Fossil Insect Faunas from Forest Sites

Maureen A Girling

The largely undisturbed woodland which extended throughout Britain in the early post-glacial period provided important habitats for wood-associated Coleoptera. In addition to wood-borers and bark beetles, many tree species harbour populations of leaf-miners, tree-fungus feeders and specialised predators which often live in the galleries of their prey. Such forest faunas have been described from a number of sites including Hampstead Heath where associated with late Mesolithic settlement there is evidence of mixed deciduous woodland with lime (Tilia) an important tree species. Fossil beetle studies can provide a sensitive index of the disturbance of woodland areas and this is illustrated at Hampstead Heath where the sample monolith extended up through the elm-decline horizon. The wholesale removal of woodland, and in particular the dead and decaying wood which provides an important habitats for many forest insects, is reflected in the major change in the British beetle fauna from the Neolithic onwards. There is a growing list of forest beetles which are now extinct in Britain and whose European distributions are correspondingly reduced, and a higher number of species which are at present found rarely in limited areas of woodland.

Composition of forest insect faunas

Woodland ecosystems offer an especially rich concentration of habitats for insects, a factor best demonstrated by Coleoptera which exhibit the greatest diversity of any insect order. Many beetles have adapted to forest niches, with numbers of families exhibiting exclusively wood-dependent life-histories and it is possible that dead wood provided the original habitat in which Coleoptera evolved, before radiating to the other terrestrial and aquatic environments they have conequered. The major types of forest beetle may be summarised according to their feeding habits.

i. Wood-borers. These are woodland beetles whose larvae feed by burrowing into wood, excavating galleries which damage and can kill the tree, particularly in the case of saplings. Wood attacked in this way is also

susceptible to invasion by other insects and rot-inducing fungi, for which reason, this group is of economic importance in forest management. Wood-boring insects are divided into those which attack living trees and others which feed on dead wood, although these are not exclusive and some species live in healthy, moribund and dead trees. A major family of wood-borers are Cerambycidae, or long-horn beetles which live principally in living trees, as do those Curculionidae or weevils, whose larvae develop in wood. Dying and dead wood feeders are divided into those which prefer sappy, decayed or well-rotted trunks and branches, examples of which are Lucanidae, the 'stag-beetle' family and such Scarabaeidae, as Gnorimus spp., and those species which also attack dry wood. This latter category includes beetles which infest seasoned, worked timber and are now known principally as household or building pests, the most notable being Anobium punctatum (Deg.) ('woodworm' or 'furniture beetle'), Xestobium rufovillosum (Deg.) ('deathwatch beetle'), Lyctus spp. ('powder-post beetles') and Nacerdes melanura (L.) ('the wharf-borer'). The fossil history of these timber pests demonstrates that they have been favoured by man's activities which have promoted them from relative unimportance in the early forest faunas to abundant representation in settlement and urban sites. Such is the case for A. punctatum (Girling 1980 a), and the significance of human influence in extending the northern limit of X. rufovillosum in Britain has been discussed by Buckland (1975). One category of wood-boring beetles which should not be overlooked is the root feeders. Certain wood-dependent Elateridae live in tree roots, and there are reports of chafers devasting plantions of saplings (Chrystal 1937, Zhuravlev and Osmolovskii 1949, Rozhkov 1970).

ii. Bark-beetles. Scolytidae, or bark-beetles live under bark, excavating intricate systems of galleries into the sap-wood. Although the actual damage caused is less serious than by wood-borers which tunnel into the heart-wood, their attack does render the trees liable to disease or other infestation and the most serious example of this is the introduction to elms by Scolytus scolytus (F.) of the virus responsible for Dutch elm disease. Many scolytid species are strong fliers, therefore isolated occurrences in fossil assemblages should be viewed with caution.

iii. Leaf-feeders. Phytophagous families include numbers of beetles which specialise on deciduous leaves and the needles of various conifers. Foliage of broad-leaved trees is skeletonised by leaf-mining weevils such as Rhynchaenus and leaf-rolling species Rhynchites lay eggs in tubes of rolled leaves which provide the larval food source. Chrysomelidae can often occur in sufficient numbers to defoliate trees, for instance willows in the case of Galleruca and Phyllodecta. The seeds, nuts and buds of forest trees also provide a food source appropriated by particular species, instanced by Curculio nucum L. the nut weevil which develops in hazel nuts or acorns.

iv. Predators. Occupying the same ecological niches as the wood and leaf-feeders are their predators. These specialised beetles live under bark and in the galleries of prey species, feeding on beetle larvae and other arthropods. Predators include some of the rarest species on the list of British Coleoptera, and others are now extinct in this country. Cleridae, Eucnemidae, Cucujidae, Colydiidae and Rhizophagidae are families dominated by predators although not all species live solely by predation, and the feeding habits of some of them are disputed by entomologists. Predators live in a variety of deciduous and coniferous species, some of them displaying a preference for a single or a limited number of tree types. The state of the wood is also important, with certain insects selecting dead, sun-dried trunks and branches, whilst others require wet, decayed trees with heart-rot or other fungus attack. It is significant, however, that those species now represented by relict populations are typically inhabitants of dead wood. As well as their removal in general clearance of woodland areas, dead trees and branches are also under constant threat where settlements produce a requirement for building materials and fuel, and in recent managed forests, the deliberate tidying-up of dead trees has destroyed many vestiges of this important beetle habitat.

Predaceous insects are not confined to these specialised locations and foliage, loose bark and leaf-litter support arthropod populations which are an abundant food source for numbers of Carabidae and Staphylinidae. The large

metallic ground beetle Calasoma inquistor (L.) feeds voraciously on defoliating caterpillars, especially of the oak totricid Tortrix viridana (L.), in search of which it clambers into the oak crown. Silphidae, a family usually associated with carrion, includes one specialist feeder on tree caterpillars, Xylodrepa quadrimaculata (Scop.) usually found on oak. Other predators which often inhabit tree crowns include the small carabid Bembidion harpaloides.

A forested environment provides limited occurrences of particular habitats such as tree-fungus, colonized by a small suite of Sphindidae and other insects. Wood-ant nests, and those of other ant species which live in dead wood have an associated beetle fauna comprising certain rare Pselaphidae and Colydidae. Also, mammals within a forest supply dung and carrion to those small number of Silphidae and Scarabaeidae which are characteristically forest dwellers.

