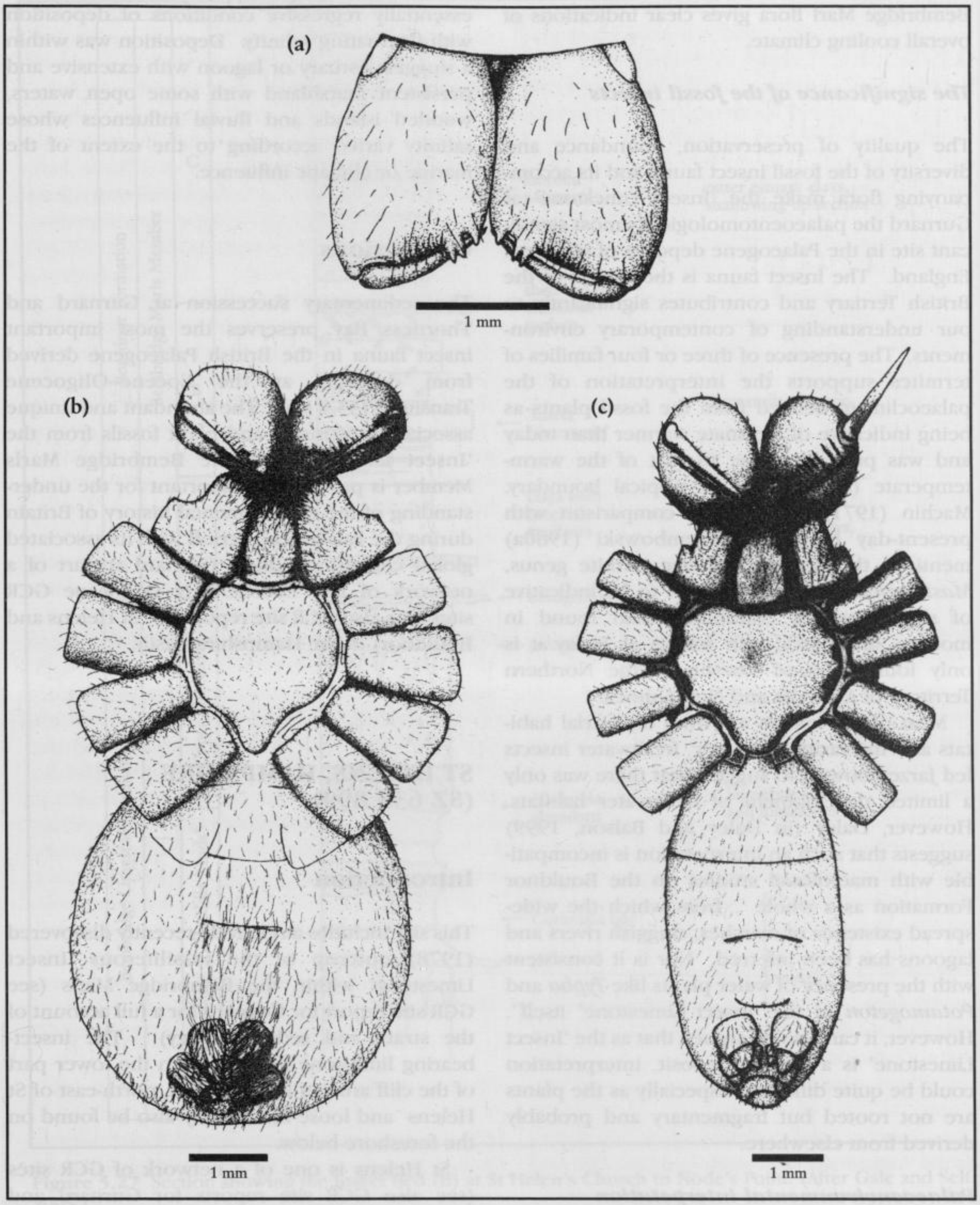


Figure 5.26 *Vectaraneus yulei* gen. et sp. nov., upper Eocene, Bembridge Marls, Isle fo Wight. Reconstruction of (a) chelicerae, anterior view, and (b, c) body, ventral view (b, female and c, male). (From Selden, 2001b.)

