
Insect Faunas of Late Devensian and Flandrian Age from Church Stretton, Shropshire

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Phil. Trans. R. Soc. Lond. B 1972 **263**, 327-367

doi: 10.1098/rstb.1972.0003

References

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INSECT FAUNAS OF LATE DEVENSIAN AND FLANDRIAN AGE FROM CHURCH STRETTON, SHROPSHIRE

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(Communicated by *F. W. Shotton, F.R.S.* – Received 13 July 1971)

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Invertebrate faunas consisting mainly of insects, from deposits in the Church Stretton valley, are described and discussed. These deposits fall into two periods: (*a*) Late Devensian, which follows an episode of glaciation and precedes a period of accumulation of frost-shattered gravel fans; and (*b*) Flandrian, which post-dates the gravels and has been placed in the post-Glacial pollen zones VI and VII. The faunas of these two episodes are dealt with separately in Parts I and II respectively.

PART I. From two sites in which sequences containing clays, peats and silts were examined five radio-carbon dates are available, the oldest being $13\,555 \pm 620$ years B.P. and the most recent $11\,000 \pm 200$ years B.P. The faunas include a substantial number of species not now found in Shropshire, many not in Britain. Inferences on the changing ecology and thermal environment of the area are drawn from these faunas and are compared with the pollen analytical zones. This comparison shows that, according to the insects, the warmest part of the episode was late zone I, and that zone II (the Allerød), often considered

Vol. 263. B. 852. (Price £1.10; U.S. \$2.86) 32

[Published 10 February 1972]

to be the climatic optimum of the period, appears to have been a time of gradually deteriorating summer temperatures.

PART II. Deposits from three late Flandrian sites are discussed. Although only one radiocarbon date was obtained, of 8101 ± 138 years B.P., pollen analysis was carried out by Rowlands throughout each sequence and this showed that the earliest deposit, at Little Stretton, dated from zone VIa and at all three localities deposition continued into zone VIIb. An examination of the insect assemblages shows that completely different biotopes, from open pasture to dense woodland, were existing side by side in the Church Stretton valley in late Flandrian time. Summer temperatures at least as high as those of today are inferred. The possibility exists that during the period represented here the climate was even warmer than that of the present but until more information is available it is not possible to be more definite on this point.

PART I. LATE DEVENSIAN DEPOSITS

1. INTRODUCTION

The faunas discussed here were collected from sites at two different localities whose relationship is shown in figure 1. The stratigraphy and palynology of the sites have been dealt with in detail by Rowlands (1966) and Rowlands & Shotton (1971), and material for entomological investigation was collected in conjunction with the field work of these two authors.

The first of these deposits, referred to here as C(hurch) S(tretton)₁, consisted of a series of 'peats' and clays underlying valley fan gravels exposed at SO 456941 in the wall of a trench being dug for a main sewer. Samples were taken from a thickness of 1.67 m (5 ft 6 in) visible above standing water in the trench, about $3\frac{1}{2}$ kg (8 lb) of material being collected from each 15 cm layer. From a series of pollen samples collected only a few centimetres away from this section it was determined that the upper 35 cm fell into pollen zone II and the 30 cm below this belonged to zone Ic (Rowlands & Shotton 1971). A preliminary examination of this material showed that it was imperative to collect more before the opportunity was lost and so the site was revisited within a few days. Even so, the trench had been back filled and it was not possible to collect at the same spot as before. Also, the bottom of the trench had become a morass in which accurate work was impossible. A series of samples was collected, therefore, by means of a 10 cm bucket auger from a point about 6 m northeast from the site of CS₁, on a step beside the trench from which the topsoil and most of the fan gravel had been removed, these being impenetrable to the auger. Samples were collected from the base of the fan gravel downwards for 2.9 m, when the proportion of pebbles and water made sample recovery impossible. This series of samples is called here CS₂. At the same time a bulk sample of about $13\frac{1}{2}$ kg (30 lb) was cut from the side of the trench, from what was thought to be the richest part of the section, between 0.76 and 1.22 m below the gravel.

As pollen was not examined from the auger hole, correlation between CS₁ and CS₂ could only be done approximately by comparison of the contained insect faunas and of the lithology. The resulting correlation, shown in table 1 (p. 344) is discussed later.

Under the direction of Professor F. W. Shotton and the late Mr T. H. Whitehead, three boreholes were sunk in the Church Stretton valley to elucidate the Pleistocene stratigraphy of the area (see Rowlands & Shotton 1971). One of these, referred to as RS₂, at SO 459939, encountered organic deposits both above and below fan gravels similar to those of the sewer trench. The upper deposit was of Flandrian age (zones VI and VII) and contained an insect fauna which is discussed in Part II. The lower, consisting of organic silts lying on boulder clay, could be assumed to be of similar Late Devensian age to the subgravel deposits of the sewer trench. These were sampled throughout, the size of the samples depending largely on the exigencies of the drilling operation.

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The position and numbering of the samples collected from all the Devensian sections described above, together with their lithologies, are shown in figure 2.

All the material from these sites was disaggregated, either in water or in hot sodium carbonate solution and washed over a 300 μm sieve to remove the finer material. When the residue

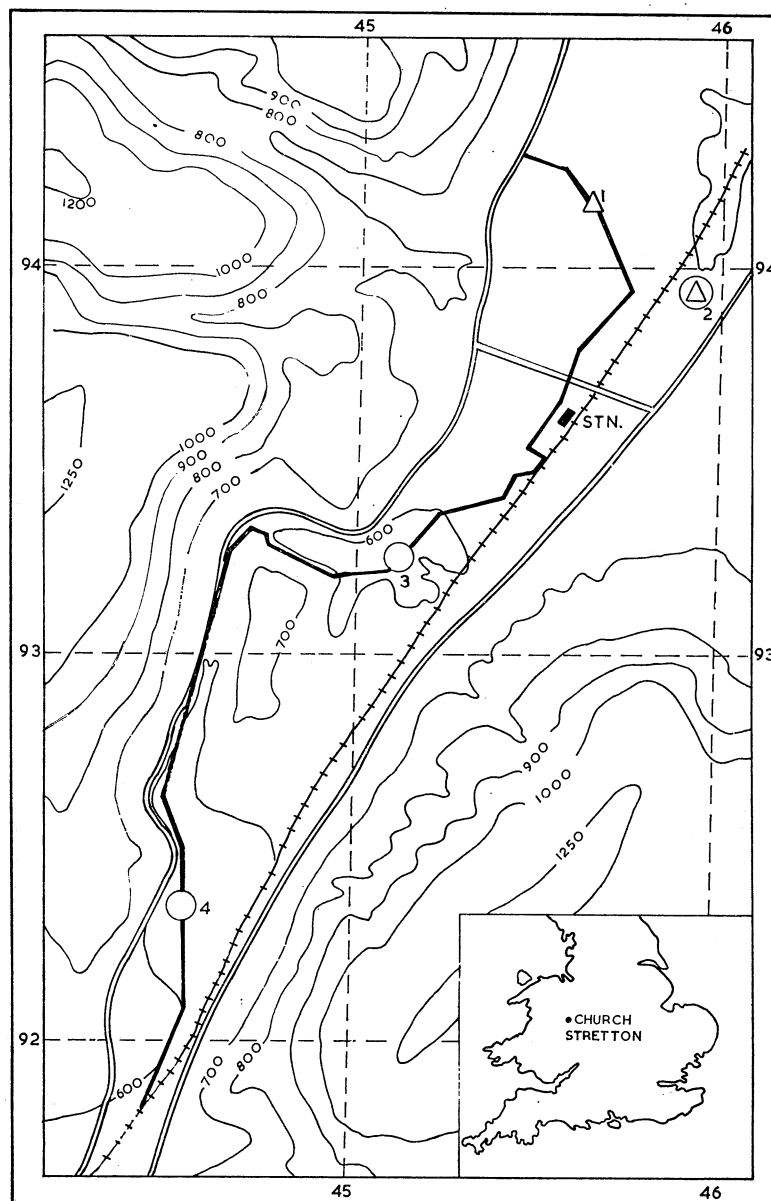


FIGURE 1. Topography of the Church Stretton valley showing the location of the fossil insect sites. Δ , Late Devensian sites; \circ , Flandrian sites. 1 CS_1 and CS_2 , 2 RS_2 , 3 Worldsend, 4 Little Stretton. —, Line of the sewer trench; ----, boundaries of National Grid 1 km squares (Map SO).

consisted of only a small quantity of organic material this was sorted directly under a binocular microscope but if, as in the case of the 'peat', much vegetable matter was left, it was first subjected to paraffin flotation (see Coope & Osborne 1967) and then the flotant sorted. All the invertebrate remains recovered were mounted, either dry or, in a few instances, in canada balsam and the collection is housed in the Geology Department, Birmingham University.

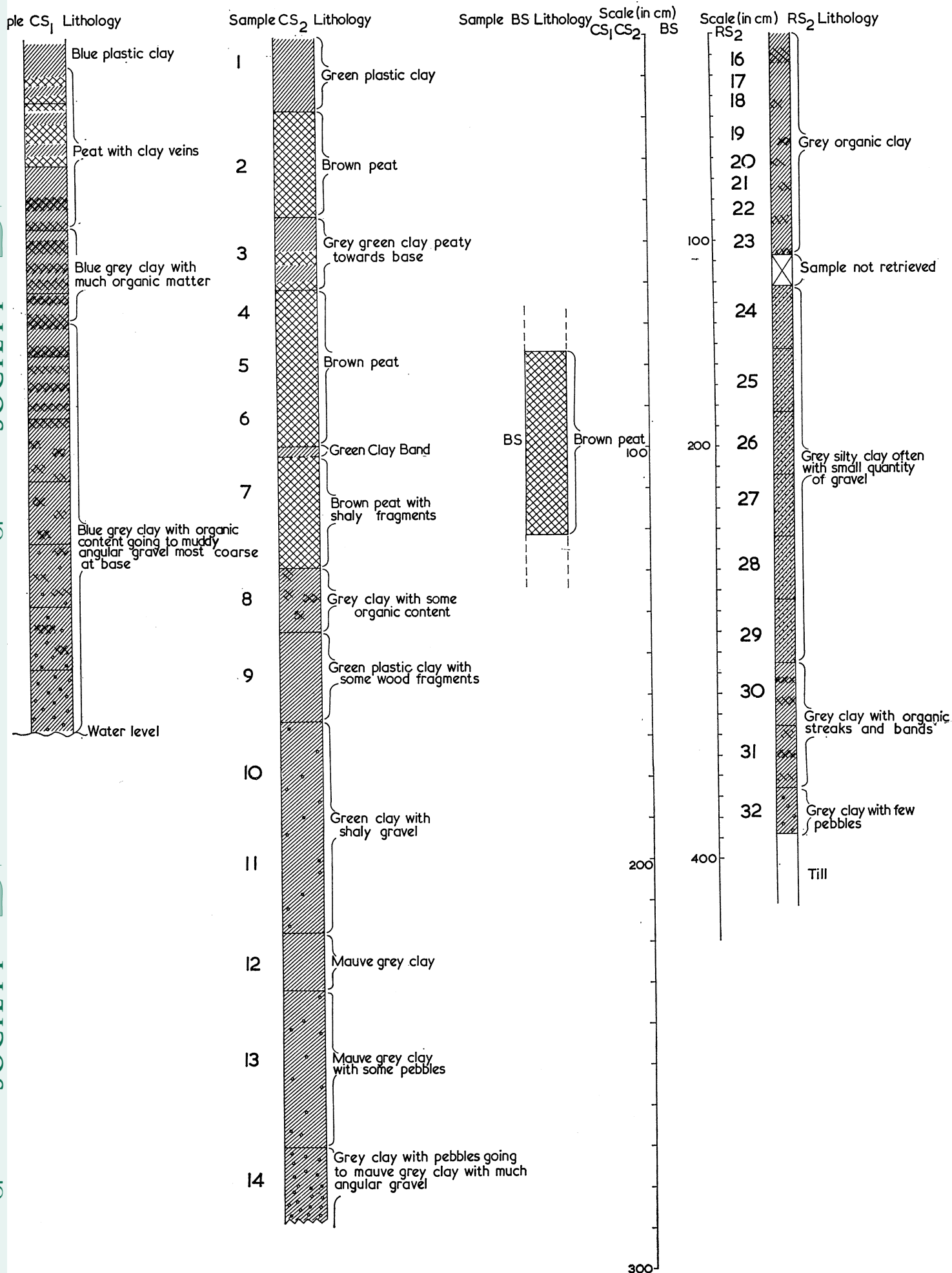


FIGURE 2. Lithologies and sampling intervals of the Late Devonian sections.

2. THE FAUNAS

(a) Faunal lists

A feature of these deposits was the fine state of preservation, not only of the very robust beetle remains, but also of the many fossils of other invertebrate animals. In order to gain a comprehensive picture of the environment of the time an attempt has been made to list as many of these other elements as possible. In some groups, e.g. the Coleoptera, it was possible to estimate the number of individuals represented in each sample but in others, the Polyzoan *Cristatella mucedo* being an example, numbers of fossil fragments recovered do not relate directly to numbers of individuals present. In the following list, therefore, where estimation of minimum numbers of individuals per sample was possible, these are the figures given. The groups dealt with in this way are: Odonata (dragonflies), Raphidiidae (snakeflies), the caddis *Phryganea obsoleta*, the Hemiptera (bugs), the Coleoptera (beetles) and the Formicidae (ants), all of which are insects whose fossil remains are those of the adult animal. In the remainder of the fauna each group has been listed according to what parts were found and the numbers given are as follows:

- 1 *Cristatella mucedo*. Numbers of statoblasts from each sample.
- 2 ?*Lepidurus arcticus*. Numbers of mandibles recovered.
- 3 *Daphnia* sp. Numbers of ephippia per sample.
- 4 *Sialis* sp. Numbers of larval mandibles.
- 5 Trichoptera. Remains of both larvae and imagines of this group were recovered which, with the exception of *Phryganea obsoleta* referred to above, could neither be specifically identified nor grouped in any way. On account of these factors no figures are given and only the samples in which Trichoptera were found are listed.
- 6 Chironomidae. Numbers of larval head capsules.
- 7 Miscellaneous Hymenoptera. Heads and pronota of adult insects constituted the majority of the fossils in this group and these, like the Trichoptera remains, could neither be identified nor associated with each other. The numbers given in the list are those of the most numerous skeletal part per sample.

In a few instances fossil specimens were so abundant that to pick them all out would have been a waste of time. In these cases the letter 'n' is used to show that large numbers of uncounted specimens were present.

For reasons of economy of space a layout using a separate column for each sample has not been used. Instead only those samples from which fossils were recovered are listed against the name of each taxonomic unit, and the number of individuals represented or fragments found follows the sample number after an oblique line (solidus). This system is also used in the faunal list in part II of this paper.

In the following list and also in that in part II the insect nomenclature is based primarily on Kloet & Hincks (1945). Names of non-British species, indicated in the lists by an asterisk (*) are taken mainly from Hansen *et al.* (1960), Hoffmann (1950-62), Reitter (1908-16) and Stichel (1955).

