

Scolytus scolytus (F.) and the possible role of elm disease in the early Neolithic.

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Scolytus scolytus (F.) (destructor Ol.) is a small bark beetle whose major host is elm (Ulmus). Attacks on a variety of other deciduous trees including hazel (Corylus), hornbeam (Carpinus) and ash (Fraxinus) have been recorded (Michalski 1973) but most authors in Britain cite elm (Fowler 1891, Duffy 1953). The beetle is found over the whole of Europe up to the start of the taiga and in Central Asia. In common with other Scolytidae, the larvae feed by excavating galleries between the bark and sap wood, the radial pattern of these channels varying between species. S.scolytus almost always attacks dead wood, breeding in living trees only in unusual conditions, and infestations alone are not greatly injurious to healthy trees although they lead to rapid destruction of the bark on dead trees. After pupation, recently emerged adults feed on twigs of living elms and although this causes scarring, it is not otherwise deleterious. The importance of S.scolytus is that it is the major carrier of Ceratocystis ulmi, the fungus responsible for Dutch Elm Disease. S.multistriatus (Marsh.) is also, but to a lesser extent, implicated in the spread of the disease. The fungus is introduced into the larval galleries where its fructifications are of two kinds; asexual stalks and sexual

flask-shaping fruiting bodies. It spreads to the channels, or tracheids, of the current year's wood growth where toxins cause the production of tyloses, usually found in the dead heart wood, which block the drainage and hence the nutrient supply. This leads to the death of the affected bough and to the whole tree unless the infection can be sealed off. Interference with the elm's hormone production results in the curved twigs which are characteristic of Dutch Elm Disease blighted trees. The requirement of dead, including felled, wood for the larval development of S.scolytus restricts the spread of the disease at this stage, but the habit of twig feeding by young adults serves to carry the fungal spores to healthy trees when the beetles have emerged from infested wood. C.ulmi also travels via the root systems of suckered elms and such attacks are rapidly fatal to the clones. Elm species which readily throw out suckers, U.procera and U.minor, are thus more susceptible than U.glabra which reproduces by seed, and in the current epidemic of Dutch Elm Disease (1965 to the present) U.procera, the "English" elm has been the most affected species, infection arising both from insect attack and transfer via root suckers especially in hedgerows.

Archaeological context of the S.scolytus record

A number of records of Scolytus species have been made from archaeological and interglacial deposits (e.g. Kelly and Osborne 1965) but S.scolytus remained unknown until two elytral (wingcase) apices were identified among the insect remains from West Heath Spa, Hampstead, London (Girling and Greig 1985). Here, sediments uphill from a Mesolithic site (Collins and Lorimer in press) were deposited as the infill of a spring-fed

hollow. Investigations of pollen, plant macrofossils and insect remains have demonstrated that the basal sediments are pre-elm decline in age and represent an episode of dense forest growth (Girling and Greig 1977). In the lowest samples, between 120 and 100 cm, values for tree pollen average 96%, and when figures are corrected for the proportion of lime (Tilia), a low pollen producer because it is insect pollinated, it is shown to be the dominant forest tree (Greig in press). The beetle remains accord well with the pollen evidence and a number of tree-dependent species occur with their hosts. Of significance is the tiny bark beetle Ernoporus caucasicus Lind. a lime feeder. Hosts of other bark beetles are also present including that of Kissophagus hederæ (Schm.), ivy and Acrantus vittatus, elm, and pollen evidence indicates the availability of hazel (Corylus), the food plant of the nut-weevil, Curculio nucum.

The elm decline horizon has been identified at 95-90 cm, with reductions in elm pollen from 9 - 1% and an overall decrease in tree pollen to 50%. Coinciding with this event, changes can be observed in the insect fauna, the most significant of which are the decrease in the numbers of tree-obligate species and the first appearance of dung beetles. The pollen and insect evidence suggests a process of opening up of the forest and grazing areas provided in the clearings. One consequence of the reduction of tree cover on the thin soils developed on the Bagshot Sands substratum, the immediate appearance of Ericales or heath-forming communities, itself could argue for cultivation leading to depletion of nutrients and accelerated soil degradation. One of the traditional views of the Neolithic elm decline as the activity of early farming communities is thus

supported by the successive changes in the vegetation and insects at Hampstead. The remains of Scolytus at the site were recovered approximately 15 cm below the elm decline horizon.