Forest associations of the British beetle fauna

The high populations of insects within forests is a reflection of the biomass of this ecosystem. The undisturbed forest which cloaked Britain before its removal by man, further encouraged insect diversity by the variety of its component broadleaved trees. The importance of the forest element of the British beetle fauna can be illustrated by surveying the proportion of families with wood-associated members. Of the 96 families listed in Kloet and Hincks (1977), 14 can be considered exclusively wood-dependent and at least 14 other contain significant numbers of forest beetle species. Examples of exclusively wood dependent families include Eucnemidae, Scolytidae and Platypodidae. In addition, there are records from post-Glacial Britain of one further family, Rhysodidae which no longer has representative species in this country. The second category encompasses families such as Curculionidae and Scarabaeidae, various species of which demand trees or decayed wood and frequently occur in such numbers as to rate as forestry pests.

Interpreting forest environments from beetle data

A fossil assemblage of beetles with a strong woodland element presents fewer interpretative problems than those of certain other archaeological palaeo-environments. The exclusive dependence on wood as, for instance, a larval food source, indicates tree growth in the vicinity of the deposit, at least within the range of the dispersal flight of the winged component species. Many wood-dwelling beetles are, however, flightless, the elytra of the characteristically flattened bodies being fused, and these imply closer proximity of woodland unless water transport of insect remains by streams or rivers is indicated. Where tree-dependent beetles are present, there are several pointers to the wooded landscape which may range from dense forest to woods with clearings, isolated copses in a cleared area, hedgerows, shrubby regrowth and carr fringing lakes or fens. The proportion of stenotopic forest beetles provides the first indicator of the density of tree cover, and where this is high and combined with significant numbers of decayed wood inhabitants, primary undisturbed woodland is implied. Deposits where this forest type is suggested are those which often contain records of beetles which are now rare or absent from Britain. Another pointer to the completeness of tree cover is the evidence supplied by other phytophages if these are present in the fauna. Where no understory species occur amongst the beetle host-plants dense canopy may be excluding sunlight except where this is broken by rough or steep terrain, streams or fallen trees. As forests become affected by clearance, increasing numbers of light demanding shrubs and herbs are recorded in food plant lists.

As well as the form of the forest, evidence can be surmised on its compositio providing a valuable local compliment to the more regional data from pollen analysis. Specific tree hosts are cited for certain beetles and where this is well documented it can be used as a reliable index in assessing forest composition. It should be remembered, however, that species near the limit of their range, or under stress from competition, may display a more pronounced fastidiousness in feeding habits than populations in more favourable areas. Where British records represent the edge of the geographical distribution a check

should be made on ecological records in mainland Europe to ensure that food plants correspond in both parts of the range. This is of consequence where postulated warmer post-glacial conditions might have benefited beetles in otherwise marginal areas. Differences can also occur because the greater variety of forest trees in Europe provides food plant opportunities which do not occur in Britain.

Studies on oaks have demonstrated that they support an enormous invertebrate fauna (Morris and Perring 1974), including a large number of wood and leaf feeding beetles, although lepidopterous caterpillars are the most notorious of the oak pests, responsible for defoliation, and even death of trees where their numbers reach plague proportions. Attacks on oak by geometer or looper moths frequently stimulate the growth of a second crop of leaves, an effect also caused by swarms of adult chafer beetles. Visible signs of insect infestation are obvious from the yield of galls on oak trees; oak apples, oak marbles, oak artichokes, oak cherries and leaf spangles are vegetable growths generated by various hymenopterous wasps and there are also gall-producing midges. Many other deciduous trees have rich, associated faunas although numbers of insect species do not approach those of oak, and beech, elm and willow figure frequently in host-tree lists of forest beetles.

It is possible to make an assessment of forest composition from the host tree data of a fossil fauna. Such a numerical assessment was applied to beetles from a wood peat at Stileway in the Somerset Levels (Girling, in press). Here, all the wood-dependent species were considered and their host trees awarded points according to their importance; 3 for a single named host, 2 points for frequent, but not exclusive attack and 1 point where a number of trees are involved. In addition, obligate tree species were indicated. Figure I is the histogram based on the host trees of the Stileway beetles, and it provides a guide to the likely form of the woodland at the site, with oak, willow and hazel positively indicated. The frequency of occurrence of the various trees cannot, however, be easily