Bembridge Marl flora gives clear indications of overall cooling climate.

The significance of the fossil insects

The quality of preservation, abundance and diversity of the fossil insect fauna and its accompanying flora make the 'Insect Limestone' at Gurnard the palaeoentomologically most significant site in the Palaeogene deposits of southern England. The insect fauna is the largest of the British Tertiary and contributes significantly to our understanding of contemporary environments. The presence of three or four families of termites supports the interpretation of the palaeoclimate derived from the fossil plants as being indicative of a climate warmer than today and was probably close to that of the warm-temperate (subtropical) to tropical boundary. Machin (1971) suggested a comparison with present-day Florida. Jarzembowski (1980a) mentions the presence of one termite genus, *Mastotermes*, which is thought to be indicative of slightly wetter conditions than found in modern subtropical rain forests as today it is only found around Darwin in the Northern Territory of Australia and New Guinea.

Most of the insects are from terrestrial habitats and the rarity of aquatic, freshwater insects led Jarzembowski to suggest that there was only a limited development of freshwater habitats. However, Daley (in Daley and Balson, 1999) suggests that such an interpetation is incompatible with macrofossil studies on the Bouldnor Formation as a whole '...from which the widespread existence of marshes, sluggish rivers and lagoons has been inferred. Nor is it consistent with the presence of water plants like *Typha* and *Potamogeton* in the 'Insect Limestone' itself'. However, it can also be argued that as the 'Insect Limestone' is a unique deposit, interpretation could be quite different, especially as the plants are not rooted but fragmentary and probably derived from elsewhere.

Palaeoenvironmental interpetation

Interpretation of the sedimentology of the Bembridge Marls Member of the lower part of the Bouldnor Formation suggests that deposits were brackish to freshwater sediments laid down under relatively shallow and quiet-water depositional conditions. The palaeontology supports such a view so that overall there were essentially regressive conditions of deposition with fluctuating salinity. Deposition was within a sluggish estuary or lagoon with extensive and persistent marshland with some open waters, wooded islands and fluvial influences whose salinity varied according to the extent of the marine or climatic influence.

Conclusions

The sedimentary succession at Gurnard and Thorness Bay preserves the most important insect fauna in the British Palaeogene derived from deposits at the Eocene–Oligocene Transition (33.9 Ma). The abundant and unique association of insect and plant fossils from the 'Insect Limestone' in the Bembridge Marls Member is particularly important for the understanding of the environmental history of Britain during the Palaeogene Period with its associated global climatic cooling. Gurnard is part of a network of late Eocene/early Oligocene GCR sites (see also GCR site reports for St Helens and Bouldnor) in the Hampshire Basin.

ST HELENS, HAMPSHIRE (SZ 638 899)

Introduction

This site includes a relatively recently discovered (1978) outcrop of the fossiliferous 'Insect Limestone' within the Bembridge Marls (see GCR site report for Gurnard for a full account of the strata and sedimentology). The insect-bearing limestone is exposed in the lower part of the cliff around Node's Point, north-east of St Helens and loose blocks may also be found on the foreshore below.

St Helens is one of a network of GCR sites (see also GCR site reports for Gurnard and Bouldner) of latest Eocene or earliest Oligocene age in the Hampshire Basin from which a diversity of more than 250 fossil insects has been found within the Bembridge Marls. It is also the most distant insect-rich site from the classical exposure of the Bembridge Marls in Thorness Bay, lying 18 km to the ESE.