Identification of the beetle remains

The Scolytus elytral fragments from West Heath Spa were filmy and fragmented, in keeping with the poor preservation which typified insect assemblages from the basal samples. In Britain the genus Scolytus is represented by six species and these can be readily keyed into two groups on elytral characters. S.scolytus and one other species, S.ratzbergi are thus separable from the remaining species and other characters relating to the head, elytra and dorsal abdomen allow their differentiation. A summary of the elytral characters employed in the keys of Fowler (1891), Duffy (1953) and Michalski (1973) are given below.

Elytral striae distinct, punctures of striae larger than those of interstices.....scolytus, ratzbergi

Elytral striae not distinct, punctures of striae equal to or smaller than those of interstices....intricatus(Ratz.), mali(Bech.), multistriatus (Marsh.) and rugulosus (Mull.)

Sides subparallel, slightly constricted at the posterior. Striae depressed with rows of circular or elongated rectangular hollows, and closely punctured. Punctures on interstices irregular, sometimes in slightly depressed furrows and those on 1-3 confusedly scattered. Apical and postero-lateral margins smooth or finely granularratzbergi

Sides parallel behind mid-point with apices slightly emarginate at suture and margins smooth. Punctures of striae depressed, dense and well defined. Interstices broad, punctures widely spaced and variable in size but always smaller than those of the striae. Striae and interstices become obsolete at apex. Puncturation at sides and apex irregular.....scolytus

In spite of the poor preservation of the Scolytus elytra, they were clearly referable to the scolytus/ratzbergi group and

the keys indicated that the elytra of the two were sufficiently distinct to allow their separation. In the identification of disarticulated remains of beetles, however, reliance cannot be placed upon keys as the entomologists frequently have much more clear cut characters to work with, often relating to the appendages, than the morphological variation on the major skeletal elements (head, pronota and elytra) which is primarily employed in the naming of Quaternary and archaeological remains. (In the case of scolytus/ratzbergi, the heads display marked differences and the tubercles on the 3rd and 4th abdominal sternites are pronounced, particularly in males of the latter species and entire beetles present little difficulty in their recognition.) Fossil remains of beetles and other insects can be confidently identified only by directly comparing them with modern, correctly named, specimens, and it is usual to refer to a number of examples of each species. This is particularly relevant in the bark beetles which exhibit considerable size variation within species, a factor dependent upon the condition of the wood in which the larvae developed. Identification of the Scolytus remains was carried out at the Coleoptera section of The British Museum (Natural History), London, where both British and World collections of Scolytus were examined in conjunction with the identification keys. On this basis, the elytral apices were identified as S.scolytus. Examples of modern elytra of S.scolytus and S.ratzbergi corresponding to the fossil remains are shown in plates 1 - 4 to demonstrate the morphological characters on which the identification was based.