FAUNAL LIST

| | BS | CS ₁ | CS ₂ | RS ₂ |
|---|----|---------------------------------------|---|--|
| POLYZOA | | | | |
| <i>Cristatella mucedo</i> Cuvier | — | E/3, D/55 | 7/1 | 32/n, 31/n, 30/1 29/3, 28/1 |
| CRUSTACEA | | | | |
| *? <i>Lepidurus arcticus</i> Pal. | — | — | 1/40 | — |
| <i>Daphnia</i> sp. | — | K/2, I/7, H/2, G/7, C/5, B/n, A/11 | 14/4, 13/2, 6/1, 5/32 4/36, 3/18, 2/50, 1/13 | 32/n, 31/n, 30/26, 29/10, 25/2, 24/1 22/2, 21/2, 20/11, 19/5, 18/3, 17/8, 16/9. |
| INSECTA | | | | |
| Megaloptera | | | | |
| <i>Sialis</i> sp. | — | E/1, D/3 | 14/1 | 31/7 |
| <i>Agulla xanthostigma</i> (Schummel) | 2 | — | — | — |
| Odonata | | | | |
| probably Zygoptera | 10 | D/3, C/2, B/1 | 8/1, 7/1, 6/1, 5/1, 4/1 3/1, 2/1 | 32/1 |
| Trichoptera | | | | |
| <i>Phryganea obsoleta</i> Hagen | — | C/2, B/1 | — | — |
| gen. et sp. indet. | — | K, I, G, D, C, B | 5, 4, 3, 2, 1 | 31, 30, 29, 28, 25, 22, 21, 16 |
| Hemiptera—Heteroptera | | | | |
| <i>Legnotus picipes</i> (Fall.) | 1 | — | 12/1 | — |
| <i>Sehirus luctuosus</i> M. & R. | 4 | D/1, C/1, B/5 | 9/1, 8/1, 4/1, 2/1 | — |
| <i>Odontoscelis fuliginosa</i> (L.) | 2 | E/1 | 9/1 | — |
| * <i>Sciocoris</i> cf. <i>homalonotus</i> Fb. | 4 | — | — | — |
| * <i>Plinthisus pusillus</i> (Sch.) | — | — | — | 32/4, 31/4 |
| Lygaeidae indet. | 8 | H/1, E/1, C/1 | 13/1, 9/6, 8/3, 3/1 | 32/3, 31/3 |
| <i>Dictyonota</i> ? <i>fuliginosa</i> Costa | — | J/1, E/1 | — | — |
| <i>Onchocila</i> sp. | — | — | — | 18/1 |
| Tingidae indet. | — | E/2, D/1 | 12/1 | — |
| <i>Gerris</i> sp. | 4 | — | 7/1 | — |
| <i>Saldula</i> sp. | 9 | F/1 | 9/1, 6/3, 5/1 | — |
| <i>Chartoscirta</i> sp. | 7 | — | 6/1, 5/1, 4/1 | — |
| <i>Sigara</i> ? <i>nigrolineata</i> Fieb. | — | — | — | 31/1 |
| <i>Sigara</i> sp. | — | — | — | 31/2 |
| Hemiptera—Homoptera | | | | |
| gen. et sp. indet. | 34 | E/3 | 9/1, 8/1, 5/12, 4/1, 3/1 | — |
| Coleoptera | | | | |
| Carabidae | | | | |
| <i>Cicindela campestris</i> L. | 1 | C/1, B/1 | 9/1 | — |
| <i>Carabus clathratus</i> L. | 1 | — | — | — |
| <i>C. problematicus</i> Hbst. | — | C/1 | 5/1 | — |
| <i>Leistus terminatus</i> (Hellwig) | 2 | C/1, B/3 | 8/1, 5/1, 4/1 | — |
| <i>Nebria nivalis</i> Payk. | — | — | — | 16/1 |
| <i>Notiophilus aestuans</i> Mots. | — | I/1, F/1 | 10/1 | — |
| <i>N. aquaticus</i> L. | — | — | — | 17/2 |
| <i>N. hypocrita</i> Putz. | 1 | — | 8/1 | — |
| <i>N. palustris</i> Dufts. | — | — | 6/1 | — |
| <i>Notiophilus</i> sp. | — | E/1, D/1, C/1, B/1 | 11/2, 5/2 | 32/1, 19/1 |
| <i>Helobium multipunctatum</i> (L.) | 1 | C/1 | — | — |
| <i>Elaphrus</i> ? <i>cupreus</i> Dufts. | 1 | — | — | — |
| <i>Elaphrus</i> sp. | — | — | — | 19/1 |
| <i>Loricera pilicornis</i> (F.) | 1 | — | 5/1 | — |
| <i>Clivina fossor</i> (L.) | — | — | 3/1 | — |
| <i>Dyschirius aeneus</i> (Dej.) | 1 | D/1 | — | — |
| <i>D. globosus</i> (Hbst.) | — | C/2, B/1 | — | 32/1 |
| <i>Bembidion varium</i> (Ol.) | 1 | — | — | — |
| <i>B. obliquum</i> Sturm | — | — | 9/1 | — |
| <i>B. quadrimaculatum</i> (L.) | — | G/1 | — | — |
| <i>B. doris</i> (Pz.) | 16 | E/2, D/4, C/5, B/6 | 8/2, 7/2, 6/3, 5/1, 4/3 3/1, 2/1 | — |

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FAUNAL LIST (cont.)

| | BS | CS ₁ | CS ₂ | RS ₂ |
|---|----|---|------------------------------------|------------------|
| Coleoptera (cont.) | | | | |
| Carabidae (cont.) | | | | |
| <i>B. octomaculatum</i> (Gze.) | — | I/1, F/1, E/1 | 8/1 | — |
| <i>B. aeneum</i> Germ. | — | E/1, D/1, B/1 | 13/1, 11/1, 10/1, 8/1, 5/1, 3/1 | — |
| <i>B. unicolor</i> Chaud. or <i>guttula</i> (F.) | 1 | B/5 | — | 31/3 |
| * <i>B. dauricum</i> Mots. | — | — | — | 16/1 |
| * <i>B. ibericum</i> Ploc. or <i>grisvardi</i> | 1 | — | 9/1 | — |
| <i>Bembidion</i> sp. | 3 | J/1, I/1, H/2, G/2, F/2, E/2, D/3, B/1 | 10/1, 8/2, 5/1, 1/1 | 18/1 |
| <i>Trechus secalis</i> (Payk.) | 5 | C/1, B/2, A/2 | 7/1, 4/1 | — |
| <i>T. quadristriatus</i> (Sch.) or <i>obtusus</i> Er. | 1 | B/2 | 7/1, 6/2, 4/1, 2/1 | — |
| <i>T. rubens</i> (F.) | — | C/1 | — | — |
| <i>Patrobus septentrionis</i> Dej. | 1 | C/1 | — | — |
| <i>P. assimilis</i> Chaud. | 3 | C/1, B/3, A/1 | 7/1, 5/1, 2/1 | — |
| <i>Patrobus</i> sp. | — | A/1 | 3/1 | — |
| <i>Harpalus</i> ? <i>rubripes</i> (Dufts.) | — | — | 3/1 | — |
| <i>Harpalus</i> sp. | 2 | — | — | — |
| <i>Amara equestris</i> (Dufts.) | 3 | — | — | — |
| * <i>A. torrida</i> (Ill.) | — | — | — | 31/1 |
| <i>Amara</i> sp. | 1 | E/1, D/2 | 8/1, 6/1 | 17/1 |
| <i>Feronia nigrita</i> (F.) | — | — | 3/1 | — |
| <i>F. gracilis</i> (Dej.) | — | A/1 | 4/2 | — |
| <i>F. strenua</i> (Pz.) | — | D/1 | — | — |
| <i>F. strenua</i> (Pz.) or <i>diligens</i> Sturm | 3 | A/1 | 2/1 | — |
| <i>Feronia</i> sp. | 2 | B/3 | 9/1, 5/3 | — |
| <i>Calathus fuscipes</i> (Goeze) | 2 | — | — | — |
| <i>C. ?melanocephalus</i> (L.) | 1 | E/1, D/1, C/1, B/2 | 9/1, 3/1 | 32/1, 31/1 |
| <i>Agonum fuliginosum</i> (Pz.) | 8 | C/?1 | 4/?2, 2/2 | — |
| <i>A. gracile</i> (Gyll.) | 2 | — | — | — |
| <i>A. thoreyi</i> Dej. | 1 | — | — | — |
| <i>Agonum</i> sp. | 3 | D/2, B/3 | 7/1, 6/2, 5/6, 4/3, 3/1 | — |
| <i>Lebia chlorocephala</i> (Hoff.) | 1 | — | — | — |
| <i>L. ?crux-minor</i> (L.) | 1 | — | — | — |
| <i>Dromius linearis</i> (Ol.) | 1 | — | — | — |
| <i>Lionychus quadrillum</i> (Dufts.) | — | B/1 | — | 32/1 |
| * <i>Cymindis angularis</i> Gyll. | — | E/1, D/2, B/1 | 9/1, 8/1 | — |
| Halipidae | | | | |
| <i>Haliplus</i> sp. | — | B/1 | — | 31/1 |
| Dytiscidae | | | | |
| <i>Laccophilus</i> sp. | — | B/1 | — | — |
| <i>Hygrotus inaequalis</i> (F.) | — | D/2 | 9/1 | — |
| <i>Coelambus impressopunctatus</i> (Schall.) | — | D/1 | — | — |
| <i>Deronectes assimilis</i> (Payk.) | — | — | — | 32/2 |
| <i>D. ?griseostriatus</i> (Deg.) | — | J/1, I/1 | — | — |
| <i>Hydroporus</i> ? <i>granularis</i> (L.) | 1 | — | — | — |
| <i>H. dorsalis</i> (F.) | 4 | A/1 | 6/1, 4/1 | — |
| <i>Hydroporus</i> sp. | 19 | I/1, H/1, D/9, C/4, B/3 A/1 | 14/1, 5/1, 4/10, 2/2, 1/1 | 28/1, 25/1, 19/1 |
| <i>Agabus affinis</i> (Payk.) or <i>unguicularis</i> Thom. | — | — | 4/2 | — |
| <i>A. undulatus</i> (Schrank) | 1 | — | — | — |
| <i>A. arcticus</i> (Payk.) | — | — | — | 31/3 |
| <i>A. sturmii</i> (Gyll.) | 2 | — | — | — |
| <i>A. bipustulatus</i> (L.) | 2 | D/1, B/1 | 7/1, 6/1 | — |
| <i>Agabus</i> sp. | 28 | B/1, A/1 | 7/1, 6/1, 4/1, 3/2, 2/1 | — |
| <i>Ilybius</i> sp. | 14 | E/1, D/1, C/1, B/1, A/2 | 6/2, 5/1, 2/1 | 31/1 |

FAUNAL LIST (*cont.*)

| | BS | CS ₁ | CS ₂ | RS ₂ |
|-------------------------------------|----|--------------------------------|---|--|
| Coleoptera (<i>cont.</i>) | | | | |
| Dytiscidae (<i>cont.</i>) | | | | |
| <i>Rantus</i> sp. | 2 | D/1, A/1 | 8/1, 4/2 | — |
| <i>Colymbetes</i> sp. | 1 | D/1, C/1 | 7/1 | 31/1 |
| <i>Dytiscus</i> sp. | 3 | C/1 | — | — |
| <i>Graphoderes</i> sp. | 1 | — | 8/1 | — |
| <i>Acilius sulcatus</i> (L.) | 1 | — | — | — |
| Gyrinidae | | | | |
| <i>Gyrinus minutus</i> F. | 1 | D/1 | 4/1 | — |
| <i>Gyrinus</i> sp. | 1 | D/1, C/1 | 9/1, 8/1, 7/1 | 32/1, 31/1 |
| Hydrophilidae | | | | |
| <i>Ochthebius bicolon</i> Germ. | 1 | — | — | — |
| <i>O. minimus</i> F. | 79 | E/3, D/27, B/19, A/5 | 8/10, 7/2, 5/10, 4/7 | — |
| * <i>O. foveolatus</i> Germ. | — | — | 9/1 | — |
| <i>Ochthebius</i> sp. | — | H/1, C/3 | 9/1, 5/5, 2/1 | 31/1 |
| <i>Hydraena riparia</i> Kug. | 7 | D/9, C/2, A/2 | 8/3, 5/2, 4/2 | 31/2 |
| <i>H. gracilis</i> Germ. | 2 | — | 5/1 | 32/2, 31/4 |
| <i>Hydraena</i> sp. | — | H/1 | 9/1, 7/1, 2/1 | — |
| <i>Limnebius</i> sp. | 10 | F/1, E/1, D/5, C/3 B/2, A/2 | 11/1, 10/3, 9/2, 8/1, 7/1, 6/1, 5/1, 4/2 | 31/1 |
| <i>Helophorus nubilus</i> F. | 2 | E/1, D/2, B/2 | 9/1, 8/1 | — |
| <i>H. aquaticus</i> (L.) | 7 | D/1, A/1 | 3/1 | — |
| <i>H. brevipalpis</i> Bedel | 4 | D/2, B/1 | 1/1 | — |
| <i>H. flavipes</i> F. | 37 | D/3, C/5, B/1 | 5/1, 4/1 | — |
| <i>H. nanus</i> Sturm | 2 | E/1, D/1, B/4 | 2/?1 | — |
| <i>H. strigifrons</i> Th. | ?1 | — | 6/1 | 24/?1 |
| * <i>H. glacialis</i> Villa | — | — | — | 29/1, 27/1, 25/1, 22/1, 21/2, 20/2, 19/1, 18/2, 17/3, 16/2 |
| * <i>H. fennicus</i> Payk. | — | — | — | 29/?1, 28/1, 19/1 |
| <i>Helophorus</i> sp. | — | — | 9/2, 8/4, 7/1 | 31/2, 27/1 |
| <i>Hydrochus brevis</i> (Hbst.) | 2 | B/2 | 5/1, 4/1 | — |
| <i>Coelostoma orbiculare</i> (F.) | 1 | — | — | — |
| <i>Cercyon</i> sp. | 42 | D/4, C/2, B/12, A/4 | 11/1, 8/2, 7/1, 6/8, 5/4, 4/3, 2/2 | 31/2, 27/1 |
| <i>Hydrobius fuscipes</i> (L.) | 10 | D/2, A/2 | 7/1, 6/1, 4/1 | — |
| <i>Anacaena</i> sp. | 1 | — | — | — |
| <i>Laccobius</i> sp. | 8 | D/1 | 5/1 | 31/1 |
| <i>Enochrus</i> sp. | — | D/2 | 7/1, 6/1 | — |
| <i>Berosus affinis</i> Brulle | 3 | — | 4/1 | — |
| Silphidae | | | | |
| <i>Thanatophilus</i> sp. | 1 | — | — | — |
| <i>Silpha tyrolensis</i> Laich. | 2 | — | — | — |
| <i>Phosphuga atrata</i> (L.) | 3 | D/1, A/1 | 7/1, 6/1 | — |
| <i>Choleva</i> or <i>Catops</i> sp. | — | D/1, B/1 | — | — |
| Leiodidae | | | | |
| <i>Leoides</i> sp. | 1 | D/1 | — | 31/1 |
| <i>Agathidium laevigatum</i> Er. | — | D/1 | — | — |
| <i>A. ?marginatum</i> Sturm | — | — | — | 32/1 |
| <i>Agathidium</i> sp. | 3 | — | 6/1 | — |
| Ptiliidae | | | | |
| <i>Acrotrichis</i> sp. | 1 | — | 5/1, 4/1, 2/3 | — |
| Staphylinidae | | | | |
| <i>Proteinus</i> sp. | — | — | — | 25/1 |
| <i>Eusphalerum minutum</i> (F.) | 10 | — | 5/1, 4/2 | — |
| <i>Eusphalerum</i> sp. | — | B/2 | — | — |
| <i>Omalius caesum</i> Grav. | — | B/2 | — | — |
| <i>O. excavatum</i> Steph. | — | F/1, E/1, D/1, B/1 | 2/1 | — |
| <i>Deliphrum tectum</i> (Payk.) | — | — | 2/1 | — |
| <i>Olophrum consimile</i> (Gyll.) | 16 | B/3 | 6/4, 5/3, 4/2, 3/4, 2/6 | — |
| <i>O. fuscum</i> | 3 | — | — | 28/2 |