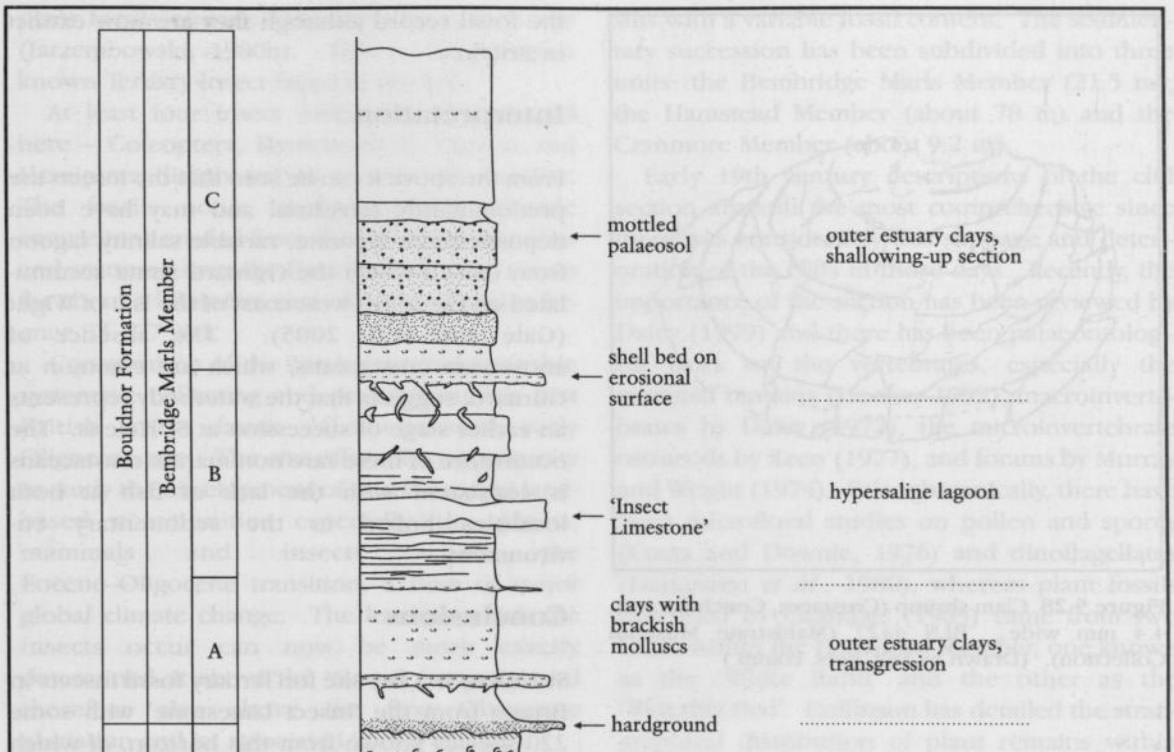


Figure 5.27 Section showing the Insect Bed (B) at St Helen's Church to Node's Point. (After Gale and Self, 2005.)

Description

The low, slipped cliff between St Helens and Node's Point provides a 250 m exposure of the uppermost Bembridge Limestone and lower Bembridge Marls. The succession is condensed compared to that seen in the nearby fine section of the Bembridge Beds in Whitecliff Bay. A single 0.1 m-thick micrite in the Insect Bed has yielded insect remains (Figure 5.27) and dips gently southwards (from *c*. 8–0.5 m above cliff base) towards the axis of the Bembridge Syncline.

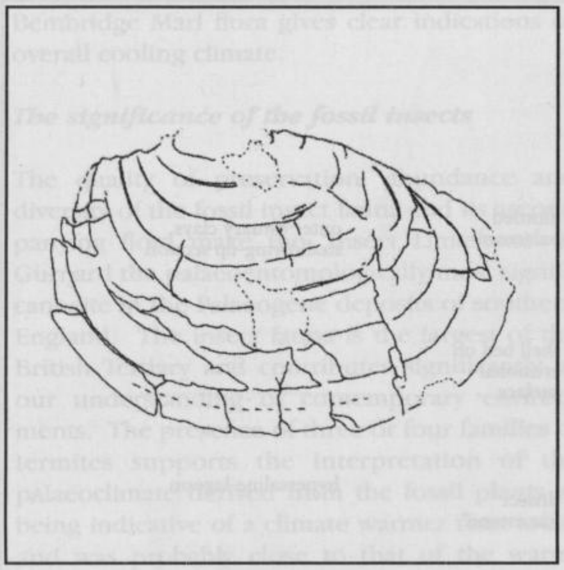


Figure 5.28 Clam shrimp (Crustacea, Conchostraca), 4.4 mm wide. BLN 4427 (Maidstone Museum Collection). (Drawn by Self, pers. comm.)