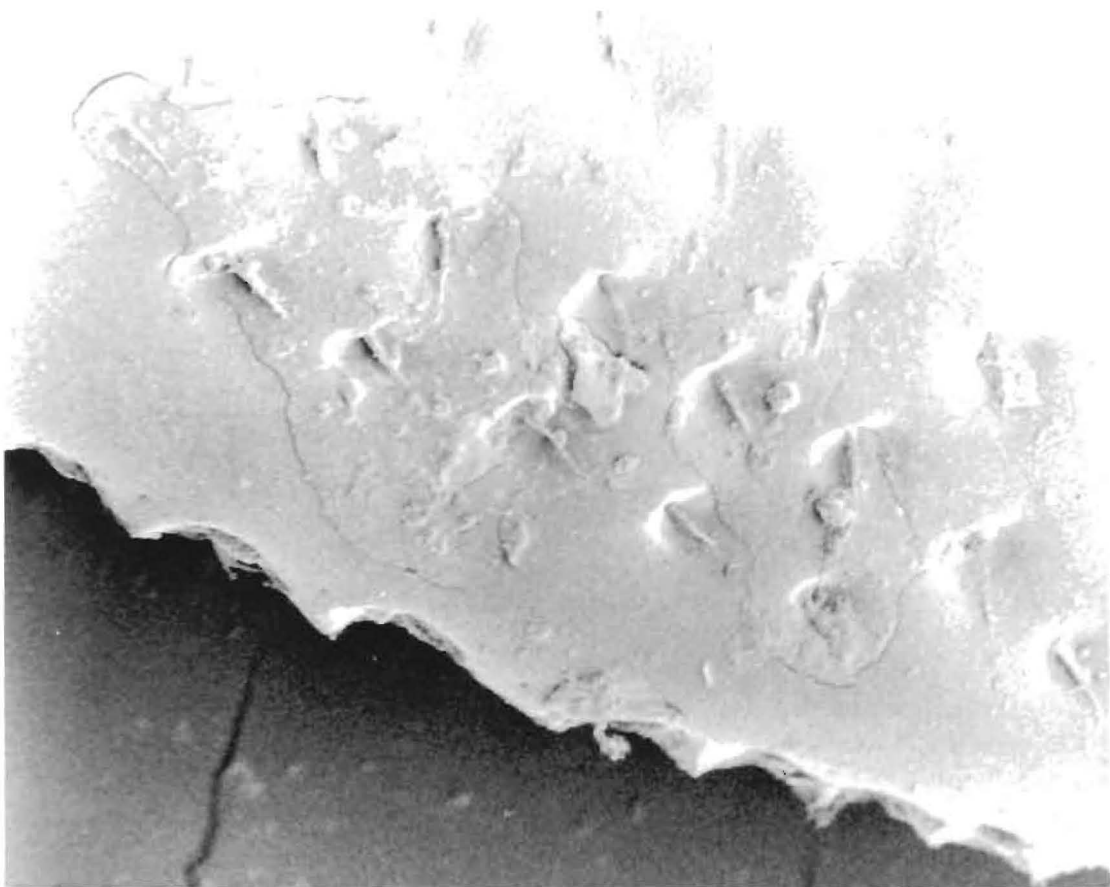
The recognition of S.scolytus is of intrinsic interest as there are no previous fossil records from Quaternary or