INSECT FAUNAS OF LATE DEVENSIAN AND FLANDRIAN AGE 335

FAUNAL LIST (cont.)

| | BS | CS ₁ | CS ₂ | RS ₂ |
|---|----|---------------------------------|---|--|
| Coleoptera (cont.) | | | | |
| Staphylinidae (cont.) | | | | |
| <i>Olophrum</i> sp. | — | D/1, A/3 | 4/5, 1/1 | 16/2 |
| <i>Arpedium brachypterum</i> (Grav.) | — | — | 1/1 | 30/1, 29/3, 28/1, 22/3, 21/7, 20/1, 19/1, 17/2, 16/3 |
| <i>Acidota crenata</i> (F.) | 3 | D/2, B/1 | 8/1, 7/2 | — |
| <i>A. cruentata</i> (Mannh.) | 1 | D/1, B/3, A/1 | 1/1 | — |
| <i>Lesteva ?longelytrata</i> (Gze.) | 4 | G/1, D/11, C/4, B/4 | 10/2, 9/3, 7/2, 6/3 | — |
| <i>L. pubescens</i> Mannh. | — | — | 3/1 | — |
| <i>Geodromicus</i> sp. | — | K/1 | — | — |
| <i>Anthophagus caraboides</i> (L.) | 4 | E/1, D/2, C/2 | — | — |
| * <i>A. bicornis</i> (Block) | 8 | — | 3/1 | — |
| <i>Eudectes whitei</i> Sharp | — | — | — | 18/1 |
| * <i>Boreaphilus henningianus</i> Sahlb. | — | — | 1/1 | 20/1, 17/1 |
| * <i>Pycnoglypta lurida</i> (Gyll.) | — | C/1 | 3/1 | — |
| <i>Trogophloeus</i> sp. | 21 | B/3, A/4 | 9/1, 8/1, 6/1, 5/5, 4/3 | 32/1, 31/1 |
| <i>Oxytelus rugosus</i> (F.) | 2 | B/2, A/1 | 5/1, 4/1 | — |
| <i>O. ?laquaeatus</i> (Marsh.) | 1 | — | — | — |
| <i>O. nitidulus</i> Grav. | 1 | — | 8/1, 5/1 | — |
| <i>Platystethus cornutus</i> (Grav.) | 1 | G/1, F/2, E/1, D/1 | 11/1, 10/1, 9/6, 8/2 | — |
| <i>Bledius</i> sp. | 1 | D/1 | 9/3, 8/1 | 31/1 |
| <i>Stenus junco</i> F. | 12 | D/2, C/2, B/6, A/2 | 6/4, 5/1, 4/2 | — |
| <i>S. ?crassus</i> Steph. | — | — | 2/1 | — |
| <i>S. binotatus</i> Ljungh | 1 | — | — | — |
| <i>Stenus</i> sp. | 18 | H/1, D/3, C/1, B/6, A/3 | 8/1, 6/3, 5/5, 4/5, 3/2, 2/3 | 32/1, 30/1, 16/1 |
| <i>Euaesthetus bipunctatus</i> Ljungh | — | E/1 | 8/1 | 31/1 |
| <i>E. ruficapillus</i> Bois. & Lac. | 1 | J/2/1 | — | — |
| <i>E. laeviusculus</i> Mannh. | — | D/2, C/1, B/2 | 8/1 | — |
| <i>Scopaeus</i> sp. | — | — | 8/1 | — |
| <i>Lathrobium terminatum</i> Grav. | 5 | D/2 | 6/3, 5/1, 3/1 | — |
| <i>Lathrobium</i> sp. | 6 | E/1, D/1, C/1, B/2 | 8/1, 7/2, 6/2 | — |
| <i>Leptacinus sulcifrons</i> (Steph.) | — | — | 2/1 | — |
| <i>Xantholinus tricolor</i> (F.) | — | D/1 | — | — |
| <i>X. linearis</i> (Ol.) or <i>longiventris</i> Heer | 7 | D/4, C/1, B/5 | — | — |
| <i>Xantholinus</i> sp. | 2 | B/1 | — | — |
| <i>Gyrohyphus punctulatus</i> Gze. | — | C/1 | — | — |
| <i>Gyrohyphus</i> sp. | — | B/2 | — | — |
| <i>Philonthus decorus</i> (Grav.) | 3 | — | — | — |
| <i>P. ?micans</i> | — | B/4 | — | — |
| <i>Philonthus</i> sp. | 7 | — | 11/1, 5/3 | — |
| <i>Gabrius</i> sp. | — | G/1, D/2 | 13/1, 6/2, 5/3, 4/2 | — |
| <i>Quedius</i> sp. | 4 | D/1, B/2 | 13/1, 12/1 | 32/1 |
| <i>Tachyporus? obtusus</i> (L.) | — | — | — | 29/1 |
| <i>Tachyporus</i> sp. | — | — | 9/1, 5/1, 4/1 | — |
| Tachyporinae indet. | 3 | — | 7/1 | 19/1, 16/1 |
| <i>Tachinus ?laticollis</i> Grav. | 1 | — | — | — |
| <i>T. ?marginellus</i> (F.) | 2 | — | — | — |
| <i>T. corticinus</i> Grav. | 2 | — | — | — |
| <i>T. elongatus</i> Gyll. | 2 | A/1 | — | — |
| <i>Tachinus</i> sp. | — | C/2 | 7/1, 6/2, 5/2, 3/2 | — |
| <i>Gymnusa brevicollis</i> (Payk.) | 2 | — | 6/1 | 32/1 |
| <i>G. variegata</i> Kies. | — | B/1 | — | — |
| <i>Zyras humeralis</i> (Grav.) | — | C/1 | — | — |
| <i>Lomechusoides strumosa</i> (F.) | — | D/2 | — | — |
| Aleocharinae indet. | 72 | I/1, H/1, G/1, F/1 D/16, C/5 | 13/2, 12/1, 11/1, 8/6, 6/2, 5/11, 4/19, 3/3, 2/19 | 30/3, 29/1, 28/4, 27/1, 25/2, 24/1, 23/1, 22/1, 21/5, 20/4, 19/10, 18/8, 17/6, 16/5 |

FAUNAL LIST (*cont.*)

| | BS | CS ₁ | CS ₂ | RS ₂ |
|--|-----|-----------------|---------------------------------|------------------|
| Coleoptera (<i>cont.</i>) | | | | |
| Histeridae | | | | |
| <i>Hister</i> sp. | — | D/3 | 9/1, 8/2 | 32/1 |
| Cantharidae | | | | |
| <i>Cantharis rufa</i> L. | — | — | 9/1 | — |
| <i>Cantharis</i> sp. | 2 | C/1 | 8/1, 7/1 | 32/1 |
| <i>Rhagonycha</i> sp. | 2 | — | — | — |
| Dasytidae | | | | |
| <i>Dolichosoma lineare</i> Rossi | — | — | 6/1 | — |
| Elateridae | | | | |
| <i>Elater</i> sp. | — | A/1 | — | — |
| * <i>Hypnoidus rivularis</i> Gyll. | — | E/1 | 10/1 | 32/1, 31/1, 17/1 |
| <i>Agriotes obscurus</i> (L.) | 4 | B/1 | 4/1 | — |
| <i>Corymbites</i> sp. | — | — | 4/1 | — |
| <i>Dalopius marginatus</i> (L.) | 3 | — | — | — |
| gen. et sp. indet. | — | K/1 | 6/1 | — |
| Eucnemidae | | | | |
| <i>Dirhagus pygmaeus</i> (F.) | 1 | — | — | — |
| Buprestidae | | | | |
| <i>Trachys</i> sp. | 1 | — | — | — |
| Helodidae | | | | |
| gen. et sp. indet. | — | D/1, B/15, A/12 | 6/3, 5/9, 4/11, 3/3, 2/4 | — |
| Dryopidae | | | | |
| <i>Dryops</i> sp. | — | D/1 | 9/1, 8/3, 7/1 | — |
| <i>Elmis maugei</i> Bedel | — | — | — | 31/1 |
| <i>Esolus parallelipedus</i> (Muell.) | 1 | D/1 | 4/1, 3/1 | 31/3 |
| <i>Limnius troglodytes</i> Gyll. | ? 1 | D/?2 | — | 32/1, 31/2 |
| <i>Riolus nitens</i> (Muell.) | — | — | — | 32/1, 31/5 |
| <i>Latelmis volckmarii</i> (Pz.) | — | D/1 | — | 31/7 |
| Georissidae | | | | |
| <i>Georissus crenulatus</i> Rossi | — | — | 8/1 | 32/1 |
| Heteroceridae | | | | |
| <i>Heterocerus</i> sp. | 1 | — | — | — |
| Byrrhidae | | | | |
| <i>Simplocaria semistriata</i> (F.) | — | F/1, D/1, C/2 | 11/1, 7/1 | 32/2, 31/1 |
| <i>Morychus aeneus</i> (F.) | — | D/1 | — | — |
| <i>Byrrhus ? fasciatus</i> (Forst.) | 1 | D/2, C/1 | 9/2 | — |
| <i>B. arietinus</i> Steff. | — | C/1, B/1 | — | — |
| <i>B. pilula</i> L. | — | B/1 | — | — |
| <i>Byrrhus</i> sp. | — | D/1, A/1 | 8/1 | — |
| <i>Porcinolus murinus</i> (F.) | — | E/1, D/3, C/1 | — | — |
| Nitidulidae | | | | |
| <i>Brachypterolus pulicarius</i> (L.) | 3 | C/1, B/1 | 5/1 | — |
| <i>Meligethes</i> sp. | 1 | — | — | — |
| Cucujidae | | | | |
| <i>Monotoma conicollis</i> Aube | — | B/1 | — | — |
| * <i>Airaphilus elongatus</i> Gyll. | — | H/1, D/1 | — | 32/2, 31/3 |
| Cryptophagidae | | | | |
| <i>Cryptophagus</i> sp. | 1 | E/1, B/2 | 5/1 | — |
| <i>Atomaria</i> sp. | 15 | B/4, A/14 | 7/2, 6/6, 5/2, 4/4, 3/2, 2/1 | — |
| Phalacridae | | | | |
| <i>Phalacrus nigrinus</i> (Marsh.) | 24 | B/11, A/4 | 6/4, 5/2, 4/6 | — |
| <i>Phalacrus</i> sp. | — | E/1 | — | — |
| Lathridiidae | | | | |
| <i>Lathridius lardarius</i> (Deg.) | — | B/1 | — | — |
| <i>Enicmus</i> sp. | — | A/1 | 5/1 | — |
| <i>Corticaria</i> group | 2 | B/4, A/5 | 6/3, 5/1, 3/1, 2/1 | — |
| Colydiidae | | | | |
| <i>Myrmecixenus vaporariorum</i> G.M. | — | B/1 | — | — |

INSECT FAUNAS OF LATE DEVENSIAN AND FLANDRIAN AGE 337

| FAUNAL LIST (<i>cont.</i>) | | | | |
|--|----|--|--|--------------------------------------|
| | BS | CS ₁ | CS ₂ | RS ₂ |
| Coleoptera (<i>cont.</i>) | | | | |
| Colydiidae | | | | |
| <i>Orthocerus clavicornis</i> (L.) | — | D/2 | — | — |
| Coccinellidae | | | | |
| <i>Scymnus</i> sp. (sens. lat.) | 5 | K/1, I/1, G/1, F/1, E/2, D/1, A/2 | 11/1, 5/1 | — |
| <i>Coccinella</i> cf. <i>septempunctata</i> L. | 1 | C/1, B/2 | 13/1, 9/1 | — |
| Aspidiphoridae | | | | |
| <i>Aspidiphorus orbiculatus</i> Gyll. | — | B/1, A/1 | — | — |
| Ciidae | | | | |
| <i>Cis</i> ? <i>boleti</i> (Scop.) | 1 | — | — | — |
| Anthicidae | | | | |
| <i>Anthicus</i> sp. | — | — | — | 32/1 |
| Mordellidae | | | | |
| <i>Mordellistena</i> sp. | 1 | — | — | — |
| Tenebrionidae | | | | |
| <i>Crypticus quisquilius</i> (L.) | — | — | 4/1 | — |
| Scarabaeidae | | | | |
| <i>Geotrupes</i> sp. | — | D/1 | — | — |
| * <i>Aphodius obscurus</i> (F.) | 1 | — | — | — |
| <i>Aphodius</i> sp. | 6 | K/1, I/1, H/1, G/1, F/3, E/2, D/3, C/2, B/1, A/1 | 14/1, 13/3, 12/2, 11/3, 10/4, 9/1, 8/3, 4/1, 3/2, 2/1, 1/1 | 32/3, 23/1 |
| <i>Serica brunnea</i> (L.) | 11 | A/1 | 4/1 | — |
| <i>Potosia cuprea</i> (F.) | — | B/1 | 6/1 | — |
| Cerambycidae | | | | |
| <i>Lamia textor</i> (L.) | — | B/1 | — | — |
| Chrysomelidae | | | | |
| <i>Macrolea</i> sp. | — | — | — | 31/2 |
| <i>Donacia versicolorea</i> (Brahm) | 9 | D/1, C/4 | 8/1, 7/3, 4/1 | — |
| <i>D. obscura</i> Gyll. | 13 | D/2 | 8/1, 5/1, 4/1 | — |
| <i>D. ? simplex</i> F. | 6 | — | — | — |
| <i>Donacia</i> sp. | — | — | — | 31/2 |
| <i>Plateumaris sericea</i> (L.) | 30 | D/2, C/3, B/2, A/2 | 7/3, 5/2 | — |
| * <i>Chrysolina ? limbata</i> F. | 1 | A/1 | — | — |
| <i>Chrysolina</i> sp. | — | — | 9/1 | — |
| * <i>Adoxus obscurus</i> L. | 3 | D/5, B/6, A/1 | 8/5, 7/1, 6/2, 1/1 | — |
| <i>Phaedon</i> sp. | — | — | 5/1 | — |
| <i>Prasocuris phellandrii</i> (L.) | 2 | D/2 | — | — |
| <i>Phyllodecta</i> sp. | 8 | — | — | 18/1, 17/1 |
| <i>Galeruca tanacetii</i> (L.) | — | D/1, C/1 | — | — |
| <i>Haltica</i> sp. | — | D/1 | — | — |
| <i>Chalcoides</i> sp. | 5 | — | 6/1 | — |
| <i>Mantura matheusii</i> (Curtis) | 2 | — | — | — |
| <i>Mantura</i> sp. | — | D/1 | 9/1, 8/1 | — |
| <i>Chaetocnema</i> sp. | — | G/1, F/1 | 13/1, 12/1 | — |
| Bruchidae | | | | |
| <i>Bruchus ? loti</i> Payk. | — | B/1 | — | — |
| <i>Bruchidius unicolor</i> (Ol.) | 4 | E/2 | — | — |
| <i>B. unicolor</i> var. <i>debilis</i> (Gyll.) | | C/1, B/1 | 9/1, 8/1, 7/1 | — |
| Curculionidae | | | | |
| <i>Caenorhinus tomentosus</i> (Gyll.) | 1? | D/1 | — | — |
| <i>Deporaus betulae</i> (L.) | — | — | 4/1 | — |
| <i>Apion curtirostre</i> Germ. | — | — | 5/1, 4/1 | — |
| <i>Apion</i> cf. <i>platalea</i> Germ. | 1 | — | — | — |
| <i>Apion</i> sp. | 7 | F/1, D/1, C/1, B/8, A/3 | 9/1, 8/5, 7/2, 6/1, 1/1 | 32/2, 31/3, 19/1, 18/1 17/1, 16/1 |
| <i>Otiorrhynchus rugifrons</i> (Gyll.) | 1 | D/3, C/1, B/1 | 8/1, 5/1, 3/1, 2/1 | — |
| <i>O. ovatus</i> (L.) | 2 | C/1, B/10 | 6/1, 4/1 | 31/1 |
| <i>Trachyphloeus bifoveolatus</i> (Beck) | — | D/1, C/21 | — | — |