The insects have not been studied in detail, but at least five orders are represented, and should provide valuable information on palaeoecological diversity in and surrounding the ancient water body in which the 'Insect Limestone' was deposited. The 'Insect Limestone' forms the most productive insect-bearing horizon in the British Tertiary deposits.

The entomofauna here includes beetles (Coleoptera); true flies (Diptera) for example crane-flies (Tipulidae), fungus gnats (Sciaridae), 'dance'-flies (Empididae); Hymenoptera including weaver ants (Formicidae: *Oecophylla* sp.), bugs (Hemiptera) such as jumping plant lice (Psylloidea); and *Mastotermes anglicus*, a termite (Isoptera) belonging to a now relict tropical genus found in north Australia and New Guinea.

The insects are accompanied by plant remains, ostracods, the gastropod *Galba* and more significantly, the only Tertiary conchostracan (clam shrimp) known from Europe (Figure 5.28). The latter is rare (being known only from less than six specimens). These non-marine crustaceans have a bivalved carapace remarkably convergent with that of lamellibranch molluscs although made of chitin. As a result of this organic proteinaceous composition, conchostracans often occur with insects in the fossil record although they are now extinct in Britain.

Interpretation

From the above it can be seen that the insects are predominantly terrestrial and may have been deposited in a separate, variable salinity, lagoon from that in which the Gurnard strata accumulated on the north-west coast of the Isle of Wight (Gale and Self, 2005). The absence of anostracan crustaceans, which are common at Gurnard, suggests that the waterbody represents an earlier stage of succession at St Helens. The occurrence of these rare non-marine crustaceans is consistent with the lack of fish at both localities linked to the sedimentary environment.

Conclusions

St Helens is a key site for Tertiary fossil insects in Britain from the 'Insect Limestone' with some 220 species known from this horizon, of which the most common is a tree ant *Oecophylla* and the best-known, a termite *Mastotermes anglicus*. This site is unique in Europe for Tertiary conchostracan Crustacea. The arthropods are found within the Bembridge Marls of late Eocene–early Oligocene age (c. 33 Ma). The site also has great potential for future research in improving our knowledge of the palaeontology of the 'Insect Bed', a unique horizon in the British Tertiary record.

BOULDNOR, HAMPSHIRE (SZ 382 907)

Introduction

The cliff section in the Hamstead Member within the upper part of the Bouldnor Formation in the Solent Group at Bouldnor on the Isle of Wight straddles the Eocene–Oligocene boundary. The site has long been known for its diverse fossil biota of vertebrates (reptiles, mammals, birds) along with plant remains (Cleal *et al.*, 2001) and a variety of 'shelly' invertebrates, especially gastropods. However, modern work shows that this member also contains an insect fauna associated with freshwater ostracods and plant fossils of early Oligocene (Rupelian) age (Jarzembowski, 1980b). This is the youngest known Tertiary insect fauna in the UK.

At least four insect orders are represented here – Coleoptera, Hymenoptera, Diptera and Hemiptera distributed in at least six families. The fossils occur in fine-grained sideritic concretions eroded from the Hamstead Member and scattered over the foreshore by wave action for about a kilometre east of national grid reference SZ 377 904.

Conservation of the site is essential to enable systematic collecting and research on this first British insect fauna of unequivocal early Oligocene age. The site offers the opportunity to study the development of nearshore and land-based communities especially the plants, mammals and insects across the Eocene–Oligocene transition, a time of major global climate change. The level at which the insects occur can now be more exactly determined at above the 'Grand Coupure' and therefore also above the first Oligocene glaciation and its associated faunal changes.

Bouldnor is the only site where there is a more-or-less complete succession of the Bouldnor Formation and the only place where the Hamstead Member is exposed. These are the youngest strata of the local Palaeogene sequence and the site is one of the best localities for the study of low-energy, brackish and freshwater clastic depositional environments along with its diverse fossil biota. In addition to the fossil arthropod importance of this site, the area is also selected for the GCR for the Tertiary Palaeobotany, Palaeogene, Aves, Tertiary Mammalia and Tertiary Reptilia selection categories.