Plates 1 and 2

1. Scolytus scolytus. left elytron X 40

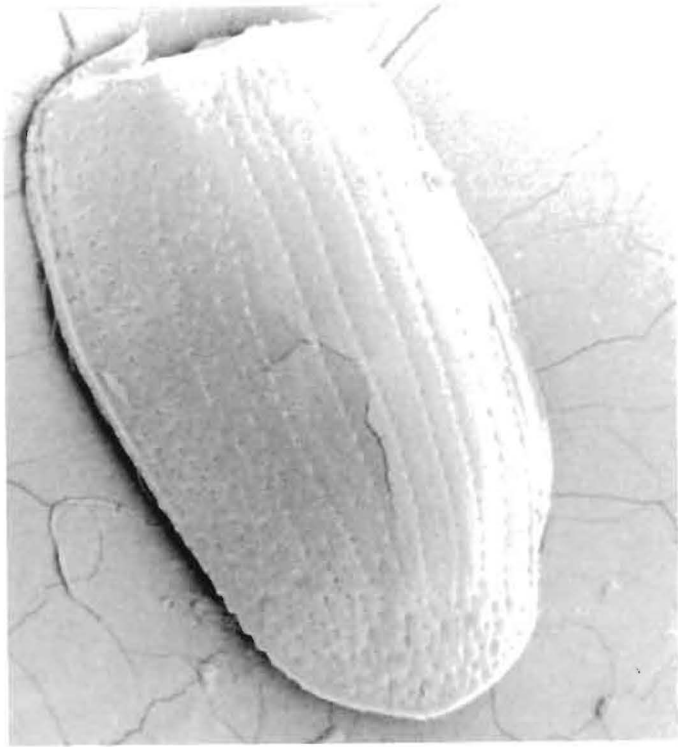


2. S.scolytus, elytral apex X 200

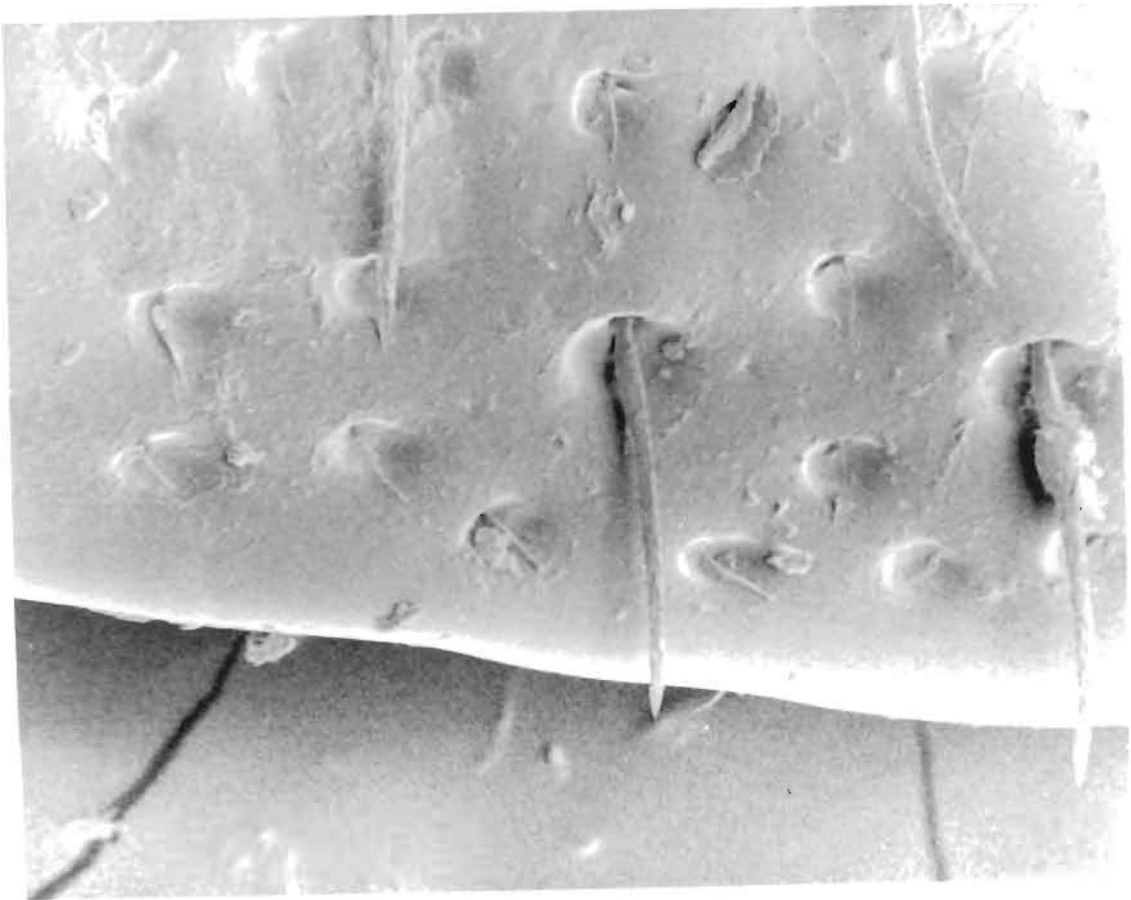


Plates 3 and 4

3. Scolytus ratzeburgi, left elytron X 40



4. S.ratzeburgi, elytral apex X 200



Scanning electron micrographs, M.A Girling

archaeological deposits. This factor partly reflects the relatively low number of suitable sites which have been fully analysed but it might also indicate a change in population levels of the beetle. S.scolytus is found more commonly in open landscapes than closed woodland, preferring isolated trees and those in hedgerows and copses, and it is likely to have become more abundant as deforestation of the primeval forest progressed.

Implications for the elm decline episode.

The S.scolytus record from West Heath Spa is also significant because of its relationship to the elm decline horizon at the site. A number of hypotheses have been forwarded to explain the marked decline of elm pollen to half its former level, which occurred across Europe at about 5,000 bp., within a period of 300-400 years (see Smith 1970, 1981, Edwards 1979). Recent research is showing that pollen of trees other than elm are affected (Beckett and Hibbs 1979). As the decline marks the boundary of von Post's Atlantic and sub-Boreal periods, held by him to represent a change to greater continentality, climatic explanations for the event found early favour. A straightforward temperature reduction is not supported by corresponding declines in other thermally sensitive trees, however, and even allowing for varying effects of climatic change over the whole of their geographical ranges, particularly at their northern and altitudinal limits, the evidence is inconclusive. The theory that man was the causal agent of the elm decline has been widely discussed. Direct tree clearance, possibly aided by fire, for shifting agriculture was initially proposed, but the more elaborate theory of stripping foliage for cattle fodder goes further to explain the otherwise huge acreage