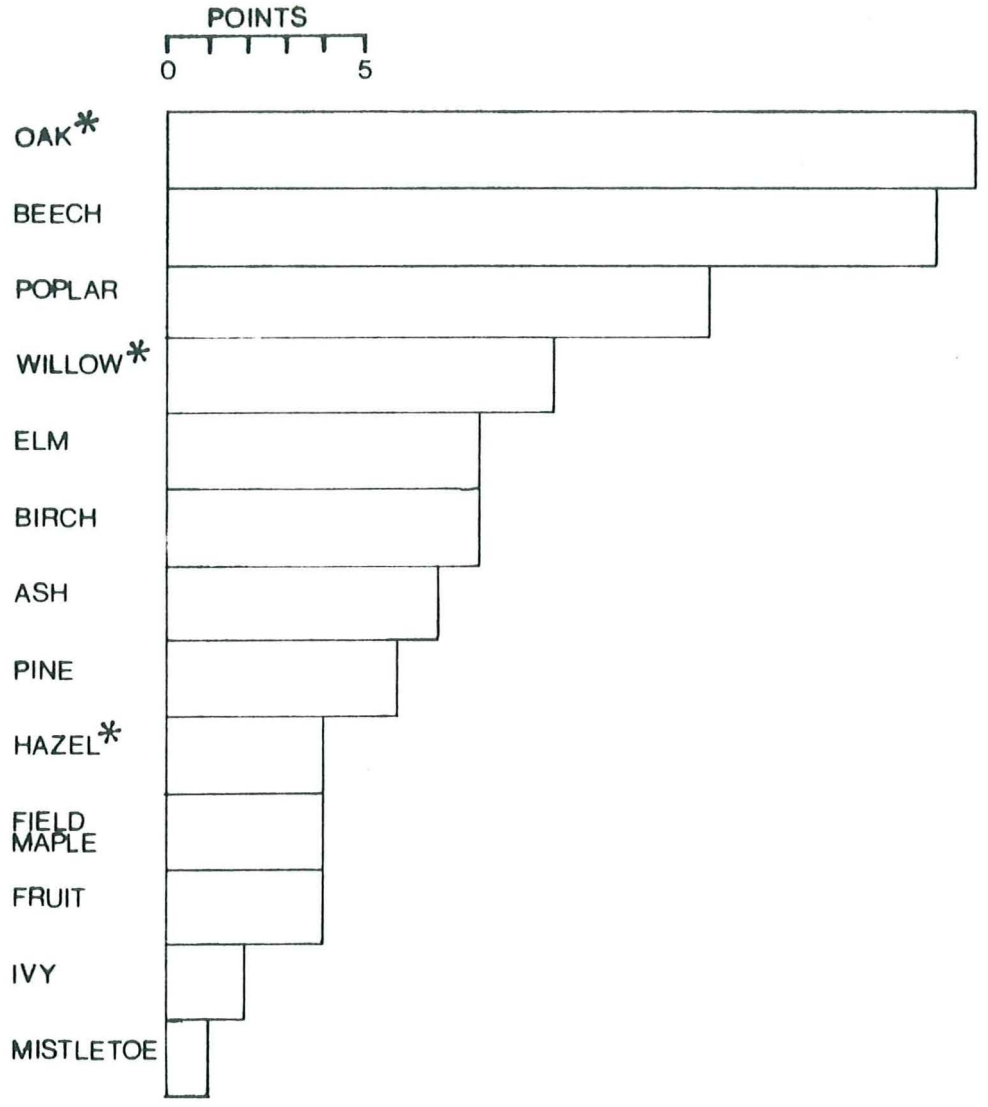


FIGURE 1

Host trees based on requirements of the beetles from Stileway

3 = single host
2 = important host
1 = one of several hosts
* indicates an obligate host

predicted from such data as they reflect the susceptibility of tree species to beetle infestation. Such might be the case for beech, the second commonest species in the histogram. Fagus arrived comparatively late in the post-glacial cycle of Britain, with sporadic records in pollen zone VI in southern England followed by low frequencies in VIIa, attaining values of 10% only in Hampshire. (Godwin 1975). The tree is, however, a low pollen producer which flowers only intermittently and its pollen does not appear to be easily transported. It is not a typical component of mixed deciduous forest. The canopy shades out other species and, in shallow soils, its roots form a dense, fibrous mat, which leads it to become the dominant species in poor heathy or calcareous soils. Although Somerset is one area where beech later became a common species on the limestone, values in pollen spectra are low when the Stileway peats were deposited (Beckett and Hibbert 1979), and it is unlikely that the tree would have grown easily on the waterlogged clay soils of the site, although the higher limestone rock of Meare Island could have provided suitable localities. Other trees, for instance, Alnus have a low level of beetle attack, and rarely figure commonly in host plant lists although the tree might be common near a site. It follows that beetles do provide a wealth of data about forest environments, but are even more valuable when used as part of a multidisciplinary investigation.

History of the British forest beetle fauna

i. Post-glacial climatic recovery

Beetles are sensitive climatic indicators because of their mobility which allows them to respond quickly to environmental change, and their often precise geographical distributions related to temperature regimes, length of seasons and rainfall or snow cover figures (Coope 1965, 1970, 1977). Studies of beetle faunas have demonstrated sudden climatic warming in the middle and late stages of the Devensian (last) ice age (Coope et.al. 1961, Girling 1974, Coope and Angus 1975, Osborne 1972, Coope and Brophy 1976). Investigation of the earliest beetle faunas of post-glacial Britain have demonstrated that here, climatic amelioration was rapid, leading to an imbalance between the thermophilous insects and the slowly migrating forest vegetation which typifies European temperature regimes

(Osborne 1974, 1980a). Both Midlands sites of Lea Marston and West Bromwich have produced insect faunas dated to about 9500 years BP which indicate summer temperatures at least as warm as those at present, and include two beetles now extinct from Britain, a further species whose nearest occurrence is South West Ireland and a head and pronotum of a beetle with no known match which is tentatively assigned to an undescribed species of the little-studied genus Leucohimatium (Osborne 1974). Woodland beetles are present in both faunas, demonstrating that Betula, Pinus and Salix had arrived by 9500 yrs BP, but, significantly, no records were made of species with obligate hosts amongst the thermophilous broad-leaved trees. Their arrival is attendant upon the establishment of the major forest trees. The thermal record of zone IV is better illustrated by open ground flora, and in particular, by aquatic plants than by arboreal pollen, but Coleoptera enable a more precise climatic reconstruction with July temperatures estimated by Osborne (1974, 1976) to be at least 15°C.

ii. Mesolithic forest

In contrast to the numerous pollen studies from sites of zone IV-VIIa age, spanning the Mesolithic, only two archaeological sites have associated beetle studies; those of Seamer Carr (Osborne and Girling, unpublished data) and the late Mesolithic site at West Heath, Hampstead. Here in conjunction with the excavation of the flint assemblage (Lorrimer 1976, Collins in preparation) a nearby marsh localised on a spring-line slightly uphill from the site was investigated for environmental remains (Girling and Greig 1977, and in preparation). Close correspondance has been recorded between the pollen evidence for mixed deciduous forest dominated by Tilia (see also Greig, page xx in this volume) and the beetle fauna from the zone VIIa samples, with frequent interdependence of wood obligates and their host trees. The major example is provided by the commonest bark beetle, Ernoperus caucasicus Lind. which in Britain feeds exclusively on lime. This tiny species was first identified as a fossil from Shustoke (Kelly and Osborne 1964) but has subsequently been found living in

Moccas Park, Herefordshire and at a nearby locality (Allen 1969, Cooter 1980). Its fossil record indicates that it was formerly widespread and often common, a factor undoubtedly related to the importance of lime as a forest tree in South and Midland England. Concurrence of the pollen and beetle record in VIIa and higher samples at Hampstead is further demonstrated by Pogonocherus hispidus (L.), a holly feeder, the ivy bark beetle Kissophagus hederae (Schmitt) and the commonest weevil, Strophosomus melanogrammus (Forst.) which often, but not invariably, occurs on oak saplings. The overall evidence from the beetles is of mixed deciduous forest with little evidence for ground vegetation except pondside plants.

iii. The elm-decline

Although there is an increasing body of pollen evidence for anthropogenic disturbance of Mesolithic forest (eg Dimbleby 1962, Simmons 1969, 1975, Smith 1970) there is general agreement that the zone VIIa/b transition marks the beginning of major forest clearance (Iverson 1941). As the Hampstead samples extend upwards, changes in the beetle fauna can be related to pollen boundaries allowing a rare opportunity to relate these data. Two previously investigated forest beetle faunas from Church Stretton and Shustoke also span the zone VIIa/b transition (Osborne 1972, Kelly and Osborne 1964). Important forest beetles from these sites, and from wood peats in the Somerset Levels of mainly zone VIIb age (Girling 1979, 1980b, in press) include numbers of decaying wood species and Osborne (1972) has suggested that this dead wood fauna from the VIIb Worldsend peats might be related to a phase of clearance, with the overlying gravels resulting from erosion of the deforested hillside of Church Stretton. At Hampstead, preliminary investigations suggest that this faunal element increases at and after the elm decline. In considering forest clearance, by prehistoric communities Rackham (1976) suggests their primitive tools might have been inadequate for removing large trees, and that stumps and trunks which would not burn would have been left to decay, cultivation proceeding around them.