Description

The whole succession of the Bouldnor Formation extends from Bouldnor Cliff and its north-easterly continuation in Hamstead Cliff for about 3.2 km to Hamstead Ledge. In recent decades there has been considerable slippage of the fine-grained and relatively unconsolidated sediments resulting in cliff collapse and destruction of the lithological succession and other parts of the outcrop are overgrown resulting in intermittent exposures (Figure 5.29). The section comprises a complete sequence of the Bouldnor Formation (almost 110 m thick, see Figure 5.30) and mostly consists of muds and silts with a variable fossil content. The sedimentary succession has been subdivided into three units: the Bembridge Marls Member (21.5 m), the Hamstead Member (about 78 m) and the Cranmore Member (about 9.2 m).

Early 19th century descriptions of the cliff section are still the most comprehensive since there was considerably less slippage and deterioration of the cliffs in those days. Recently, the importance of the section has been reviewed by Daley (1999) and there has been palaeontological work on the vertebrates, especially the mammal remains (Hooker 1992), macroinvertebrates by Daley (1972), the microinvertebrate ostracods by Keen (1977), and forams by Murray and Wright (1974). Palaeobotanically, there have been microfloral studies on pollen and spores (Costa and Downie, 1976) and dinoflagellates (Liengjaren *et al.*, 1980), whereas plant fossils described by Chandler (1963) came from two levels within the Hamstead Member, one known as the 'White Band' and the other as the 'Waterlily Bed'. Collinson has detailed the stratigraphical distribution of plant remains within the underlying Bembridge Marls Member (1983).

Lithology and succession

The Bouldnor Formation is predominantly comprised of black, grey and green muds and muddy silts with varying fossil content. There are two discrete lignitic horizons: the 'Black Band', which marks the base of the Hamstead Member (Figure 5.29), is a carbonaceous mud with freshwater molluscs (e.g. *Unio* and *Viviparus*) and rootlets that penetrate the underlying bed. The *Nematura* Bed is another black lignitic clay, but contains a distinctive brackish-water gastropod fauna. Above the *Nematura* Bed there is a 10.8 m-thick green clay that contains the ironstone band from which the insect fauna has been recovered near the White Band.

Until recently, there was no known lithological representative of the 'Insect Limestone' in this section. Now a nodular representation has been found as seen at Hamstead Ledge. Elsewhere the 'Insect Limestone' occurs close to the base of the Bembridge Marls. The foreshore and cliffs between Hamstead Ledge and Bouldnor were defined by Insole and Daley (1985) as the type area both for the Bouldnor Formation and the Hamstead Member.