FAUNAL LIST (*cont.*)

| | BS | CS ₁ | CS ₂ | RS ₂ |
|--|----|--------------------------------------|---------------------------|--|
| Coleoptera (<i>cont.</i>) | | | | |
| Curculionidae (<i>cont.</i>) | | | | |
| <i>Phyllobius</i> sp. | 6 | D/1, C/1, B/2, A/1 | 2/1 | — |
| <i>Brachysomus echinatus</i> (Bonsd.) | 2 | A/7 | 3/3, 2/2 | — |
| <i>Strophosomus</i> sp. | — | A/1 | — | — |
| <i>Barynotus squamosus</i> Germ. | 1 | — | — | — |
| <i>Sitona decipiens</i> (Lind.) | 2 | D/?1, C/?1 | 10/1, 9/?1, 8/?1 | 32/5, 31/5 |
| <i>Sitona</i> sp. | — | — | 4/1 | — |
| * <i>Cyphocleonus trisulcatus</i> Hbst. | — | B/2 | — | — |
| <i>Bagous</i> sp. | 1 | D/2, B/1 | 9/1 | 32/1, 31/4 |
| <i>Dorytomus</i> sp. | — | — | 4/1 | — |
| <i>Notaris aethiops</i> (F.) | — | A/1 | 6/1 | — |
| <i>Grypidius equiseti</i> (F.) | 1 | — | — | — |
| <i>Phytonomus arator</i> (L.) | — | — | 8/1 | — |
| <i>P. plantaginis</i> (Deg.) | — | D/1 | — | — |
| <i>Cryptorrhynchidius lapathi</i> (L.) | 1 | D/1, C/1, B/1 | 8/1, 6/1 | — |
| <i>Limnobaris pilistriata</i> (Steph.) | 2 | — | 6/1, 5/1 | — |
| <i>Ceuthorhynchus</i> sp. | 2 | D/1, B/1, A/1 | 13/1, 8/2 | 31/1 |
| <i>Rhinoncus inconspicuum</i> (Hbst.) | — | C/1 | — | — |
| <i>Litodactylus leucogaster</i> (Marsh.) | — | E/1, D/2 | 9/1, 8/2, 7/1 | — |
| <i>Eubrychius velatus</i> (Beck) | — | D/1, C/1 | 10/?1 | 31/2 |
| <i>Phytobius comari</i> (Hbst.) | 2 | C/2, A/1 | 5/2 | — |
| <i>Phytobius</i> sp. | 1 | C/1 | — | — |
| <i>Orobites cyaneus</i> (L.) | — | D/1, C/1 | 8/1 | — |
| * <i>Mecinus ?heydeni</i> Wenck | — | B/1 | — | — |
| <i>Gymnetron beccabungae</i> (L.) | — | — | 6/1 | — |
| <i>Gymnetron</i> sp. | 3 | C/2, B/2 | 8/1, 7/3, 6/1, 5/1 | — |
| <i>Rhynchaenus salicis</i> (L.) | — | — | 4/?2 | 20/1 |
| * <i>R. flagellum</i> Erics. | — | — | — | 20/1 |
| <i>R. *flagellum</i> Erics. or <i>foliorum</i> (Muell.) | — | — | — | 22/1, 19/1, 18/2 |
| <i>Rhamphus pulicarius</i> (Hbst.) | 1 | D/1, B/1 | 6/1 | — |
| Diptera | | | | |
| <i>Dilophus</i> sp. | — | K/1, H/1, D/5 | 13/1, 11/1, 9/2, 7/3, 6/1 | — |
| Chironomidae indet. | — | I/16, H/3, G/4, E/19, D/55, C/730 | 4/9, 2/50, 1/30 | 32/n, 31/n, 30/8, 28/12, 27/5, 22/2, 21/3, 20/16 19/3, 16/14 |
| Hymenoptera | | | | |
| <i>Formica lugubris</i> Zett. | 6 | D/7 | 5/2 | 31/1 |
| <i>Formica fusca</i> (group) | 9 | — | 9/6, 8/9 | 32/3, 31/4 |
| <i>Formica</i> sp. | 73 | C/11, B/15 | 6/1 | — |
| <i>Tetramorium caespitum</i> (L.) | — | — | 5/1, 4/2 | — |
| <i>Myrmica</i> sp. | 18 | C/1 | — | — |
| * <i>Camponotus herculeanus</i> L. | 3 | — | — | — |
| Hymenoptera indet. | — | D/15, B/15 | 13/1, 12/2, 4/2 | 29/2, 28/1, 22/1, 19/1, 18/2 |

(b) Notes on selected species

With an assemblage of this size it is impracticable to list the habits, environmental requirements and taxonomic status of every species. Some species, however, must be discussed in detail if the implications of these faunas is to be understood. To keep the length of this section to a minimum many interesting species which are deserving of special mention have been omitted. Among these are most of those which no longer occur in Britain, but which have been recorded frequently from British Middle Devensian (Weichselian) sites, and also many species still found in these islands but with a very restricted distribution. When possible the more interesting animals are mentioned briefly in the discussion of the implications of the faunas.

HEMIPTERA

Odontoscelis fuliginosa

At least four individuals of this bug were recovered. Heads and pronota were exceptionally well preserved with their pubescence still intact, and large fragments of scutellum were also found.

In Britain today *O. fuliginosa* is mainly a coastal sand dune species and has been recorded from Lancashire, Suffolk, Kent, Hampshire and Pembroke. Stichel (1955) says that it is found on the soil and amongst the roots of a wide variety of herbaceous plants. Widely distributed on the continent from Norway and Sweden in the north to Greece, Crete and the Iberian Peninsula in the south, it has also been found in Egypt and as far east as Mongolia and Siberia.

Sciocoris cf. *homalonotus*

Four heads, four pronota and a scutellum, all well preserved, were assigned to the genus *Sciocoris* but not to a British species. They resembled, but failed to exactly match three or four European species, of which *homalonotus* was closest.

Members of this genus generally live in warm, sunny places, often on sandy ground, in the soil around the bases of plants. According to Stichel (1955) *homalonotus* has a southern and continental distribution today, having been recorded from southern France, Spain, Portugal, Morocco, Algeria, Tunisia, Sardinia, Italy, Czechoslovakia, Jugoslavia, Albania, Hungary, Romania, Bulgaria, southern Russia and Iran.

Plinthisus pusillus

At least eight examples of this distinctive little bug were recovered, represented by heads and pronota, often joined, and a number of elytra.

Although not found in Britain it is widespread in Europe, having been recorded from Germany, Finland, Norway, Sweden, Austria, Czechoslovakia, Poland, Hungary, Jugoslavia, and S. Russia. Stichel (1955) says it is found amongst moss and lichen in dry sandy places, on heather moors and under *Herniaria*, *Potentilla* and *Thymus*.

COLEOPTERA

Nebria nivalis

This species was only introduced to the British List in 1950 (Blair) and even now only a bare half dozen specimens have been taken in this country. All these records have been from mountainous areas, around 1000 m, in Inverness-shire or Ross and Cromarty (see Johnson 1967).

In Europe *nivalis* is a northern and arctic species, found in the mountains of Norway and Sweden, on the Kola Peninsula and farther east into Siberia. Lindroth (1945) says it is found at the margins of perennial snowdrifts and beside melt-water streams. It will venture on to snow to search for insects frozen there.

Bembidion octomaculatum

It is many years since the last capture of this species in Britain and it is probably extinct in this country. Even during the latter half of the nineteenth century a few specimens only were taken, mostly from localities in the London area, now built over, and Fowler (1887) referred to it as one of the rarest of the British Carabidae. In Scandinavia also, records are very few and all

are from the extreme south of Sweden. Farther south in Europe it becomes more common, extending as far as Greece and Crete and into north Africa.

The species lives beside water, often by small pools which dry up in the summer.

Bembidion dauricum

Only one fragment of this species, an elytron, was found. In Europe today it has a pronounced northern distribution and until lately was not known to occur south of the Arctic Circle in Scandinavia. It has recently been recorded, however, from the mountains of southern Norway (C. H. Lindroth, personal communication). It is a xerophilous species, usually found on a sandy or fine gravel substrate with very sparse vegetation (Lindroth 1945).

Bembidion ibericum/grisvardi

Two pronota of a *Bembidion* were recorded which, though very distinctive, could not be matched with any British species nor with any of the exotic northern *Bembidions* previously recorded from Quaternary deposits. They were identical, however, with the pronota of *B. ibericum*, a species found in Spain and Portugal, and with its close relative *B. grisvardi* which is found today in certain valleys in the French Alps and the Massif Centrale.

Cymindis angularis

A number of fragments of *C. angularis*, mostly well preserved heads and pronota, were recovered, representing at least six individual beetles.

The species is one of open, sunny situations, particularly grassland on chalky or sandy soils. It is frequently found under stones or low plants, such as *Thymus* and *Calluna*. It is widely distributed in Europe as far north as latitude 64° N in Fennoscandia, and south to the French Alps and N. Italy. In the more southern parts of its range it appears to be a montane species, ascending to a height of 2000 m.

Ochthebius foveolatus

A solitary pronotum of this species was recovered. On the continent it has a markedly southern distribution, its range extending only as far north as mid-France, mid-Germany and the Caucasus. It is found mainly in mountainous areas in clear, rapidly flowing streams.

Helophorus fennicus

This is the species referred to in Hansen *et al.* (1960) as *H. fennicus* Payk. and now equated with *H. sibiricus* Mots. by Angus (1970).

This insect is a northern species in Europe today, its range only extending as far south as 62° N in the mountains of southern Norway. It is found in ponds and ditches and Strand (1946) records it from the edges of melting snow.

Anthophagus bicornis

Heads, pronota and elytra of at least nine individuals of this species were found.

Its present-day range does not extend northwards into Scandinavia, but it is widespread and not uncommon in mid- and southeast Europe, particularly in the mountains. It is often found on flowering bushes such as broom, rowan and whitethorn.

Airaphilus elongatus

A number of well-preserved heads, pronota and elytra were recovered which plainly belonged to a species of *Airaphilus*. Though the synonymy of this group is somewhat confusing these specimens could be matched exactly with individuals in the British Museum's collection which in turn tallied with Lindberg's (1943) description of *A. elongatus* Gyll. (= *geminus* Kr. = *ruthenus* Solsky). All have the pronotum shagreened and hardly longer than broad, and elytra without shagreenation which are only three times as long as wide. The Church Stretton specimens also have the short, triangular head assigned to *geminus* Kr. by Portevin (1931), and are comparable with *geminus* Kr. of Reitter (1911), but are definitely not the species called by him *elongatus* Gyll.

Since its original discovery in the Church Stretton deposits *A. elongatus* has been found in a number of late Glacial sites. Today it has a rather restricted distribution in south and mid-Europe and north Africa. The most northerly part of its range is the southern extremity of Sweden and it appears to be absent from Western France, Holland, Britain and eastern Europe generally, occupying a corridor up the centre of the continent from Greece and Italy. This distribution seems to suggest a thermophilous species and it is treated as such here, but with some reserve for, as Dr Coope has pointed out (personal communication) he has found it in late-Glacial deposits, sometimes in company with an assemblage of species which would otherwise suggest a cold environment. Its distribution is possibly governed, therefore, by factors other than climate.

A. elongatus is found in wet marshy places and in grassy spots, sometimes under stones but more often in accumulations of dead vegetation.

Aphodius obscurus

A single elytron of this very distinctive species was recovered.

According to Balthazar (1964) *A. obscurus* is found in sheep, goat and chamois dung in the alpine and subalpine zones but is nowhere common. Its range includes the mountains of middle Europe, the Pyrenees, the northern Apennines, the Balkan mountains, Asia Minor and the Caucasus.

Cyphocleonus trisulcatus

This is a species which, in common with a number of others recorded from Church Stretton, would appear to be quite capable of living in Britain today if it could get here. It is widespread in Europe, though not present in either Fennoscandia or the Mediterranean region, and is found as high as the subalpine zone. According to Hoffmann (1950) the larval foodplant is *Chrysanthemum leucanthemum*, on which the adult is also found.

At least two individuals were present at Church Stretton, represented by a pronotum and three well-preserved elytra.

Mecinus ? heydeni

A single elytron of a *Mecinus* which, while wet, possessed traces of a blue coloration seems almost certain to belong to *M. heydeni*. This species has already been recorded from a late-Glacial deposit at Rodbaston, Staffordshire, by Ashworth (1969) and the Church Stretton specimen, though less well preserved matches well with his. A positive identification is not made however, as the blue colour, which may still be discerned on the Rodbaston examples, has completely vanished from the Church Stretton specimen.

M. heydeni is very rare on the Continent today. It has been found in France, Belgium, Germany, Sweden and Denmark according to Hoffmann (1958), and Allen (1948) in a paper introducing *Mecinus janthinus* Germ. on to the British List, suggests, after comparing the geographic ranges of the two species, that *heydeni* might ultimately be discovered in Britain.

The larvae of *heydeni* live in the stems of *Linaria vulgaris* and the adult is found on the leaves of the same plant.

Rhynchaenus flagellum

This species and *R. foliorum* are very closely related and are most easily distinguished on the number of joints in the flagellum of the antenna, *foliorum* having seven and *flagellum* only six. Although in fossil material this character is most unlikely to be preserved the degree of rugosity at the base of the rostrum also appears to be diagnostic. Parts other than the head appear to be indistinguishable when found as fossils. The single head from RS₂ proved to be *flagellum* and, although absolute certainty is not possible, it seems highly likely that the pronota and elytra from the same and adjacent samples, are this species also.

Flagellum is a northern species inhabiting Fennoscandia from latitude 60° N as far north as the Kola peninsula. It has not been recorded in Denmark, Germany, France or Britain.

The foodplants of this species are *Salix herbacea* and *S. polaris*. In the light of recent discoveries of otherwise northern species, as relicts on high mountains in Scotland (e.g. *Nebria nivalis*, *Phyllopecta polaris*), and its extremely close resemblance to our common *R. foliorum*, it seems quite probable that *R. flagellum* will in time be found in the Scottish Highlands.