of forest which would need to be removed in order to depress the elm pollen by half (Iversen 1941, Troels-Smith 1960). Whilst population levels postulated for the early Neolithic are vastly inadequate for direct felling of elm, foliage stripping by the same population would be more effective in reducing pollen output as this interferes with flowering of the trees. Rowley-Conwy (1982) argues that the figures for both men and cattle required to account for the elm pollen reduction by foliage stripping is still unacceptably high. Parallels exist in Europe for foliage feeding of cattle, and although this is by no means confined to elm, its use by Neolithic farmers is more understandable than selective clearance of that one particular tree, unless pure stands of elm (Morrison 1959) are envisaged. Foliage fed cattle are usually thought to have been stockaded but if, as Smith (1981) points out, hobbled cattle were simply turned out into the forest and supplied with leafy branches, additional browsing on bark would be especially injurious to elm, the bark of which pulls off in long strips. Rackham (1980) has observed that apart from trees affected by Dutch Elm Disease, damage by horses and pigs is the only other cause of death in elms. The tree pollen would be further depressed by ring barking through herbivore grazing. Mesolithic forest disturbance has long been recognised (Simmons 1975, Simmons et al 1981) but a growing catalogue of sites where pre-elm decline cereal pollen has been recognised (Edwards and Hiron 1984) indicate that the elm decline does not represent the spread of cultivation as an innovative technique although it might signify the start of widespread adoption of arable farming.

One other proposal to account for the elm decline has been

disease (Watts 1961) and this is receiving much attention at present because of the devastation caused by the current outbreak in Europe (Ten Hove 1968, Smith 1981, Rackham 1980, Groenman von Waateringe 1983). Ceratocystis ulmi, responsible for the present outbreak, does not have to be the pathogenic fungus involved, but it appears likely to be the case. Elm is more susceptible than any other tree to wood-rotting fungi but it usually recovers from wound and heart-rot by regeneration. Effects of C.ulmi are more severe, resulting in the death of a bough or the entire tree in as little as a single season. (Rackham 1980, has, however, observed that self-generating pollards are arising from stumps of disease -killed trees.) C.ulmi is genetically unstable, mutation and gene-recombination resulting in more aggressive strains. Evidence suggests that the present Dutch Elm Disease fungus has been reimported from North America where a particularly virulent strain had arisen (Gibbs and Brasier 1973), whereas previous outbreaks of the disease such as that of the 1930's, involved a less aggressive strain than that presently operating. In Britian the loss of non-woodland elms during the current Dutch Elm Disease outbreak greatly exceeds 50% and the arguement that the Neolithic elm decline represents a disease epidemic caused by a particularly virulent strain of C.ulmi is persuasive. The forested landscape of that period would, however, have been very much less conducive to the spread of the desease and this should be borne in mind when considering the evidence.

Dutch Elm Disease epidemics are currently spread across much of Europe, including France, Austria, Switzerland and Italy and the combination of the rapidity with which the disease is

drastically reducing elm populations and its geographical extent (if it continues to spread outwards from its strongholds) are perhaps analogous with the pattern of the Neolithic elm decline. Whilst we can only suggest that disease was involved, it is clear that any fungus or other pathogen responsible would, by necessity, have been extremely virulent. C.ulmi is thought to have reached Europe from Asia this century but this is disputed by Rackham (1980) who described tree ring and documentary evidence of earlier outbreaks. Accepting this premise, possible dates for the origin of the disease in Europe can be considered. It is perhaps feasible that it has been indigenous in the elm population for at least as long as the present post-glacial period, migrating with the forests as they spread northwards from their glacial refugia. It could, however, be conjectured that the Neolithic elm decline represents a first attack of the disease in Europe, its effects particularly severe in an elm population which would have had no resistance. Disease epidemics in human populations are always most serious at their first appearance (Zinsser 1934), and an event such as the elm decline would be more typical of a response to a new pathogen than to an aggressive strain of an existing disease.