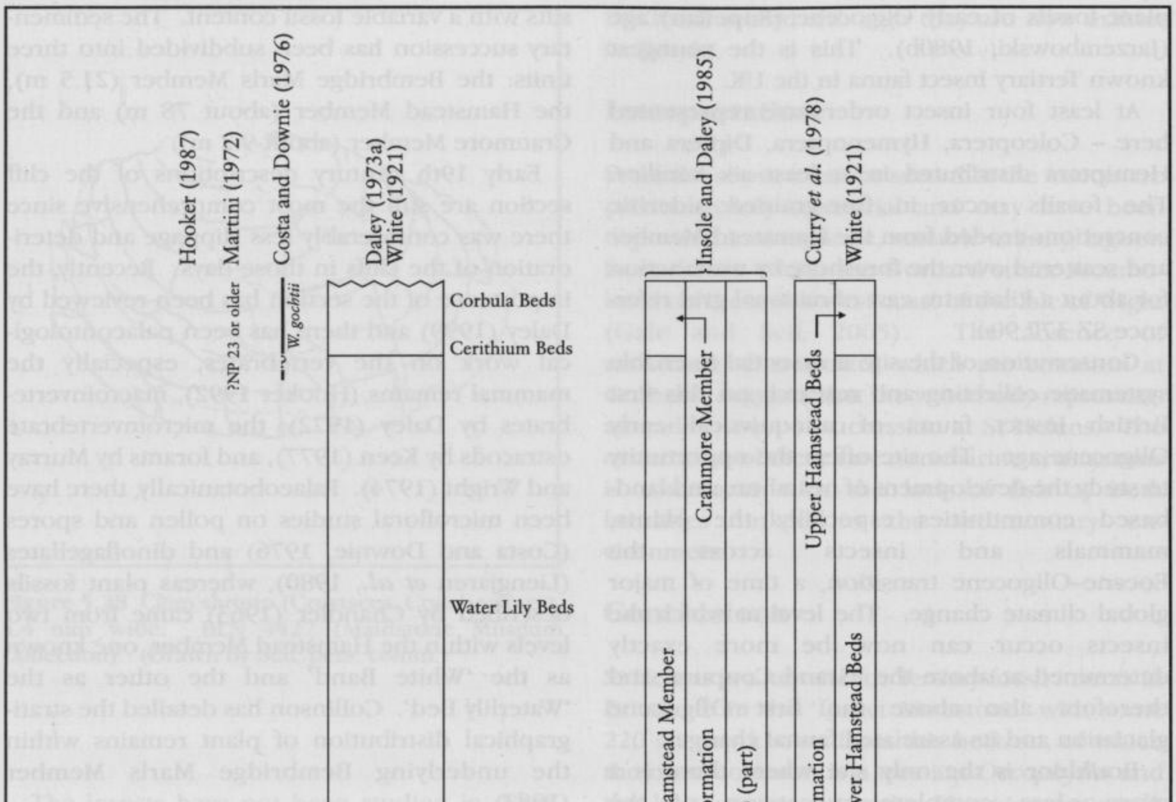


Figure 5.29 Lithostratigraphical succession of the Bouldnor Formation in Bouldnor and Hamstead cliffs, Isle of Wight as interpreted by the authors indicated. (From Cleal *et al.*, 2001.)

Interpretation

Sedimentology

Detailed sedimentological work has only been undertaken for the Bembridge Marls Member (Daley and Edwards, 1974). However, a similar lithological succession in the Hamstead Member suggests similar environmental conditions with quiet-water conditions. The generally fine-grained sediment reflects a very low-lying hinterland with a lack of tectonism or rejuvenation of landscapes. Varve-like layering indicates vertical sedimentation perhaps associated with tidal activity but with occasional interruptions of higher energy flow reflected by the introduction of laterally continuous shell coquinas, some of which might result from storm deposition.

The association of these sediments with brackish and freshwater faunas suggests the presence of brackish and freshwater lagoons (Figure 5.30), the upper reaches of which were sufficiently riverine and isolated from the sea to have experienced freshwater conditions. The 'Black Band' with rootlets which marks the base of the Hamstead Member is indicative of very shallow waters and possible short-lived subaerial conditions. Similarly, some red-mottled horizons within the member may have originated from contemporary exposure and weathering or a drop in the water table.

Palaeontology

The site is particularly important palaeontologically because nowhere else in Britain are rocks of this age and facies exposed and thus they provide an unique opportunity for the palaeoecological study of a variety of animal and plant communities from brackish to freshwater environments of Palaeogene age.

The insects from the ironstone band are small but well-preserved remains and include beetles, true flies and an ant (Figure 5.31). Of these groups, the beetles include a weevil (curculionoid); the flies include a crane-fly (limoniine) and owl-midge (psychodid) resembling species from the Bembridge Marls whereas there is also a dance-fly (empidid) which resembles extant *Ocydromia* and *Leptopeza*; the flying ant is referable to the species *Leucotaphus permancus* also known from the Bembridge Marls but species of