Camponotus herculeanus

Dr Pontin who identified the Church Stretton ants says (in litt.) that, although he believes this species to be *herculeanus* it is not possible to be absolutely certain in the absence of any abdominal segments.

There exist a few ancient records of *C. herculeanus* in Scotland, but Donisthorpe (1927) does not consider them valid. During this century there have been a number of introductions of this species into Britain, both accidental and deliberate, but none have become established. It is an alpine and northern species on the continent, often associated with pine woods.

3. CORRELATION OF THE DEPOSITS

CS₁ and CS₂, although only a few metres apart, showed considerable difference in both overall thickness and in the thickness of their various beds, and it is not immediately obvious how an accurate correlation should be drawn between them. Certain points of similarity in each section where correlation was possible, however, were obvious and these are used here to divide the columns up into a series of broad units for subsequent discussion. Finer correlation was considered both unwise and unnecessary.

In figure 3 the relative positions of the samples from each section are shown and the lengths of the columns represent the number of invertebrate taxa recognized. Clearly small differences in these lengths are of little significance, as these could be accounted for by the varying size of the samples and accidents of collection and preservation. The sudden rise in numbers at the F/E and 10/9 boundaries, after a period of uniformly low numbers, is so marked, however, that it must be significant and represent the same event in both columns.

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The next point which can easily be identified in both sections is a lithological one. This is where the grey silty clay gives way quite abruptly to brown peat, at the D/C and 6/7 junctions.

If these two points are regarded as places where the two sections can be correlated it follows that samples E and D can be equated with 9 and 8. This is borne out by an examination of their faunas. At these levels in the two sections a number of species occur for the first time and are then found regularly through a number of consecutive samples. Amongst these are *Donacia versicolore*, *D. obscura*, *Plateumaris sericea*, *Adoxus obscurus*, *Otiorrhynchus rugifrons* and *Cryptorhynchidius lapathi*, all of which are phytophagous. Again in samples B and 6, 5 and 4 a number species are introduced simultaneously in each section, including *Hydrochus brevis*, *Olophrum consimile*, *Oxytelus rugosus*, *Phalacrus nigrinus* and *Otiorrhynchus ovatus*.

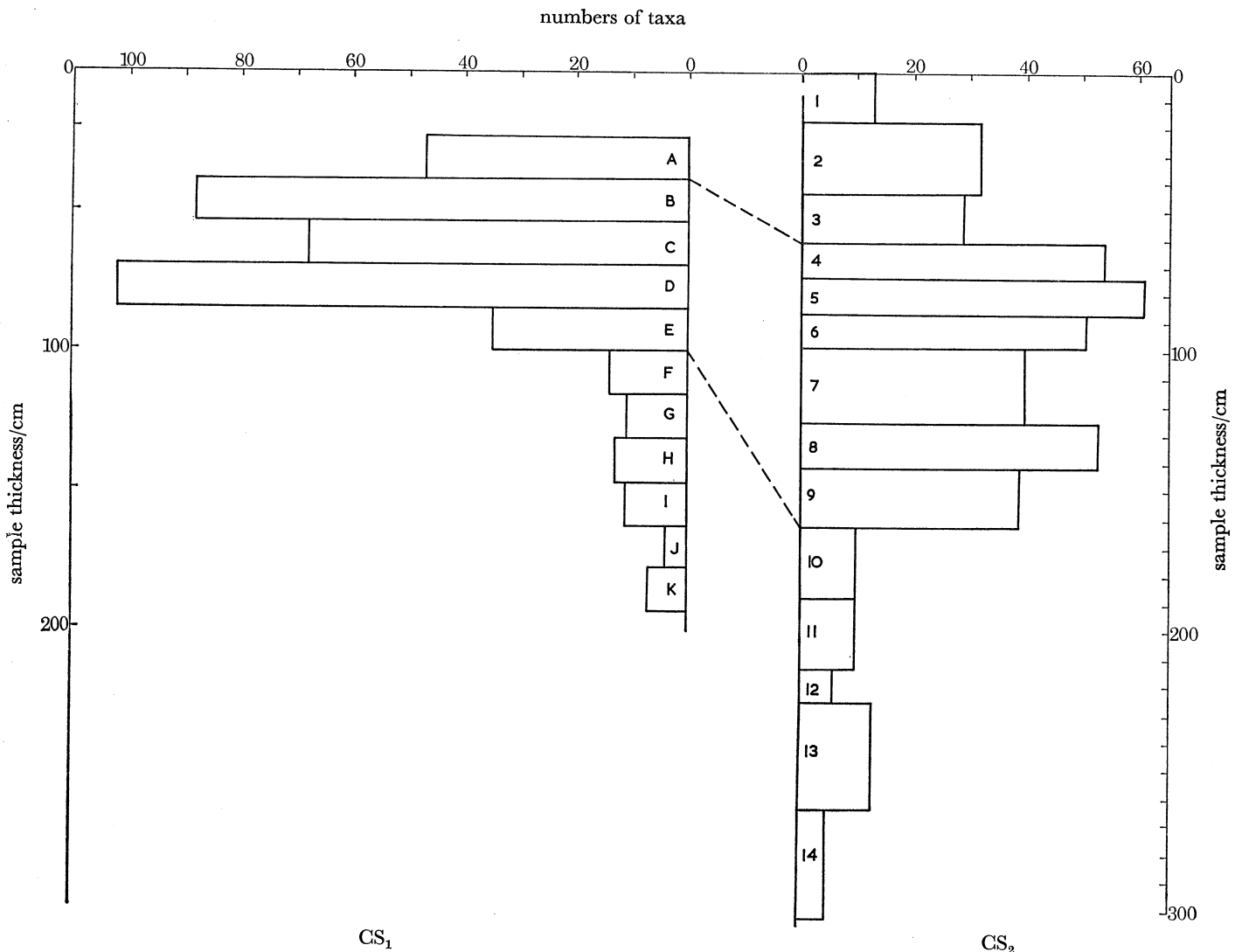


FIGURE 3. Comparison of numbers of taxa per sample from CS₁ and CS₂.
---, Lines joining points of suggested correlation.

At the B/A and 4/3 boundaries there occurs a sharp drop in numbers of taxa, similar in reverse, though not so marked, as the sudden rise earlier, and this may represent another point at which the columns may be matched.

In CS₁ collecting ended at the top of the organic material (sample A) but in CS₂ a sample was collected from above this level. There is no fauna in CS₁ equivalent to that contained in this top sample from CS₂ containing as it does such elements as ?*Lepidurus arcticus*, found nowhere else in these deposits, and the northern beetles *Arpedium brachyterum* and *Boreaphilus henningianus*. Apart from these species the fauna is a very meagre one, almost everything else having apparently died out.

In the subsequent discussion of the environmental and climatic changes demonstrated by these faunas the two sewer trench sections are correlated in accordance with the preceding paragraphs and are dealt with in the stages shown in table 1.

TABLE 1. SUGGESTED CORRELATION BETWEEN THE SAMPLES OF THE TWO SEWER TRENCH SECTIONS

| stage | samples | |
|-------|-----------------|-----------------|
| | CS ₁ | CS ₂ |
| VI | — | 1 |
| V | A | 3/2 |
| IV | B | 6/5/4 |
| III | C | 7 |
| II | E/D | 9/8 |
| I | K/J/I/H/G/F | 14/13/12/11/10 |

The bulk sample (B.S.), both from its position and its lithology appears to include all stage IV, with some from the top of III and the bottom of V. An examination of the fauna supports this for, with the sole exception of one *Bembidion grisvardi/ibericum*, none of the species which are found exclusively in stages I, II or III are recorded from B.S. and only a small number of those which are otherwise confined to stage V.

In the borehole, RS₂, sampling was carried out at rather crude intervals, as collecting an insect fauna from the site was entirely secondary to obtaining information concerning the local stratigraphy. Between samples 31 and 30, however, a dramatic change in the fauna can be seen which is very like that seen between stages V and VI in the sewer trench sections.

Samples 32 and 31, which are very similar to each other, therefore appear to belong to stage V and possibly the top of IV, while samples 30 to 16 would seem to be equivalent to VI and to some period of succeeding time.

Five radiocarbon dates have been measured from places in these three sections and they are consistent with the cross correlation suggested above. The positions from which these dates were obtained, together with the comparative positions of the stages and also the boundaries of the pollen zones (Rowlands & Shotton 1971), are shown in figure 5.

4. INFERENCES DRAWN FROM THE FAUNAS

(a) Ecology

Stage I (CS₁ K to F and CS₂ 14 to 10)

All the samples referred to this stage consisted of clay with a content of gravel, increasing downwards. Organic matter was present but in too small amounts to allow a radiocarbon date.

Rowlands (1966) says that neither pollen nor plant macrofossils were found in this part of the sequence and infers from this that the water had not been colonized by vegetation. The larger samples examined later for insect remains, however, did contain some plant fossils, among

which were the oogonia of *Chara* and fruits of *Carex*, *Hippuris*, *Myriophyllum* and, most abundant, *Potamogeton*. The weevil *Eubrychius velatus*, which lives on submerged aquatic plants, was present. It would seem, therefore, that at this time plants were growing in the water but the absence of any of the beetle species which live on vegetation having aquatic roots and subaerial leaves, the *Donacias*, for instance, suggests that the margins of the water had not yet acquired a growth of such plants as *Phragmites*, *Sparganium* or *Typha*.

A few water beetles, some caddis flies, chironomid midges, *Daphnia* and one representative of the alder fly, *Sialis*, make up the rest of the aquatic fauna.

Among the terrestrial members of the fauna the Elateridae, Chrysomelidae and Curculionidae, six species altogether, are all phytophagous and so imply the presence of some vegetation apart from that in the water. Similarly, the abundance of *Aphodius* species which nearly all live in the dung of herbivorous mammals, and the presence of *Cercyon* and *Platystethus cornutus*, both frequently found in this habitat, are all suggestive of terrestrial vegetation. This need not have been in the immediate vicinity of the pool, but near enough to permit large mammals to commute between this food supply and the water. *Notiophilus aestuans*, on the other hand, lives on dry, sandy or gravelly soil where the vegetation is very open. *Simplocaria semistriata* and the species of *Euaesthetus* live in moss, and most of the small Staphylinidae from this stage are usually found either in moss or accumulations of vegetable debris.

The fauna of this period suggests, therefore, a pool into which submerged vegetation had probably fairly recently migrated with only sparse vegetation around its periphery.

Stage II (CS₁ F and E, CS₂ 9 and 8)

At the beginning of this period there is a sudden expansion of the insect fauna, in both numbers of species and of individuals, and this stage corresponds to the lowest level at which Rowlands discovered pollen. The pollen spectrum commences with high values for *Myriophyllum* and Cyperaceae both of which soon diminish and almost disappear. Plant macrofossils recovered during sorting for insect remains include fruits of *Potamogeton* and *Hippuris*. The water clearly contained abundant subaquatic vegetation, confirmed by the presence of the beetles *Litodactylus leucogaster* and *Eubrychius velatus*, both of which live on submerged plants such as *Ceratophyllum* and *Myriophyllum*. *Donacia versicoloreae*, here making its first appearance, is frequently found on *Potamogeton* as well as on plants with foliage arising from the water. The Hydrophilidae recorded also favour pools with a profuse growth of aquatic plants. Reeds growing at the margins of water are the host plants of *Donacia obscura* and *Plateumaris sericea* and frequently of *D. versicoloreae*, whilst *Prasocuris phellandrii* is usually found on *Oenanthe aquatica*, another waterside plant.

A large aquatic fauna had by this time become established including, as well as many species of water beetle, dragonflies and caddises. Most of the aquatic species recorded from this episode live in still or slowly flowing water. The small number which live in running water, for instance the helmids, could well have been brought in by streams flowing off the neighbouring high ground.

The terrestrial fauna indicates a rather more diverse flora than in stage I. *Plagioderia versicoloreae*, *Cryptorrhynchidius lapathi* and *Rhamphus pulicarius* demonstrate the presence of their food plant, *Salix*. Although it is not possible to say which was the species involved it is clear that so large a beetle as *C. lapathi* (ca. 8 to 10 mm), which is a wood borer in its larval state, could not live in the stems of *Salix herbacea*.

The presence of such species as *Odontoscelis fuliginosa* (see p. 339), *Cicindela campestris* and *Cymindis angularis* (see p. 340) suggest that open, sunny situations were still to be found. The food plant of *Adoxus obscurus*, *Epilobium*, is a colonizer of open ground, which soon becomes shaded out when higher vegetation grows over it, and *Plantago major* and *P. lanceolata*, the host plants of *Phytonomus plantaginis*, are well known as weeds of cleared land. Moss must also still have been common to account for the presence of the species of Byrrhidae and certain staphylinids.

The ants *Formica lugubris* and *F. fusca* (group) are accompanied by the myrmecophilous beetle *Lomechusoides strumosa*. As these beetles are usually carried to a new nest from an old one by the ants it would seem that the hosts must have been generally distributed in the area rather than a newly established colony resulting from the chance arrival of a gravid female. *Lugubris* is one of the more northerly species of *Formica* in this country and is tolerant of very high rainfall, often nesting in marshy conditions. It may be that the requirement of high humidity is responsible for its distribution in these islands, which though for the most part northern or montane, includes such oceanic areas as south west Ireland.

In the pollen spectrum (Rowlands & Shotton 1971) small values for *Betula* are recorded from this time but no macro-remains of birch were found in the insect samples and no beetles were recovered which live on the plant.

Sample 8 from CS₂ was radiometrically dated at 13555 ± 620 years B.P. (Birm. 149). Very little organic matter was present in the clay and the measurement had perforce to be done on a very small sample, hence the large standard deviation. The sample may well have included much subaquatic vegetation, e.g. *Myriophyllum* and *Potamogeton*, producing the well-known 'hard water effect' and giving a date which exaggerates the age of the deposit.

Stage III (CS₁ D and C, CS₂ 7)

This episode is characterized by a drop in numbers of both taxa and individuals, and it is correlated with the level which provided the peak value for *Salix* in Rowlands's pollen spectrum. Amongst the plant macro-fossils from the insect samples *Potamogeton*, *Hippuris* and *Carex* are still present and fruits of *Menyanthes* make their appearance. This latter is more a plant of watery bog conditions than open water and its presence, together with the dominance of *Salix* pollen, suggests that the margins of the pool were gradually becoming filled in with vegetation and therefore drier. The lithology of the deposit, which at this stage becomes highly organic, supports this contention. It is clear, however, from the presence of such water beetles as *Agabus*, *Colymbetes*, *Dytiscus* and *Gyrinus*, and the aquatic weevils *Litodactylus* and *Eubrychius*, that open water was still present, although the pond margin had probably advanced to the proximity of the site of the sections. The species which live on littoral reeds, *Donacia obscura*, *D. versicolore* and *Plateumaris sericea*, still occurred and the last two reached their highest numbers in this episode. In contrast *Ochthebius minimus* drops in numbers from almost thirty to two examples in this layer, rising again immediately afterwards to around twenty.

The recession in numbers of species and individuals in this horizon may be due to an accident of deposition or collection, but it seems more likely that a change in the environment was the cause. It is possible that, if the extreme dominance of the flora by *Salix* shown in the pollen spectrum bears any relation to reality a very monotonous habitat would probably have resulted, due to the shading out of many of the smaller plants. This would have been reflected in the fauna, both in the absence of the species whose foodplants were no longer available and in

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the scarcity of the more heliophilous species. The possibility of a slight climatic deterioration also cannot be ruled out and this is discussed in a later section.