Continuing investigations of the faunas of the zone VIIa/b transition should provide some evidence of a possible elm disease explanation for the decline in the pollen curve, a view recently discussed by Rackham (1980). As yet, no beetle evidence exists either for increased frequency of Scolytus scolytus (F.) which should accompany an outbreak, or for the expansion of beetle inhabitant of decaying elm (for instance, the staphylinid Siagonium quadricorne Kirby) which is currently happening throughout England.

iv. Post-clearance forest continuity

Most of the British forests existing today have resulted from planting in historic times, and are not remnants of the primeval forest, or 'wildwood' of Rackham (1976). Indeed, Smith (1970) suggests that areas of early Neolithic woodland might themselves represent regeneration from Mesolithic clearance. There is evidence from Bronze Age and Iron Age beetle faunas for extensive removal of tree cover in the surrounding area, notably at the late Bronze Age Wilsford Shaft where the rich dung beetle fauna emphasised the importance of grazing (Osborne 1969). Clearly, the effects of forest clearance varied over the whole of Britain and particularly between lowland and upland areas, but from the initial concentration of tree removal on fertile, well drained soils, the process extended to heavier, lowland clays and poorly drained areas as the efficiency of ploughs and other cultivation tools improved. Although the number of beetle assemblages from archaeological sites is limited, it is notable that only two forest faunas are related to Bronze Age features. Thorne Moors, Yorkshir has a very rich beetle fauna associated with a Bronze Age trackway, one of the structures rare outside the Somerset Levels (Buckland and Kenward 1973, Buckland 1979). The second site with a forest assemblage of this age is Stileway, in the Levels, where peat deposition continued into this period, and Bronze Age activity in the vicinity is evidenced by oval platforms of hurdles spaced at intervals from the Jurassic island which may have represented attempts to stabilize especially wet areas of the peat surface, or, the more favoured explanation, were for use in hunting or wildfowling (Coles and Orme 1978). Both faunas indicate mature, mixed woodland with abundant dead wood habitats but

this evidence is overwhelming at the Thorne site, where 35 wood-boring species and numerous other tree associated beetles were recorded. The site is also important for yielding the largest concentration of old forest relict species, ("Urdwaldrelikt"of Dorn, quoted in Horion 1935) which no longer occur in Britain; 75 individuals of 6 extinctions plus one weevil identifiable only to genus were listed from the Thorne peats. A feature common to Thorne Moors and Stileway is that both forests grew in very wet conditions and in fact the Thorne forest was eventually inundated by a flooding episode which Buckland relates to changes in the configuration of Spurn Head at the mouth of the Humber. The very wet conditions of the locality might have afforded protection against the 'Landnam' clearances identified by Turner (1965) in the Bronze Age pollen spectrum of Thorne. Similarly, intense human activity, especially pastoralism, has been demonstrated for the island of Meare during the Bronze Age (Beckett and Hibbert 1979), but at Stileway, on the gentle slope of the south east part of the island, some forest survived clearance possibly because the ground was too wet to be easily, and usefully, deforested. The important dead wood fauna at Stileway is strongly suggestive of mature woodland rather than the regeneration identified after Neolithic and Bronze Age clearance elsewhere in the Levels.

v. Spread of 'culture-steppe'

Concomitant with the survival of mature forest in certain, especially unfavourable areas, there is increasing evidence for widespread forest removal in the Midlands and South England, especially on fertile and well drained soils. As well as the grassland fauna dominating the late Bronze Age site of Wilsford (Osborne 1969), Runnymede, a Thames Valley site of the same age (Longley Needham 1979) has produced a meadowland pollen suite associated with abundant dung and grassland beetles (Girling and Greig unpublished data). By the Iron Age, evidence for a dominantly cleared landscape is more extensive, evidenced by the grazing fauna of Iron Age Fisherwick (Osborne 1979) and at two Thames Valley sites of Mingie's Ditch and Farmoor which produced respectively 1% and less than 0.01% woodland beetles (Robinson 1981) substantiating the low arboreal pollen values

at the site (Dimbleby, quoted in Robinson). A similar pattern has emerged at the Iron Age ring ditch at Tattershall Thorpe excavated by Mr P Chowne where dung and grassland species predominate (unpublished data). At the Iron Age Lake Village of Meare, true woodland species made up a insignificant faunal element although the timber pest, Anobium punctatum (Deg.) was present in hundreds (Girling 1979b).

From Roman times onwards, beetle evidence for virtually treeless landscapes around settlements is substantial, and indirect evidence for the importance of cereal cultivation signified by records of food store pests, the most serious of which are imported beetles with possible Middle East or Mediterranean origins. (Osborne 1978). Their occurrence in Roman and later Britain is summarised by Buckland (1981). Since Roman times, emphasis on agricultural land use has ensured the continuation of the largely deforested landscape except where deliberate attempts to protect the dwindling woodland, from Saxon times onwards, and deliberate planting of forests first by the Norman kings for hunting, and later for shipbuilding, smelting and other industrial practices, furniture making, the process culminating in the coniferous monocultures of the present Forestry Commission.

The British beetle fauna of the cleared sites from the Bronze Age onwards display affinities with the treeless steppe faunas of central and eastern Europe and Asiatic USSR although differences are dictated by the degree of continentality of the climate. Analogous faunas existed in Mid-glacial Midland and Southern England about 43,000 years ago when rapid climatic amelioration resulted in a temperate treeless landscape whose beetle fauna showed striking similarities with that of post-Neolithic Britain (Girling 1974, 1980b, Coope and Angus 1975) although the former is climate-steppe, the latter culture steppe. The pre-Neolithic faunas more clearly resemble the temperate interlacial stages of the Cromerian, Hoxnian and Ipswichian (eg Shotton and Osborne 1965 Osborne 1980b) which offer the best models for the type of beetle fauna which might have been present in Britain today but for the interference of man.