In view of the predominantly closed forest environment of the early Neolithic, the avoidance of this habitat by both C.ulmi and S.scolytus should be considered. Both would be adversely affected by the cooler, damper microclimate under closed canopy. In such conditions, elm, especially when fallen, is prone to funguses which can thoroughly infest wood more quickly than C.ulmi. The cooler microclimate also hinders the flight of S.scolytus which needs a certain temperature threshold to fly

readily and in woodland, competition from woodpeckers, cuckoos and other predators is greater for wood-boring beetles and larvae. The debate about the actual climatic conditions which prevailed in the early Neolithic continues but insect investigations from the Somerset Levels argue for a period of higher summer temperatures combined with increased continentality (Girling 1984). Although the forest microclimate is relatively protected the warmer summers would have favoured the expansion overall of S.scolytus populations; observations of this beetle in Britain have shown that it was abundant during the hot summer of 1976 (which itself followed a warm, dry summer) and in the succeeding year. 1976 and 1984, another summer when higher than average temperatures were recorded, are both thought to have dramatically extended the spread of Dutch Elm Disease because of the increase in numbers of S.scolytus and the large numbers of days in which its dispersal flights were possible.

The presence in early Neolithic times of S.scolytus indicates that the beetle carrier of the major elm disease was available, but it remains questionable whether disease alone could have accounted for the elm decline. If the pollen evidence suggests a major disease outbreak, there is little sign that it waned and ended. Historic outbreaks of Dutch Elm Disease have ended spontaneously probably as a result of its hybridization with less aggressive strains of the fungus. One hopes that the present epidemic will follow this pattern, although so far there is little sign.

An explanation for the elm decline combining both human and disease factors (Rackham 1980) has a number of advantages over

either agency working in isolation. Elm disease causing the death of trees could provide natural clearings around the forest edges which might facilitate man's encroachment. Dead elms, whether due to disease or felling by man, would greatly increase habitat availability for S.scolytus, thus allowing more rapid spread of the disease. Elms which are growing quickly as is the case after foliage stripping, are more susceptible to C.ulmi and this practice would predispose the trees to infection by the disease. The actual injury caused by the removal of leafy branches for fodder is also likely to be significant as damaged trees are more at risk from the disease. The introduction of grazing animals into woodland could have lead to bark damage through feeding, the injured and dying trees providing more foci for the fungus and beetle. Early forest settlers could thus have assisted the immediate spread of disease in an area of infection by increasing the vulnerability of trees and the incidence of infection. Migration of the communities could also serve to spread the disease over a wider area by transport in timber of the fungus or spore-carrying beetles. Had C.ulmi already been present in the forests, the movement and activities of Neolithic man could have provided impetus for the spread of the fungus and mixing of the gene-pool could have produced a more aggressive strain. On the other hand, if the fungus were not already established in the deciduous forests of N.W.Europe, it is perhaps valid to suggest that man's wider geographic migration was responsible for its introduction. The theory of a new disease in elms with no aquired resistance combined with their increased susceptibility to infection because of man's forestry practices goes some way to explain any catastrophic reduction of elm recorded by the pollen record.

An unequivocal interpretation that a "Dutch Elm Disease" was (in part) responsible for the Neolithic Elm decline cannot be made in the absence of direct identification of C.ulmi in wood of this age. The identification at West Heath Spa in sediments below the elm decline level of S.scolytus does however indicate that the main beetle-carrier of the fungus, prerequisite in the successful spread of the disease, was indeed present. Continued investigations of deposits of this age should provide a fuller understanding of the status of this important beetle, particularly during the elm decline, and add fuel to the debate on the relative importance of man, disease and other possible contributory agents such as climate. It is perhaps valid to introduce a note of caution at this stage. Although these individual factors could singly or in combination be effective in reducing elm pollen levels, the overall impact of introducing change into a balanced ecosystem should not be underestimated. Even minor disturbances to mature, deciduous forest due to human activity or disease could have far reaching consequences. Similarly, variation in one or more climatic parameters might exert an influence which we can not isolate. Continued observation of the effects of the present outbreak of elm disease might help unravel some of the problems encountered in the fossil record of a former epidemic.

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