A radiocarbon date of $12\,135 \pm 200$ years B.P. (Birm. 158) was recorded from layer 7 of CS₂. Again *Myriophyllum* may have been responsible for some 'hard water effect', but many more littoral and terrestrial plants must have contributed their remains to the sample than in CS₂ 8. Any effect attributable to ancient mineral carbonates in solution in the water at the time of deposition is likely, therefore, to be less marked than in the previous sample.

Stage IV (CS₁ B, CS₂ 6 to 4)

During this stage the pollen spectrum showed a peak in *Betula* at the expense of *Salix*, and a small peak in Cyperaceae. Plant macro-fossils recovered from the insect samples were, near the bottom of the layer, principally *Menyanthes* and further up, *Menyanthes*, *Carex* and *Betula*. This suggests a conversion of the pool to marshy ground and the insects, to a large extent, bear this out. *Phalacrus nigrinus*, which lives on smut fungus on *Carex*, first appears at this time and rapidly becomes abundant. *Notaris aethiops* and *Limnobaris pilistriata* too, both live on Cyperaceae in marshy places. There are still a number of species which live on *Salix*, amongst which are *Cryptorrhynchidius lapathi*, *Rhamphus pulicarius* and, for the first time the large cerambycid, *Lamia textor*, a species which though apparently found in some numbers in Britain during the last century, has not been taken here now for many years and has probably become extinct. The littoral reed fauna of *Donacia* species and *Plateumaris* is still well represented and *Gymnetron beccabungae*, which lives on brooklime (*Veronica beccabunga*), was found.

Although the pool was gradually silting up, enough open water still existed to support a large water-beetle fauna. With a few possible exceptions all are still water forms.

Amongst the dry ground fauna the major additions are those species which live under fallen vegetation in various stages of decomposition. These include *Acrotrichis*, *Cryptophagus*, *Atomaria*, *Lathridius*, *Enicmus* and some new small staphylinids which together make up a large proportion of the fauna. Inhabitants of moss, too, have increased in numbers.

Despite the abundance of *Betula* pollen and seeds, no species specific to this host plant was recovered. The large non-British weevil *Cyphocleonus trisulcatus* (see p. 341), was recorded from this stage. The food plant of this beetle is *Chrysanthemum leucanthemum*, a species typical of open meadowland. Amongst the non-Coleoptera ants of the genus *Formica* were very common and their presence is correlated with the recovery of two myrmecophilous species, *Monotoma conicollis* and *Potosia floricola*.

The bulk sample (BS) is largely equated with stage IV and agrees very closely in its implications.

Stage V (CS₁ A, CS₂ 3 and 2)

This episode is marked by a sharp drop in numbers of species and individuals, affecting particularly the aquatic Dytiscidae, Hydrophilidae and the weevils *Eubrychius* and *Litodactylus*. The Donaciines also, previously well represented, occur only as a few unidentified fragments. *Notaris aethiops* and *Phalacrus nigrinus* are still to be found, however, and their presence is correlated with a high Cyperaceae pollen count and many *Carex* nutlets. No macrofossils of fully aquatic plants were recorded but seeds of *Betula* were plentiful. All the evidence suggests the complete conversion of the pool to a *Carex* marsh surrounded by dry ground, occupied principally by birch woods. Much of the beetle fauna consists of species which inhabit leaf litter or

moss, while phytophages with specific host plants are few. This may well be due to the shading effect of the birch creating a rather monotonous vegetation.

A radiocarbon date of 11790 ± 140 years B.P. (N.P.L. 81) was obtained on peaty material from sample A of CS₁ and another of 11000 ± 200 years B.P. from CS₂ 2 (Birm. 148).

Stage VI (CS₂ 1)

The lithology of this stage is quite different from that of the preceding, consisting of silty clay with some angular gravel. The contained fauna, too, is markedly different from any of the previous samples. Numbers of taxa undergo a dramatic reduction and the fauna includes such species as *Boreaphilus henningianus*, *Arpedium brachypterum* and ?*Lepidurus arcticus*, none of which has occurred before. The plant macrofossils revert to a much more aquatic assemblage, with *Chara* and *Batrachium* recorded, as well as *Carex* and *Betula*. The pollen spectrum for this period shows very high values for Cyperaceae and Graminae with a greatly reduced *Salix* count.

Lepidurus lives in water that dries up periodically and hence contains a minimum of large predatory Dytiscidae. *Helophorus brevipalpis* is a species which rapidly colonizes temporary pools by flying in. The staphylinids *Olophrum*, *Arpedium*, *Acidota* and *Boreaphilus* are found in litter or moss, whilst the only specifically identified phytophagous species, *Adoxus obscurus*, lives chiefly on *Epilobium*.

This sample follows immediately after one dated 11000 ± 200 years B.P.

RS₂ 32 and 31

Though at the top of this pair of samples a transition occurs similar to that of stages V/VI of the sewer trench the bottom cannot be precisely equated with a lower stage. It is possible that these two samples are the equivalent in time of two or three of the stages of CS₁ and CS₂. Most of the insect species from this horizon were found in the sewer trench in stages III to V, the chief difference being in the much greater number of species from the borehole which live in running water. Little purpose would be served by describing this fauna in detail as clearly, in the length of time during which it was deposited, a number of seral changes were gone through which, when the samples were washed, became inextricably mixed.

The stage V/VI boundary, however, appears sufficiently well marked to provide a point of correlation with the sewer trench sections.

RS₂ 30 to 16

In this series of samples insects were very sparse but all tended to imply a similar environment.

After sample 31 numbers of insects drop very sharply and thereafter the faunas become progressively smaller until in sample 27 nothing was found. After this, faunas started to build up again, reaching their maximum numbers just before organic deposition was cut off by the spreading fan gravels. Only *Helophorus glacialis*, a snow meltwater species and indeterminate Aleocharinae, which generally inhabit vegetable refuse, were found throughout. In the latter half of the episode, when the fauna was increasing in numbers, the non-British species *Rhynchaenus flagellum* (see p. 342) which lives on *Salix herbacea* and *S. polaris*, and possibly *Rhynchaenus salicis*, another *Salix* eater, occur. The species of *Phyllodecta* live on various poplars, aspens and willows, depending on the species involved. One example of *Eudectes whitei* was recorded from this episode. This species, formerly known as British from only a few specimens from the

Scottish highlands has recently been recorded from high ground in the Pennines by the late W. O. Steel (personal communication).

Moss fragments were recorded from some samples, and enough of this material was gleaned from sample 28 to provide a radiocarbon date of 11048 ± 376 years B.P. (Birm. 9).

(b) *Climate*

Insects are frequently very sensitive to the climate, particularly the thermal environment, in which they live. Their abundance in deposits covering roughly 3000 years of the Devensian late-Glacial promised the possibility of an evaluation of the contemporary climate independent of the conventional interpretation based on pollen analysis, but capable of comparison with it. As will be seen later, there is considerable discrepancy between the two results.

Because of the paucity of experimental data on the climatic requirements of insects, deductions about past climates are usually based on the present-day distributions of the species found as fossils. Though odd exceptional species may have either changed their habits or are not occupying all their potential range today, in such a large assemblage it is unlikely that these will amount to a very large proportion of the total.

In attempting to assess the late-Glacial climate indicated here it is principally the modern distributions of beetles in Fennoscandia which have been used, because of the wide range of thermal environments to be found in that area and on account of the ready availability of the records, which are given, by provinces, in Hansen *et al.* (1960). Maps of the distributions of those species of beetle recorded from Church Stretton, which are found in Scandinavia today, were prepared and compared with the July isotherms for 15 and 16 °C. As both these isotherm lines and the boundaries of the beetle distributions are necessarily approximate no more latitude was permitted in matching the maps with the isotherms. Only those species were admitted whose entire ranges fell within the isotherm or overlapped it by less than a complete province. A single province entirely outside the isotherm rendered the species unacceptable even though the remainder of its range was well inside. The species whose present-day distributions in Fennoscandia are south of the 15 °C isotherm are referred to in the following discussion as the 'thermophiles' and their proportional representation in each of the sewer trench stages is shown in the graph (figure 4). The numbers of thermophiles are expressed as a percentage of the total fauna of each stage, the total fauna being only those specifically identified Coleoptera whose range today includes Scandinavia. Species outside this definition are discussed in the text where necessary.

This assessment of the thermophilous species present can only give a generalized picture of the thermal environment, as it takes no account, for instance, of those phytophagous species whose distributions are limited by the range of their food plants. Microclimates, in which some species may live in isolation from the overall climate, are also ignored by this method. These factors are, so far as possible, considered subjectively during the discussion of the different stages.

Stage I

The very high percentage of thermophiles (see figure 4) would seem to indicate that this time was the warmest part of the sequence. It must be noted, however, that this percentage is based on only a small number of species, the total fauna consisting of only eleven named beetles. A number of the insects recorded favour areas with only sparse vegetation and high insolation

at ground level and it may be that this is a pioneer fauna which entered the area after a rapid amelioration in the climate before a large variety of terrestrial plants had become established. Even so temperatures must have been at least as high as those of Shropshire today, possible even higher.

Stage II

By this time, radiometrically dated $13\,555 \pm 620$ years B.P., a large and complex insect fauna was living in the Church Stretton valley. The percentage representation of thermophiles shows a marked fall from the preceding stage, but this is due to an influx of eurytherms, probably in response to the development of a more diverse vegetation cover. With the exception of *Notio-philus aestuans*, all the thermophiles of the previous stage, *Bembidion octomaculatum*, *Platystethus*

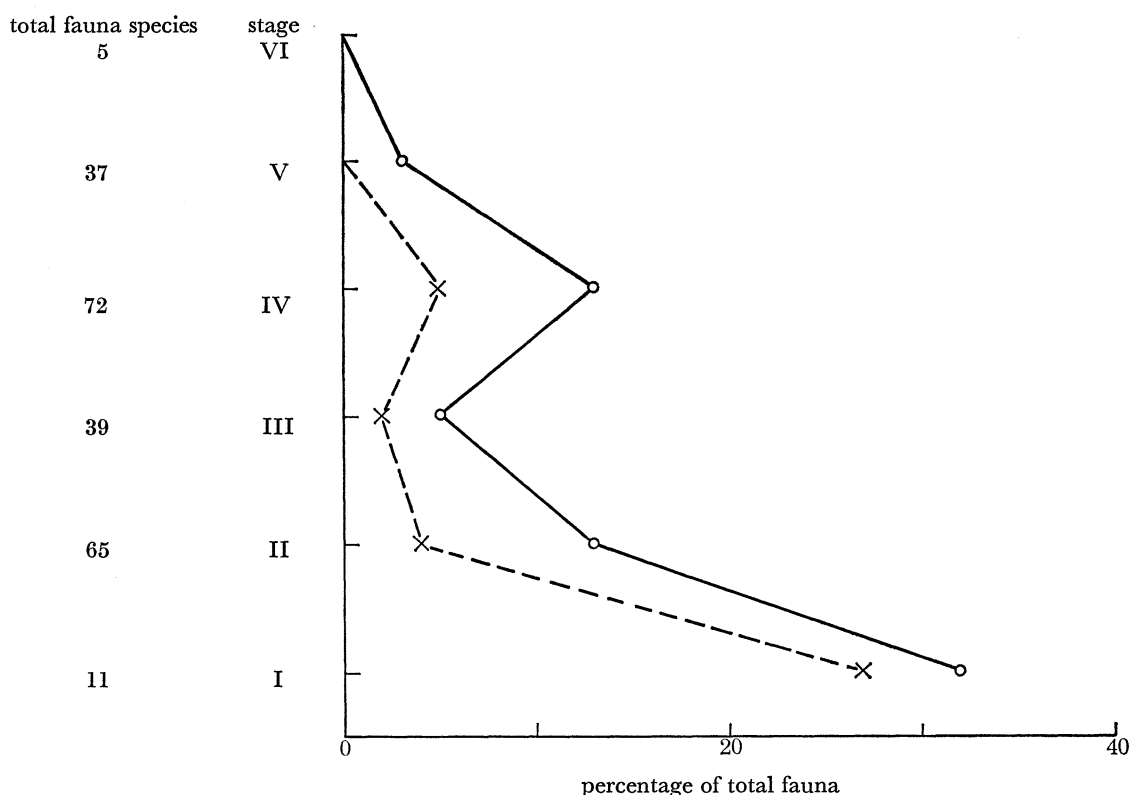


FIGURE 4. Proportion of 'thermophiles' in each stage. (The terms 'thermophile' and 'stage' are defined in the text.) Percentage of species whose range does not extend north of the July isotherms in Fennoscandia of 15 °C (O) and 16 °C (x)

cornutus and *Airaphilus elongatus*, are again found, reinforced by *Dyschirius aeneus*, *Helophorus nubilus*, *Georissus crenulatus* whilst *Morychus aeneus*, *Lomechusoides strumosa*, *Litodactylus leucogaster* and *Rhamphus pulicarius*, all recorded from this stage, are all borderline cases, not quite definitely within the 15 °C isotherm and so not included in the figures from which the graph was constructed, but having nevertheless a very southern distribution in Scandinavia. Species not found in Fennoscandia today and so not represented in figure 4 include *Bembidion ibericum/grisvardi* (see p. 340) and *Ochthebius foveolatus* (see p. 340) both having very southern ranges on the continent. The remainder of the fauna consists of widespread eurytherms, none of which give any hint of a low summer temperature.

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If stage I, for which information is a little inadequate, is excepted, this must be the warmest part of the Church Stretton sequence, with summer temperatures probably in excess of those of today.

Stage III

In this stage another drop in the thermophilous element occurs, only two species, *Brachypterolus pulicarius* and *Rhinoncus inconspicuous*, falling into this category. The exotic southern species do not occur in this stage and the non-British *Pycnoglypta lurida* makes its first appearance. This species, though not an arctic stenotherm, has a northern and montane distribution in Europe today. Its presence is compatible with the appearance of the northern British beetles *Patrobus assimilis*, *P. septentrionis* and the caddis *Phryganea obsoleta*. Temperatures at this time must have been somewhat lower than those of stages I and II, and were probably akin to those of high ground in the Lake District or southern Scotland today. The radiocarbon date 12135 ± 200 years B.P. suggests that the climatic deterioration began prior to or around 12000 years ago.

Stage IV

Despite a rise in the thermophile graph to the same level as that of stage II it seems unlikely that a marked rise in summer temperatures occurred. The southern species which are absent today from both Britain and Scandinavia were not found in this fauna and a number of beetles which in this country are confined to the north and to high ground, such as the *Patrobus* species recorded in stage III and in addition *Olophrum consimile* and *Notaris aethiops*, are recorded. Against this evidence *Berosus affinis* occurs, a southern European insect which is found as far north today as Belgium and Britain but not Scandinavia, and also the non-British weevil *Cyphocleonus trisulcatus*, not found north of the 16 °C isotherm in Sweden. *Cyphocleonus* lives on *Chrysanthemum leucanthemum* which is found as far north as Lapland, so that the beetle's distribution is not dependent on the presence of its foodplant.

From the foregoing it is considered that the climate of this stage was considerably cooler than that of stage II but not very different from that of stage III, the apparent lower incidence of thermophiles in III being probably due to the smaller size of sample.