Extinctions from the British fauna

Over 20 species of beetle recorded from post-glacial Britain have disappeared from this country, and considerably more have undergone a serious range contraction The two causal mechanisms for these extinctions are climate change and forest clearance (Osborne 1965). Our present knowledge indicates a larger proportion of forest induced extinctions, and although it is probable that climatic change has played some role in their disappearance it might not be significant within the protected environment of woodland where temperature extremes are reduced to create a more equable microclimate than that of an open landscape.

The forest extinctions are mainly composed of wood-borers and predators which develop in the galleries of their hosts. One species omitted from this list because it is a water beetle nevertheless deserves brief mention as acid pools in coniferous forests are its usual habit. Agabus wasastjernae Sahl., recorded by Osborne (1972) from zone VIIb deposits at Worldsend has since undergone a northwards retraction in range and now occurs in continental parts of Scandinavia. A simple explanation of climatic cooling is untenable in view of contemporary records for beetles whose ranges now lie predominantly south of this country. It might, however, prove to be an indicator of a more continental climatic regime although an anomalous range produced by human disruption of its primary habitat can also be proposed for A.wasastjernae as well as other woodland beetles with isolated or disjunct present day distributions.

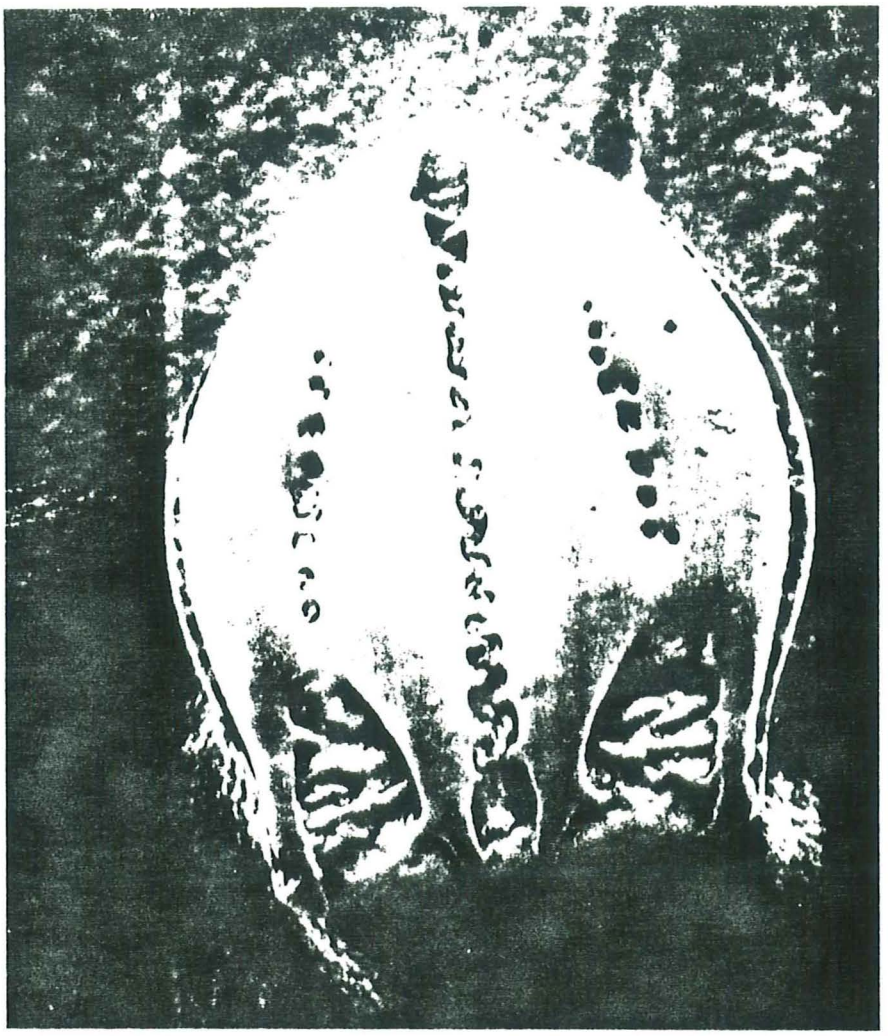
The occurrence in Mesolithic to Bronze Age sites of all known wood-dependent beetles now extict in Britain is summarised in Table I. No records have been made for this group later than the Brzone Age although Iron Age, Roman and one Medieval occurrences of the climatically-induced extinct beetles have been registered. A number of the forest extinctions are today exceedingly rare in mainland Europe a particular example being Rhysodes sulcatus F. whose steady decline has been traced within recent historic times by old collecting records (Horion 1935). The species is of entomological interest as it retains a number of primitive features of the ancestral forms of the predaceous

TABLE I

NAME	AGE MES	NEO	NEO/BA	BA	pBA
Rhysodes sulcatus F.	-	SH BP	-	TM	-
Batrisus formicarius Aubé	-	-	SW	-	-
Porthmidius austriacus Sch.	-	CS	-	-	-
Cerambyx cerdo L.	-	?BO	-	-	-
Isorhipis melasoides (Lap.)	HH	BP	-	MC TM	-
Pelta grossum (L.)	-	-	-	TM	-
Prostomis mandibularis(F.)	-	-	-	TM	-
Pycnomerus terebrans Ol.	-	CS	SW	-	-
Bothrideres contractus F.	-	-	SW	-	-
Mycetina cruciata Sch.	-	-	-	TM	-
Rhopalodontus bauderi Abeille	-	-	-	TM	-
Eremotes elongatus Gyll.	-	CS	-	-	-
E.strangulatus Perr.	-	CS	-	-	-
E.punctulatus Boh.	-	-	SW	-	-

Occurrence at British sites of wood-dependent beetles now extinct from this country

Key to sites: HH, Hampstead Heath,Girling and Greig (1977); SH, Shustoke,Kelly and Osborne (1964); CS, Church Stretton (including Worldsend), Osborne (1972); BP, Baker Platform,Girling (1980a); BO, Bog Oak records,Duffy (1968); TM, Thorne Moors,Buckland (1979); MC, Misterton Carr,Osborne (unpublished data).