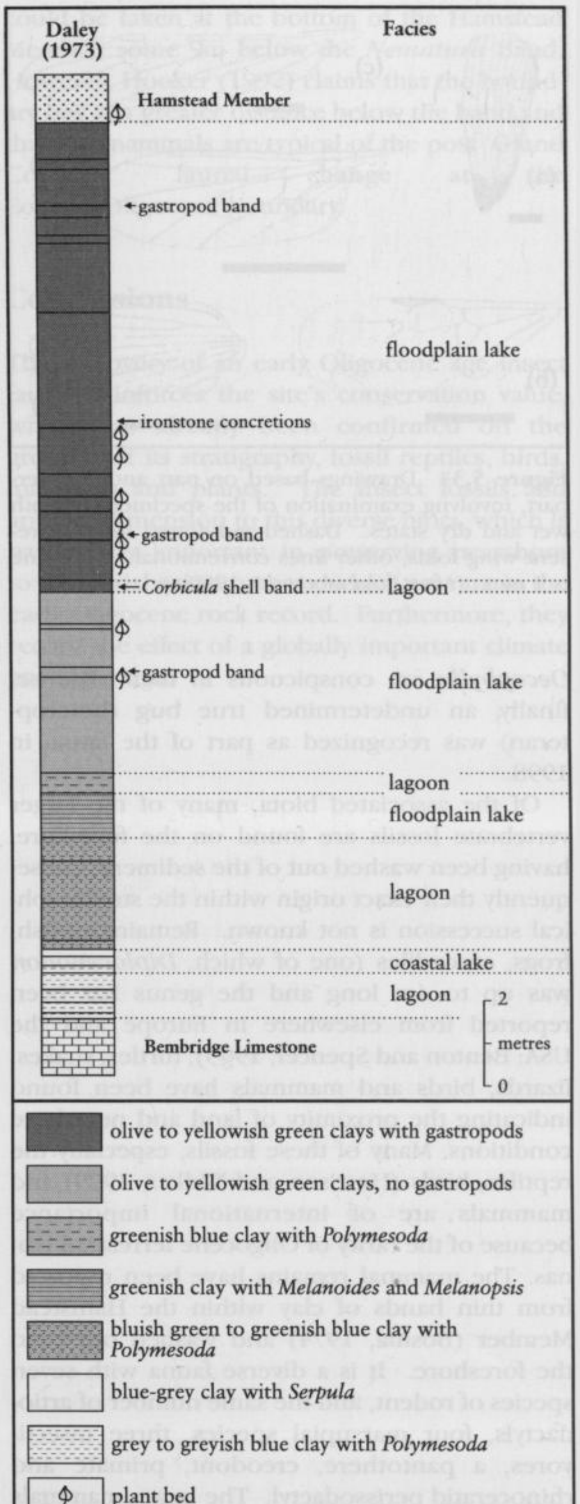


Figure 5.30 Stratigraphical section through the Bembridge Marls Member and Bouldnor Formation at Hamstead Ledge. (After Collinson, 1983; from Cleal *et al.*, 2001.)

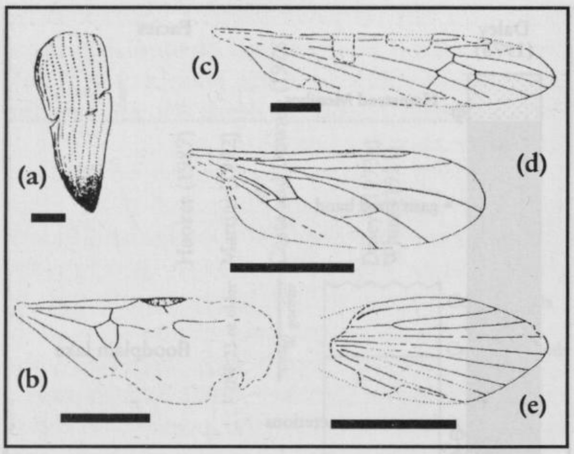


Figure 5.31 Drawings based on part and counterpart, involvng examination of the specimens in both wet and dry states. Dashed-and-dotted lines represent wing folds, other lines conventional. Scale line is 1 mm. (After Jarzembowski, 1980b.)

Oecophylla are conspicuous in their absence; finally, an undetermined true bug (heteropteran) was recognized as part of the fauna in 1998.