Stage V

This stage, with its solitary thermophile and one borderline thermophile, appears to show a further decline in summer temperatures. *Patrobus assimilis*, *Olophrum consimile* and *Notaris aethiops*, all northern or montane in this country, are represented, together with *Pycnoglypta lurida*, this time offset by no southern element. Although this stage must be cooler than the preceding ones it is far from being arctic in aspect and northern Scotland today is probably a near analogy. Two dates are available from samples of this stage, one from the top of CS₁ of 11790 ± 140 years B.P. and another from the upper part of CS₂ of 11000 ± 200 B.P. If the correlation between these two sections is correct then the date from CS₁ is an average one for the whole duration of the stage while that from CS₂ was taken from the upper part of the stage only. Their discrepancy is, therefore, not so great as a cursory glance might suggest.

Stage VI

After the rather gradual changes seen in the previous stages, with southern species slowly dwindling in importance and being replaced by widespread eurytherms or northern British elements the transition to stage VI seems particularly abrupt. The fauna suddenly becomes very scanty, only five species of beetle being named, none of these being thermophiles. Among

these five are two newcomers to the site, *Boreaphilus henningianus* and *Arpedium brachypterum*. *Boreaphilus* is no longer found in this country and in Scandinavia has a northern and montane distribution while *Arpedium*, though still living in Britain is only found in the north. This marked change, accompanied by a corresponding change in the lithology may be due to a break in deposition. In RS₂, however, a similar change in the fauna occurs with no obvious alteration in the lithology and it is possible that a rapid deterioration in the climate so reduced the local vegetation that material being deposited simply contained little organic material.

RS₂

Samples 31 and 32 are so thick that they cannot be fitted into any single stage dealt with above. The fauna suggests, however, that they cover stage V and at least some of IV and as in these stages in the sewer trench, a thermal environment similar to that of Scotland today prevailed for much of this time.

Between samples 31 and 30 a dramatic reduction in numbers of insects, both as species, and individuals, takes place. All thermophilous elements disappear and the northern and montane *Arpedium brachypterum* comes in, accompanied by very little else. This sudden change is very similar to that seen between stages V and VI in the sewer trench sections and is ascribed to a rapid deterioration in the thermal environment. Radiocarbon dates from around these levels (see figure 5), though predictably not exactly the same, are similar enough not to contradict the suggestion that these changes in the faunas of the two sites were roughly contemporaneous. From sample 30 upwards the thermal environment does not appear to have varied significantly until deposition of the organic silts ended. *Helophorus glacialis*, an arctic and montane species today, whose habitat is typically the margins of melting snow, was found throughout the remainder of RS₂. *Bembidion dauricum* (see p. 340) whose most southerly modern occurrence was an isolated specimen in the mountains of southern Norway, and *Nebria nivalis* (see p. 339), another species associated with snow meltwater, were both found near the top of the section. Two other northern and montane species, *Helophorus fennicus* (see p. 340) and *Boreaphilus henningianus* also occur and the only specifically named phytophage found, *Rhynchaenus flagellum* (see p. 342) is also non-British and northern and lives on dwarf willow. The presence of all these species and the complete absence of any thermophilous elements indicates a climate of arctic severity, probably with perennial snow, at least on the Long Mynd and other high hills.

The first few samples of this cold episode have an extremely impoverished fauna, but after sample 26 numbers start to build up gradually. This might be construed as an indication of a relaxation of the rigorous climatic régime. It is considered much more likely, however, that when the preceding thermophilous fauna was extirpated a fresh assemblage more suited to the new conditions was simply not at hand to move in, but took some time to become established.

Deposition of the organic sediments of RS₂ was eventually cut off by the spreading fan gravels from Carding Mill valley.

5. RELATION OF INFERRED CLIMATIC FLUCTUATIONS TO POLLEN ZONES

The climatic fluctuations deduced from the insect faunas of these deposits, which are discussed in the preceding section, are illustrated in the form of a curve in figure 5, together with the boundaries of the pollen zones given by Rowlands & Shotton (1971). Also shown on this figure are the salient points of the pollen spectrum, the plant macro-fossils recorded from the insect

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samples and the radiocarbon dates. It will be seen that the concept of a cold zone I followed by the warm Allerød (zone II) is not supported by the evidence from the insects (see also Coope 1970). The reverse of this would in fact seem to be more likely, that at least late zone I was the

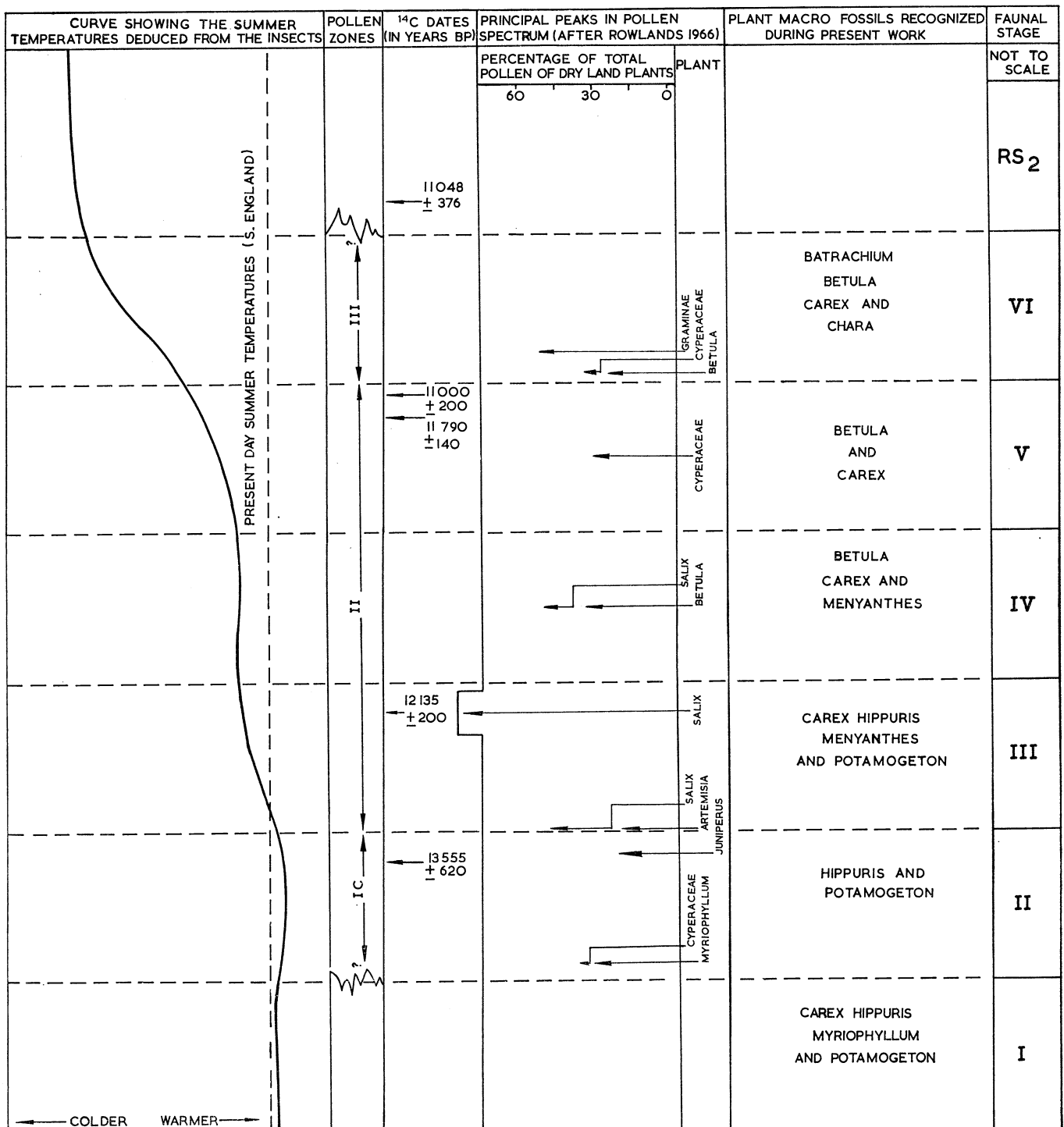


FIGURE 5. Relation between the thermal environment inferred from the Late Devensian insect faunas and the botanical evidence and radiocarbon dates.

warmest part of the episode and that zone II showed a gradually deteriorating thermal environment. In all this time no evidence of continentality of climate is presented by the insects. In fact the presence of such forms as *Barynotus squamosus* and *Formica lugubris* would seem to suggest a considerable degree of oceanicity. Thus, it would seem that zone Ic was quite warm enough to allow the growth of thermophilous trees but that, probably because of a very rapid amelioration in climate in an earlier stage, they were unable to arrive in time (see Coope, Morgan & Osborne 1971). The rapidly migrating insects, however, reached the area almost as soon as it was warm enough to allow them to survive, well in advance of even the tree birches with their easily dispersed seeds. During zone II, though summer temperatures were falling, *Betula* was able to catch up with the insects and this flora and fauna then persisted with only minor changes until the end of zone II. At this time, around 11 000 years B.P. both plants and animals agree in their evidence of a severe drop in summer temperatures with the onset of zone III. *Betula* declines rapidly in importance in the pollen spectrum and is replaced by Graminae and Cyperaceae, while the accompanying insect fauna is very sparse and consists only of eurytherms or cold requesting species.

These conclusions are strongly supported by work on deposits of similar age at Glanllynau in north Wales (G. R. Coope, personal communication). Here also exotic forms such as *Bembidion ibericum/grisvardi* and *B. octomaculatum* are encountered in the late zone I horizon, together with a fauna very similar to that of the same time at Church Stretton. As in the Shropshire site these thermophiles disappear with the entry of zone II and are replaced by a mounting number of northern forms as time goes on. The situation is so similar to that at Church Stretton and to a number of other late-Glacial sites still under investigation, that it is highly likely that it was the general pattern in Britain at this time.

PART II. FLANDRIAN SITES

6. INTRODUCTION

Three sites of Flandrian age were investigated entomologically and their locations in the Church Stretton valley are given together with those of the Late Devensian sites in figure 1, p. 329.

The first of these post-Glacial deposits came from the borehole designated RS₂ in Part I. A series of organic silts of late-Glacial age, described earlier (p. 328) were overlain by a fan of Longmyndian gravels some 10 m thick (see Rowlands & Shotton 1971) and the Flandrian peats were laid down on the top of these gravels. According to Rowlands's pollen analysis the earliest of these organic sediments was laid down in zone VIc and this deposition continued until well into zone VIIb. The core from the borehole was divided into sections 15.25 cm (6 in) in length wherever practicable, but this sample size was varied slightly at times to make sample boundaries coincide with lithological changes.

The other two sites were both in the sewer trench, to the south of RS₂. One was at Worldsend (SO 451932) where the trench cut through a bed of peat which dated back to zone VIa according to pollen analysis of samples brought up by means of a Hiller auger. Water in the bottom of the trench, however, precluded the collection of bulk samples except from the top 140 cm which almost all belonged to zone VIIb. Seven samples were collected, the basic collecting unit again being 15.25 cm with adjustments for variations in the lithology and to compensate for the presence of a large log embedded in the face. The third site, at Little Stretton (SO 446921), was found where the sewer trench encountered another peaty bed. Here,

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according to the palynology, the deposit dated back to zone VIa and a radiocarbon date from the lowest but one sample, of 8101 ± 138 years B.P. (Birm. 8) confirmed this. Again, as nearly as possible, collections were made at 15.25 cm intervals, although near the bottom small deviations from this figure were made to accommodate lithological changes.

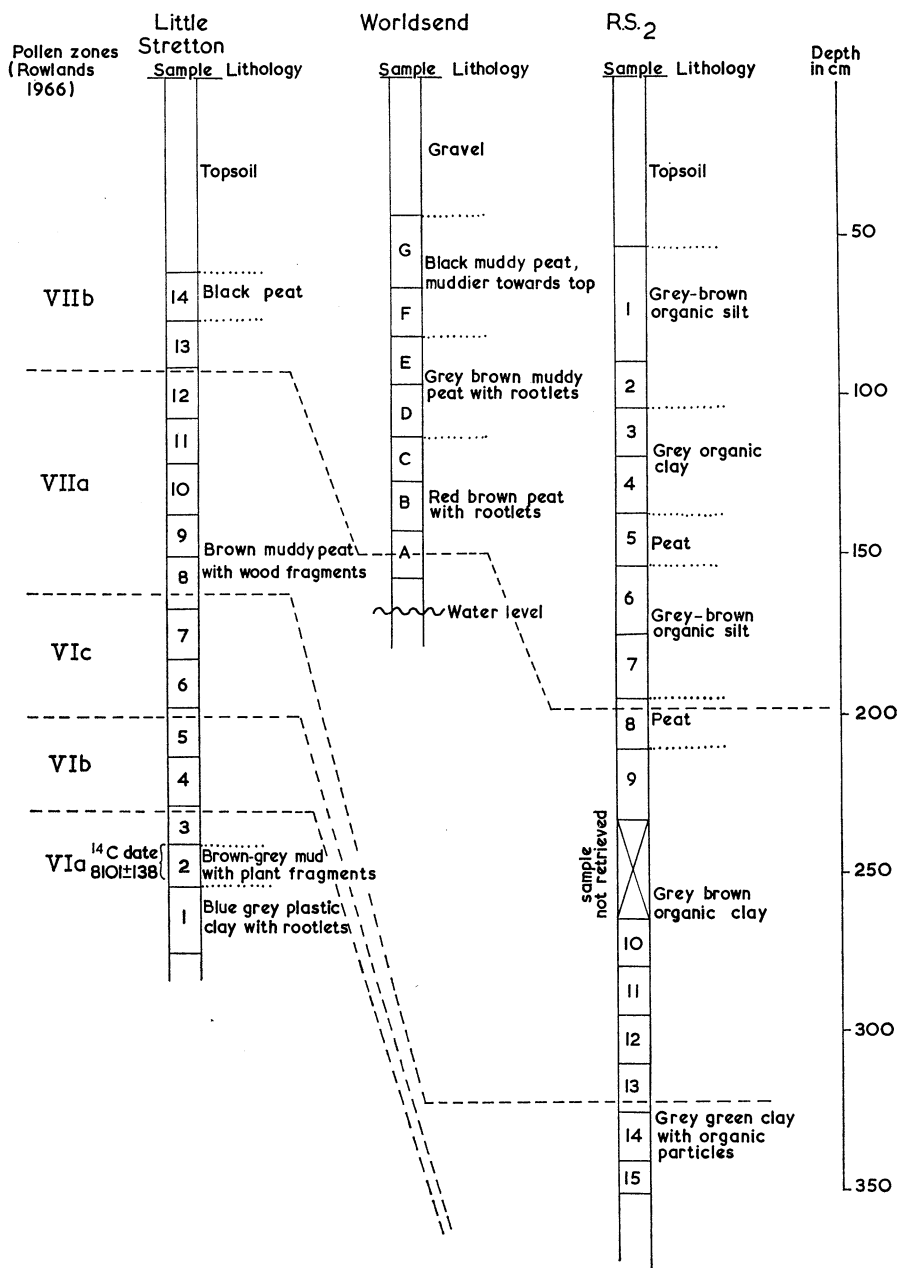


FIGURE 6. Sampling intervals and lithologies of the Flandrian sequences, with the pollen zonation according to Rowlands (1966).

Details of the lithologies of the three sites and the sampling intervals used are shown in figure 6. The pollen zonation according to Rowlands is shown here and also the position in the Little Stretton section from which the radiocarbon date was obtained.