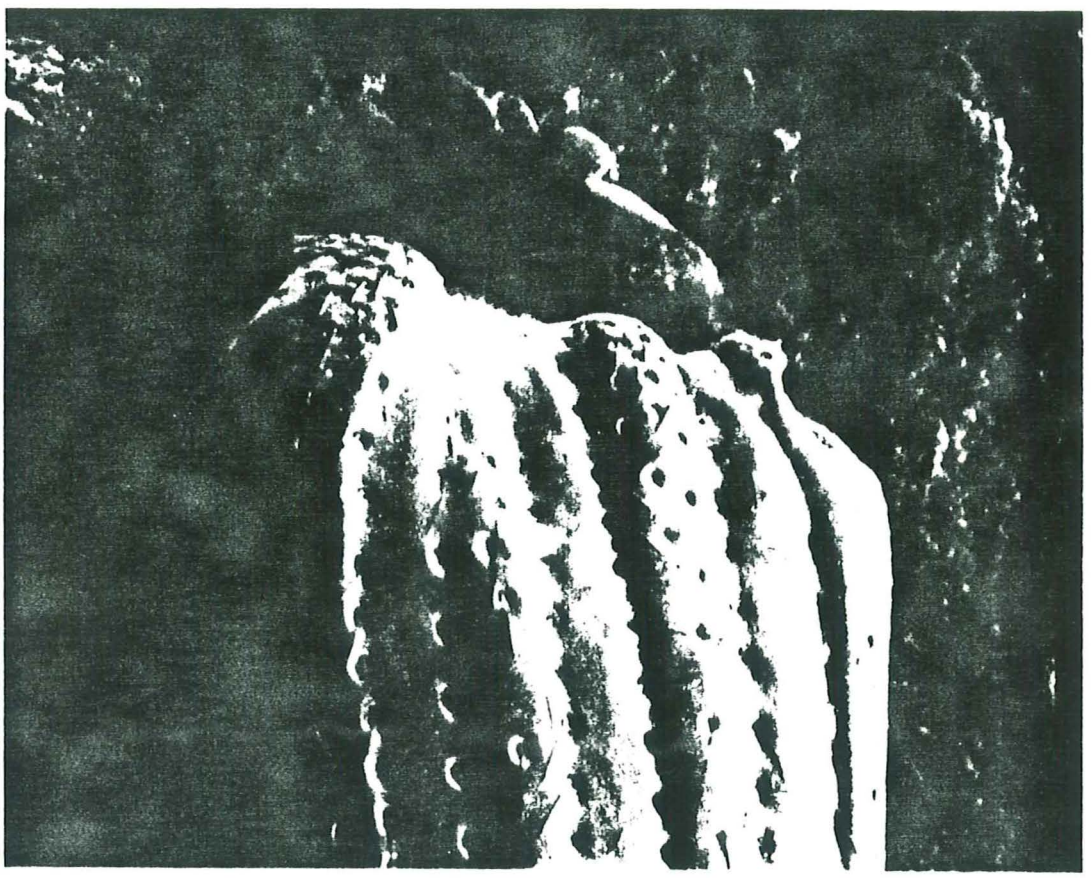


Plate 1

Rhysodes sulcatus a) pronotum and b) elytral base from the Baker Platform site of the Somerset Levels
Scanning electron micrograph (magnification)

ground-beetle and water-beetle families (Crowson 1955). Plate I shows an example of a pronotum and elytral base of R.sulcatus from the Somerset Levels. In marked contrast, Batrisus formicarius Aube is widespread in mainland Europe, reaching the coast of Northern France and this distribution demonstrates the importance of the English Channel as a barrier to re-immigration of species. This is better illustrated by certain climatically extinct beetles such as Anthicus gracilis Panz. whichhas occurred at several Somerset Levels sites (eg Girling 1979) but whose present widespread range throughout Europe suggests that suitable conditions exist at least in Southern Britain today. Its absence from this country is attributed to an episode of colder climate which eliminated the species from these shores with its return now blocked by the Channel. It may be argued that suitable habitats are present in forests such as Windsor for B.formicarius, and indeed other species listed as forest extinctions, but the lack of continuity of such environments has dislodged these beetles because of their low dispersal capacity. B.formicarius, unlike the other listed species is neither a wood (or wood-fungus) feeder or one of their predators, but has become adapted to living in ants' nests in decaying trees or stumps. This mymecophilous habit is also displayed to some extent by the predators Pycnomerus terebrans OL., Bothrideres contractus F. and Isorhipis melasoides (Lap.), the ant Lasius brunneus (Late.) often implicated in these relationships, although Dajoz (1977) questions whether the association is truly myrmecophilous in the case of the Colydiidae. At Stileway, B.contractus, figured in Plate 2, was identified alongside several species upon which it is known to prey, including Leiopus nebulosus (L.)

Elateridae are generally associated with grassland, their larvae, known as wire-worms, and often so abundant as to warrent agricultural pest-status. Porthmidius austriacus Sch. is one of a smaller number of elaterids whose larval development takes place in wood. Its only known occurrence in Britain is the zone VIIb deposits at Worldsend (Osborne 1972). Another group of wood-borers are the Cossoninae weevils of which Eremotes is a constituent genus. Today in