Of the associated biota, many of the larger vertebrate fossils are found on the foreshore, having been washed out of the sediment, consequently their exact origin within the stratigraphical succession is not known. Remains of fish, frogs, crocodiles (one of which, *Diplocynodon* was up to 4m long and the genus has been reported from elsewhere in Europe and the USA: Benton and Spencer, 1995), turtles, snakes, lizards, birds and mammals have been found indicating the proximity of land and nearshore conditions. Many of these fossils, especially the reptiles, birds (Harrison and Walker, 1979) and mammals are of international importance because of the rarity of Oligocene terrestrial faunas. The mammal remains have been reported from thin bands of clay within the Hamstead Member (Bosma, 1974) and washed out onto the foreshore. It is a diverse fauna with seven species of rodent, and the same number of artiodactyls, four marsupial species, three insectivores, a pantothere, creodont, primate and rhinoceratid perissodactyl. The larger mammals are also known from the Paris Basin and from where they were originally described. The birds include a mixture of shore birds (ducks and pelicaniforms) and terrestrials such as gamebirds, falcaniforms and a flightless ratite.

Of the microfauna, the forams are mainly indicative of hypersaline conditions although some species may indicate open marine conditions marking the deposition of the *Cerithium* Beds and the top of the Hamstead Member.

The microflora also shows a marked change at the same boundary with a decrease in pollen and spore species characteristic of a subtropical climate (e.g. the palm *Thrinax*) and an increase of northern temperate species. A more-detailed study of the dinoflagellate succession suggested to Liengjaren *et al.* (1980) that there have been three transgressive events – one associated with the 'Bembridge Oyster Bed', another with the *Nematura* 'Bed' in the Hamstead Member and a third associated with the Cranmore Member.

The Hamstead Member macroplant remains consist predominantly of the leafy shoots, cones and logs of angiosperms (18 species) and a few conifers (four species) and are typically preserved as carbonaceous films sometimes covered with a thin layer of pyrites. The angiosperm flora is dominated by aquatic plants, especially members of the water soldier, water lily and pondweed families. Although many species are also found lower down in the formation, there are some significant differences that have been associated with climate change (Cleal *et al.*, 2001). Cleal *et al.* have summarized the vegetation and environment of the Hamstead Member as a bulrush-dominated marsh with a range of other aquatic plants and surrounded by forests dominated by taxodiaceous conifers somewhat similar to that of today's cypress swamps in south-eastern USA.

Palaeoclimate

Machin's (1971) work on the microflora revealed a climatic shift away from tropical/warm temperate climates during earlier post-Bartonian times to cooler conditions. This is complemented by Buchardt's (1978) oxygen isotope temperature data derived from Palaeogene shell material which shows a sharp drop in palaeotemperature at the beginning of the Oligocene. Furthermore this cooling is supported by Collinson and Hooker's (1987) analysis of the plant record and conclusion that by the beginning of the Oligocene (Rupelian times), the dense forests of tropical aspect had given way to a more open environment with scattered trees. The Hamstead mammals also show a decrease in arborescent forms and increase in larger ground-dwelling mammals, especially browsing herbivores with a high fibre diet. Their presence re-inforces the view that there was an open, moderately wooded woodland-brushland environment (Benton *et al*., 2005.

Dating and correlation

The palaeontology of this site is important in providing correlation of British Oligocene strata with other areas of north-western Europe (see Daley and Balson, 1999 for discussion). Furthermore, the site was selected by Curry and Hailwood (1986) as typifying the English succession across the Eocene/Oligocene boundary. The famous Quercy deposits of France also span this boundary and similarly have produced a fossil biota including lizards, crocodilians and turtles. However, there have been some problems associated with the exact location of the boundary within the Bouldnor Formation. Liengjaren *et al*. (1980) have suggested that it could be taken at the bottom of the Hamstead Member, some 9m below the *Nematura* Band. However, Hooker (1992) claims that the boundary lies at a greater distance below the band and that the mammals are typical of the post 'Grand Coupure' faunal change at the Eocene–Oligocene boundary.

Conclusions

The discovery of an early Oligocene age insect fauna re-inforces the site's conservation value, which has already been confirmed on the grounds of its stratigraphy, fossil reptiles, birds, mammals and plants. The insect fossils add another dimension to this diverse biota, which is particularly important in preserving nearshore to terrestrial environments, which are rare in the early Oligocene rock record. Furthermore, they record the effect of a globally important climate cooling event.