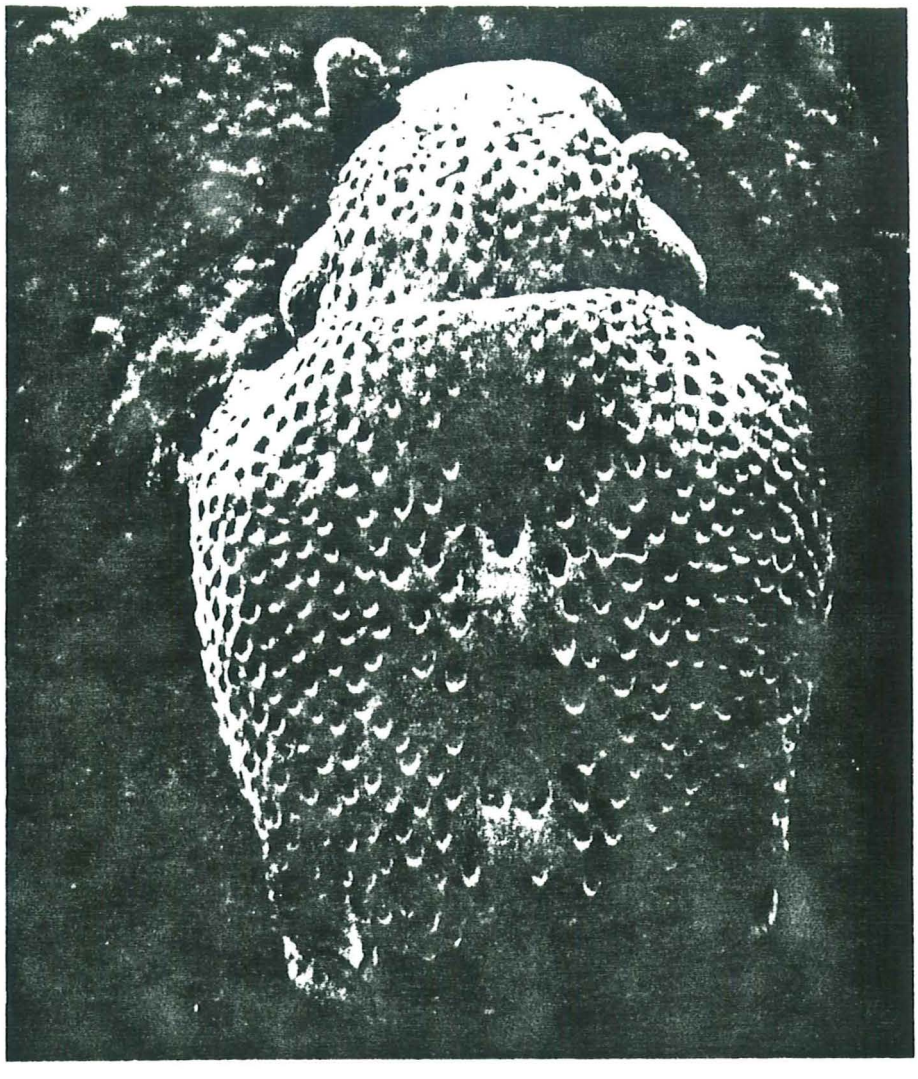


Plate 2

Bothrideres contractus head and pronotum from Stileway.

Scanning electron micrograph (magnification)

Britain, this genus is represented by a single species, E.ater (L.), known from Sherwood and the Scottish Highlands but with more recent, isolated records from forestry plantations further south. This apparently northern range is, however, belied by fossil records for the species at Hampstead Heath, Thorne Moors and the Somerset Levels. The species often feeds on conifers, but a number of deciduous trees are found amongst its hosts, and it even attacks seasoned timber. Furthermore, records of three more species have been made for post-glacial Britain; E.elongatus Gyll. and strangulatus Perr. from Worldsend and E.punctulatus Boh. from Stileway. The two former species are mainly taken on Pinus and Picea whereas E.punctulatus feeds on deciduous as well as decaying coniferous stumps (Folwaczny 1977). It would appear that the dependence of the genus on decayed wood which in turn implies mature woodland has led to the severe restriction of the whole genus resulting from forest clearance. A parallel can be drawn with another cossonine weevil, Brachytemnus submuricatus Schon. which is a common member of previous interglacial faunas, (eg Shotton and Osborne 1965, Girling 1980b). Presently, the species displays a very southern European range in Spain, Mediterranean France and Italy. It is tempting to suggest that in addition to, or possibly, instead of a straightforward climatic control, its present restricted range has been influenced by deforestation.

Cerambyx cerdo L. differs from other species listed here in that its claim to be native was initially based on old collecting records which have been questioned. Subsequently, remains of the beetle have been recovered from bog oaks. The first fossil find was by Duffy (1969) from a Cambridgeshire bog oak dated at about 4,000 years BP, although he questioned the contemporaneity of the wood and the beetle remains. Since then further bog oaks finds from Britain have been made (Harding and Hant 1978). The other extinctions are based upon studies of assemblages of insects which are continuing to furnish evidence of a much richer forest beetle fauna dating from before man's onslaught upon their habitats.

REFERENCES

Allen,A.A. (1969) Ernoperus caucasicus Lind. and Leperesinus orni Fuchs. (Col.,Scolytidae) in Britain. Entomologists' Monthly Magazine, 105, 245-49.

Beckett, S.C. and Hibbert, F.A. (1979) Vegetational change and the influence of prehistoric man in the Somerset Levels. New Phytologist, 83, 577-600.

Buckland,P.C. (1975) Synanthropy and the deathwatch: a discussion. The Naturalist, 100 (933), 37-42.

Buckland, P.C. (1979) Thorne Moors: a palaeoecological study of a Bronze Age site. University of Birmingham, Department of Geography, Occasional Publication, 8, Birmingham.

Buckland, P.C. (1981) The early dispersal of insect pests of stored products as indicated by archaeological records. Journal of Stored Products Research, 17, 1-12.

Buckland, P.C. and Kenward, H.K. (1973) Thorne Moor: a palaeoecological study of a Bronze Age site. Nature (London) 241, 405-6.

Chrystal,R.W. (1937) Insects of the British Woodlands.

Coles, J.M. and Orme, B.J. (1978) Structures south of Meare Island. Somerset Levels Papers, 4, 90-100.

Coope, G.R. (1965) The response of the British insect fauna to Late Quaternary climatic oscillations. Proceedings of the 12th. International Congress of Entomologists, London, 173, 444-5

Coope, G.R. (1970) Interpretations of Quaternary insect fossils. Annual Review of Entomology, 15, 97-120.

Coope, G.R. (1977) Fossil Coleoptera assemblages as sensitive indicators of climatic change during the Devensian (last) cold stage. Philosophical Transactions of the Royal Society of London, B, 280, 313-40.

Coope, G.R., Shotton, F.W. and Strachan, I. (1961) A Late Pleistocene fauna and flora from Upton Warren, Worcestershire. Op.Cit. 165, 389-412.

Coope, G.R. and Brophy, J.A. (1972) Late Glacial environmental changes indicated by a Coleopteran succession from North Wales. Boreas, 1, 97-142.

Coope, G.R. and Angus, R.B. (1975) An ecological study of a temperate interlude in the middle of the last glaciation, based on fossil Coleoptera from Isleworth, Middlesex. Journal of Animal Ecology, 44, 365-91.

Cooter, J. (1980) A note on Ernoporus caucasicus Lind. (Col., Scolytidae) in Britain. Entomologist's Monthly Magazine 116, 112.

Crowson, R.A. (1955) The natural classification of the families of Coleoptera (Reprinted 1967) Classey: Hampton

Dajoz, R. (1977) Coleopteres Colydiidae et Anommatidae Palearctiques (Faune de L'Europe et du Bassin Mediterraneen) Masson: Paris

Dimbleby, G.W. (1962) The development of British heathlands and their soils. Oxford Forestry Memoir, 23: Oxford.

Duffy, E.A.J (1968) The status of Cerambyx L. (Col Cerambycidae) in Britain. Entomologists Gazette, 19, 164-6.

Folwaczny, B. (1977) Bestimmungstabelle der Palaarktischen Cossoninae.

Girling, M.A. (1974) Evidence from Lincolnshire on the age and intensity of the Mid-Devensian temperate episode. Nature (London), 250, 270.

Girling, M.A. (1979a) The fossil insect assemblage from the Meare Lake Village. Op.Cit., 5, 25-32.

Girling, M.A. (1979b) Fossil insects from the Sweet Track. Somerset Levels Papers, 5, 84-93.

Girling, M.A. (1980a) The fossil insect assemblage from the Baker site. Op.Cit., 6, 36-42.

* Girling, M.A. and Greig, J.R.A. (1977) Palaeoecological investigation of a site at Hampstead Heath, London. Nature, 268, No. 5615, 45-47.

Girling, M.A. (1980b) Two late Pleistocene insect faunas from Lincolnshire. Unpublished ph.D. Thesis, University of Birmingham.

Girling, M.A. (In Press) An 'old-forest' beetle fauna from a Neolithic and * Bronze Age peat deposit at Stileway, Somerset Levels.

Godwin, H. (1975) The History of the British Flora (2nd. Ed.) Cambridge University Press: London.

Harding, P.T. and Plant, R.A. (1978) A second record of Cerambyx cerdo L. (Coleoptera: Cerambycidae) from sub-fossil remains in Britain. Entomologist's Gazette, 29, 150-2.

Horion, A. (1935) Nachtrag zu Fauna Germanica Käfer. Krefeld.

Horion, A. (1953) Faunstik der Mittel europaischen Käfer, 3. Malacodermata, Sternoxia. Eigenverlag: Munchen.

Iversen, J. (1941) Landnam: Danmarks Stenalder. Danmarks Geologiske Undersogelse, 66, 1-68.

Kelly, M. and Osborne, P.J. (1964) Two faunas and floras from the Alluvium at Shustoke, Warwickshire. Proceedings of the Linnean Society of London, 176, 37-65.

Kloet, G.S. and Hincks, W.D. (1977) A Checklist of British Insects, 2nd. Ed. Coleoptera and Strepsiptera. Royal Entomological Society: London.

Langley, D. and Needham, S. (1979) Egham: A late Bronze Age Settlement and waterfront. Current Archaeology, 68, 262-267.

Lorrimer, D. Home, (1976) A Mesolithic site on West Heath, Hampstead - A preliminary report. London Archaeologist, 2, 407-9.

Morris, M.G. and Perring, F.H. (Eds). (1974) The British Oak. Faringdon: London.

Osborne, P.J. (1964) The effect of forest clearance on the distribution of the British insect fauna. Proceedings of the 12th. International Congress of Entomologists, London, 456-57.

Osborne, P.J. (1969) An insect fauna of late Bronze Age date from Wilsford, Wiltshire. Journal of Animal Ecology, 38, 555-66.

Osborne, P.J. (1972) Insect faunas of Late Devensian and Flandrian age from Church Stretton, Shropshire. Philosophical Transactions of the Royal Society of London, B, 263, 327-67.

Osborne, P.J. (1974) An insect assemblage of early Flandrian age from Lea Marston, Warwickshire, and its bearing on the contemporary climate and ecology. Quaternary Research, 4, 471-86.

Osborne, P.J. (1976) Evidence from the insects of climatic variation during the Flandrian period: a preliminary note. World Archaeology, 8, 150-158.

Osborne, P.J. (1978) Insect evidence for the effect of man on the lowland landscape In S.Limbrey and J.G. Evans (Eds.) The Effect of Man on the landscape: the Lowland Zone, 32-34 C.B.A.: London.

Osborne, P.J. (1979) Insect remains. In C. Smith, Fisherwick, 85-97 and 189-93. British Archaeology Reports, 61, Oxford.

Osborne, P.J. (1980a) The late Devensian-Flandrian transition depicted by serial insect faunas from West Bromwich, Staffordshire, England. Boreas, 9, 139-48.

Osborne, P.J. (1980b) The insect fauna of the organic deposits at Sugworth and its environmental and stratigraphic implications. Philosophical Transactions of the Royal Society of London, B, 289, 119-33.

Rackham, O. (1976) Trees and Woodland in the British Landscape. Dent: London.

Rackham, O. (1980) Woodland Ecology. Arnold: London.

Robinson, M. (1981) The Iron Age to Early Saxon environment of the Upper Thames Terraces. In M. Jones and G.W. Dimbleby (Eds.) The Environment of Man: the Iron Age to the Anglo-Saxon Period. 251-86, British Archaeological Reports, 87: Oxford.

Roshkov, A.S. (1970) Pests of Siberian Larch. (Translated from the Russian) Keter: Jerusalem.

Shotton, F.W. and Osborne, P.J. (1965) The fauna of the Hoxnian Interglacial deposits of Nechells, Birmingham. Philosophical Transactions of the Royal Society of London, B, 248, 353-78.

Simmons, I.G. (1969) Pollen diagrams from the north York moors. New Phytologist, 56, 807-827.

Simmons, I.G. (1975) Towards an ecology of Mesolithic man in the uplands of Great Britain. Journal of Archaeological Science, 2, 1-15.

Smith, A.G. (1970) The influence of Mesolithic and Neolithic man on British vegetation: a discussion. In Walker, D. and West, R.G. Studies in the Vegetational History of the British Isles, 81-96 Cambridge University Press: London.

Turner, J. (1965) A contribution to the history of Forest Clearance. Proceedings of the Royal Society of London, B, 161, 343-53.

Zhuravlev, I.I. and Osmolovskii, G.E. (1949) Pests and diseases of shade trees. (Translated from the Russian) Sivan: Jerusalem.