These deposits were all washed and sorted in the same way as the samples from the late-Glacial sites of Part I. The highly organic nature of the samples made paraffin flotation necessary almost throughout.

7. THE FAUNAS

(a) Faunal lists

The format used here is similar to that of the lists in part I. As fossil representatives of other orders were very sparse in these deposits only the Coleoptera have been recorded, the figure following each sample letter or number and separated from it by an oblique line (solidus) is, therefore, the minimum number of individuals represented in the sample.

| FAUNAL LIST | | | |
|--|---|---------------------|------------------------------------|
| | RS ₂ | Worldsend | Little Stretton |
| Carabidae | | | |
| <i>Nebria brevicollis</i> (F.) | 11/1, 10/1 | — | — |
| <i>Notiophilus</i> sp. | — | F/1 | — |
| <i>Elaphrus cupreus</i> Duft. or <i>uliginosus</i> F. | 12/1, 11/1 | — | — |
| <i>Loricera pilicornis</i> (F.) | 3/1 | — | — |
| <i>Dyschirius globosus</i> (Hbst.) | 14/1, 12/3, 11/3, 10/2, 7/1, 3/1, 2/2 | D/1 | 7/1, 9/1, 11/1 |
| <i>Bembidion varium</i> (Ol.) | — | — | 6/2 |
| <i>B. assimile</i> Gyll. | — | — | 3/1, 4/3, 5/4, 6/3, 14/1 |
| <i>B. doris</i> (Pz.) | 12/1, 10/1 | B/2, D/1, E/1 | 4/1, 5/1, 6/3 |
| <i>B. unicolor</i> Chaud or <i>guttula</i> (F.) | 11/2, 10/1, 3/1 | — | — |
| <i>Bembidion</i> sp. | 14/1, 12/1, 11/2, 9/1, 8/1, 7/1, 6/2, 4/3, 2/2 | A/1 | 3/1 |
| <i>Trechus quadristriatus</i> (Schr.) or <i>obtusus</i> Er. | 12/1, 8/1 | — | — |
| <i>T. micros</i> (Hbst.) | — | G/1 | — |
| <i>Patrobus atrorufus</i> (Stroem) | 12/2, 10/1 | — | 4/2 |
| <i>Acupalpus ? luridus</i> Dej. | 14/1 | — | — |
| <i>Feronia nigra</i> (Schall.) | 6/1 | — | — |
| <i>F. nigrita</i> (F.) | 13/1, 9/1, 7/1, 6/1 | F/2 | — |
| <i>F. anthracina</i> (Ill.) | 11/3 | — | — |
| <i>F. minor</i> (Gyll.) | 8/1, 6/1, 4/1 | — | 6/2, 9/2, 11/2, 13/2 |
| <i>F. strenua</i> (Pz.) | 3/2 | — | — |
| <i>F. diligens</i> Sturm | 11/1, 10/4, 9/3, 8/3, 7/1, 6/1 | A/1, F/3, G/2 | 11/1 |
| <i>F. madida</i> (F.) | 3/1 | — | — |
| <i>Feronia</i> sp. | — | D/2, E/2 | 3/2, 8/3 |
| <i>Agonum viduum</i> (Pz.) | 4/1 | — | — |
| <i>A. obscurum</i> (Hbst.) | 12/1, 11/1, 9/1, 5/1, 4/1 | F/4, G/1 | — |
| <i>A. fuliginosum</i> (Pz.) | — | — | 5/5, 6/3 |
| <i>Agonum</i> sp. | 4/1 | — | — |
| Dytiscidae | | | |
| <i>Hyphydrus ovatus</i> (L.) | — | — | 11/1 |
| <i>Hydroporus bilineatus</i> Sturm | — | — | 11/1 |
| <i>H. dorsalis</i> (F.) | — | — | 8/2, 11/1 |
| <i>H. scalesianus</i> Steph. | — | C/2, D/3 | 8/1, 9/5, 10/1 |
| <i>Hydroporus</i> sp. | 9/2, 6/1, 5/2 | D/5, E/7, F/26, G/4 | 6/2, 8/7, 9/2, 11/1, 13/4, 14/1 |
| <i>Agabus undulatus</i> (Schrank) | — | — | 5/1, 8/2, 11/1 |
| <i>A. sturmii</i> (Gyll.) | — | — | 8/2, 11/1, 14/1 |
| <i>A. bipustulatus</i> (L.) | 10/1, 9/2, 4/2 | — | 6/1 |
| * <i>O. wasastjerna</i> Sahlb. | — | F/2, G/4 | — |

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FAUNAL LIST (cont.)

| | RS ₂ | Worldsend | Little Stretton |
|---|--------------------------------------|--------------------|---|
| Dytiscidae (cont.) | | | |
| <i>Ilybius</i> sp. | — | A/1 | 5/1, 11/1 |
| <i>Copelatus haemorrhoidalis</i> (F.) | — | — | 14/1 |
| <i>Rantus</i> sp. | — | — | 8/1, 10/1 |
| <i>Dytiscus semisulcatus</i> Muell. | 9/1 | — | — |
| <i>Dytiscus</i> sp. | 7/1 | — | 6/1 |
| <i>Hydaticus ? transversalis</i> (Pont.) | — | — | 8/1 |
| Hydrophilidae | | | |
| <i>Ochthebius bicolon</i> Germ. or <i>dilatatus</i> Steph. | 14/1 | — | — |
| <i>O. minimus</i> (F.) | 11/2, 6/3, 4/1 | B/6 | 8/5, 14/1 |
| <i>Ochthebius</i> sp. | 12/2, 9/1, 8/1, 5/1 | A/1 | 5/1, 6/2, 9/2, 11/2, 12/2 |
| <i>Hydraena testacea</i> Curtis | — | — | 7/2, 8/18, 9/9, 11/3, 12/2 |
| <i>H. britteni</i> Joy | 9/1, 6/3 | — | 11/1 |
| <i>H. riparia</i> Kug. | 7/2, 4/7 | — | 5/2, 6/4, 8/1 |
| <i>H. gracilis</i> Germ. | 3/1 | — | — |
| <i>Hydraena</i> sp. | 11/3, 10/2, 8/7, 4/3 | B/1, C/2 | 7/1, 8/2, 9/2 |
| <i>Limnebius truncatellus</i> (Thnb.) | 13/1, 12/1, 11/2, 8/1 5/1, 2/2 | — | 8/1 |
| <i>Limnebius</i> sp. | 12/1, 11/3, 8/1, 6/1, 3/1 | — | 8/3, 9/2, 10/1, 11/1 |
| <i>Helophorus aquaticus</i> (L.) | 4/1 | — | — |
| <i>H. brevipalpis</i> Bedel | 12/2, 2/1 | — | — |
| <i>H. flavipes</i> F. | 2/1 | — | — |
| <i>H. flavipes</i> F. or <i>strigifrons</i> Th. | 12/1 | — | — |
| <i>Helophorus</i> sp. | 11/2, 10/1, 9/1, 6/1, 4/1 2/2 | — | 10/1, 14/1 |
| <i>Hydrochus brevis</i> (Hbst.) | — | — | 8/2 |
| <i>Hydrochus</i> sp. | 6/1 | — | 9/1, 10/1, 11/1, 13/1, 14/1 |
| <i>Coelostoma orbiculare</i> (F.) | 11/1, 9/2, 6/1, 4/1 | — | — |
| <i>Cercyon</i> sp. | 10/4, 9/5, 8/5, 7/4, 6/7 5/1, 4/8 | A/3, B/4, C/4, E/3 | 5/3, 6/3, 7/2, 8/4, 10/5, 11/3, 13/4, 14/1 |
| <i>Megasternum obscurum</i> (Marsh.) | 13/1, 12/1 | — | — |
| <i>Cryptopleurum minutum</i> (F.) | 11/1 | — | — |
| <i>Hydrobius fuscipes</i> (L.) | 11/1, 9/2 | — | 14/1 |
| <i>Anacaena globulus</i> (Pk.) | 8/2 | — | — |
| <i>Laccobius</i> sp. | 2/1 | — | 11/1 |
| <i>Chaetarthria seminulum</i> (Hbst.) | 10/1, 9/1, 4/1 | — | — |
| Silphidae | | | |
| <i>Phosphuga ? atrata</i> (L.) | 9/1 | — | — |
| <i>Sciodrepa</i> sp. | — | F/1 | — |
| Leiodidae | | | |
| <i>Agathidium</i> sp. | 11/2, 10/1 | — | — |
| Clambidae | | | |
| <i>Clambus armadillus</i> (Deg.) | 6/2 | — | — |
| Scydmaenidae | | | |
| <i>Neuraphes</i> sp. | 5/1 | — | — |
| <i>Stenichnus</i> sp. | 11/1 | D/1, F/6, G/2 | — |
| Ptiliidae | | | |
| <i>Ptenidium ? punctatum</i> (Gyll.) | 5/1 | — | — |
| <i>Acrotichis</i> sp. | 14/1 | F/3 | 13/1 |
| Scaphidiidae | | | |
| <i>Scaphisoma ? boleti</i> (Pz.) | — | — | 8/1 |
| Staphylinidae | | | |
| <i>Micropeplus tessera</i> Curtis | — | F/2 | — |
| <i>Metopsia clypeata</i> (Muell.) or <i>gallica</i> Koch | — | F/1 | 5/1, 6/2 |
| <i>Phyllodrepa ioptera</i> (Steph.) | — | — | 6/2 |
| <i>P. vilis</i> (Er.) | — | A/1 | — |
| <i>Anthobium unicolor</i> (Marsh.) | 12/1 | — | — |

FAUNAL LIST (*cont.*)

| | RS ₂ | Worldsend | Little Stretton |
|--|--|--------------------------------|--|
| Staphylinidae (<i>cont.</i>) | | | |
| <i>Olophrum piceum</i> (Gyll.) or <i>fuscum</i> (Gr.) | 11/3, 10/2, 4/1 | E/1, F/3, G/1 | 5/1, 9/1, 14/1 |
| <i>Acidota crenata</i> (F.) | 10/1 | F/1, G/2 | — |
| <i>A. cruentata</i> (Mannh.) | 2/1 | F/1 | — |
| <i>Lesteva heeri</i> Fauvel | 11/1, 9/1, 8/1, 7/1, 6/1 4/2 | — | — |
| <i>L. longelytrata</i> Gze. | 2/2 | — | — |
| <i>Lesteva</i> sp. | 3/1, 2/1 | — | — |
| <i>Syntomium aeneum</i> (Muell.) | — | — | 8/1 |
| <i>Trogophloeus</i> sp. | 14/1 | — | 8/2 |
| <i>Aploderus caelatus</i> (Gr.) | 7/1, 4/1 | — | — |
| <i>Oxytelus rugosus</i> (F.) | 15/1, 11/1, 10/2, 9/2 8/1, 7/2, 6/3, 5/1, 4/7 3/7, 2/6 | — | 4/1 |
| <i>O. laquaeatus</i> (Marsh.) | 12/1 | — | — |
| <i>O. complanatus</i> Er. | 2/1 | — | — |
| <i>Platystethus nodifrons</i> Sahlb. | 9/1, 6/1 | — | — |
| <i>Bledius</i> sp. | 3/1, 2/1 | — | — |
| <i>Stenus junco</i> F. | 11/1, 4/3 | A/3 | — |
| <i>S. tarsalis</i> Ljungh | 11/1, 2/1 | — | — |
| <i>S. nitens</i> Steph. | — | — | 9/2 |
| <i>S. cicindeloides</i> (Schall.) | 10/1 | — | — |
| <i>Stenus</i> sp. | 12/2, 11/2, 10/5, 9/3, 8/2 7/2, 6/2, 5/4, 4/4, 2/1 | A/3, B/2, C/1, D/1, F/2 | 3/1, 4/1, 5/18, 6/12, 7/1 8/5, 9/2, 10/1, 11/9, 12/4, 13/1 |
| <i>Dianous coeruleus</i> (Gyll.) | 12/1 | — | — |
| <i>Euaesthetus bipunctatus</i> (Ljungh) | — | D/1 | — |
| <i>E. ruficapillus</i> Bois. & Lac. | — | A/3, F/1 | 5/4, 6/3, 7/3 |
| <i>Rugilus orbiculatus</i> (Payk.) | 10/2, 9/1 | — | — |
| <i>Lathrobium longulum</i> Gr. | 14/1, 11/1, 7/1 | — | — |
| <i>Lathrobium</i> sp. | 10/2, 9/1, 8/1, 5/1, 4/1 | B/1, C/1, D/2, E/4, F/7 G/1 | 3/1, 4/2, 7/1, 8/1, 9/1 11/1 |
| <i>Xantholinus fracticornis</i> (Muell.) | 7/1, 6/1, 4/1 | — | — |
| <i>X. tricolor</i> (F.) | — | G/1 | — |
| <i>X. linearis</i> (Ol.) or <i>longiventris</i> Heer | 15/1, 10/2, 3/1 | — | — |
| <i>Gyrophypnus punctulatus</i> (Gze.) | — | A/1, D/1 | — |
| <i>Erichsonius cinerascens</i> (Gr.) | — | — | 8/2, 9/1 |
| <i>Gabrius</i> sp. | 3/1 | — | — |
| <i>Staphylinus</i> sp. | — | F/1 | — |
| <i>Quedius</i> sp. | 11/1, 10/1, 9/1, 8/1, 4/1 3/3 | A/1 | 8/1 |
| <i>Bolitobius inclinans</i> (Gr.) | — | E/1 | — |
| <i>Tachinus</i> sp. | 11/1, 10/1, 4/1, 3/2 | — | — |
| <i>Aleochara</i> sp. | 7/1, 6/1 | — | — |
| Aleocharinae indet. | 11/3, 6/2, 2/2 | — | 1/1, 9/1 |
| Pselaphidae | | | |
| <i>Batrissodes venustus</i> (Reich.) | — | F/3 | 9/1 |
| <i>Brachygluta</i> sp. | — | F/2 | — |
| <i>Rybaxis longicornis</i> (Leach) or <i>laminata</i> Mots. | 14/1, 4/1 | — | 6/1 |
| <i>Bryaxis</i> sp. | 5/1, 4/1 | B/2, D/9, E/2, F/51, G/10 | 8/1, 9/1, 11/1 |
| <i>Tychus niger</i> (Payk.) | — | — | 6/1 |
| <i>Pselaphus heisei</i> Hbst. | — | F/6 | — |
| Histeridae | | | |
| <i>Onthophilus striatus</i> (Forst.) | 8/1, 6/1 | — | — |
| Cantharidae | | | |
| <i>Rhagonycha</i> sp. | — | — | 8/1 |

INSECT FAUNAS OF LATE DEVENSIAN AND FLANDRIAN AGE 359

FAUNAL LIST (cont.)

| | RS ₂ | Worldsend | Little Stretton |
|---|---|----------------------------------|-----------------------------------|
| Elateridae | | | |
| <i>Adelocera murina</i> (L.) | 12/1, 11/1 | — | — |
| * <i>Porthmidius austriacus</i> Sch. | — | F/2, G/1 | — |
| <i>Athous haemorrhoidalis</i> (F.) | 11/1 | — | — |
| <i>Dalopius marginatus</i> (L.) | 8/1 | — | — |
| <i>Denticollis linearis</i> (L.) | 8/1 | — | — |
| Eucnemidae | | | |
| <i>Melasis buprestoides</i> (L.) | — | F/6 | 7/1 |
| Dascillidae | | | |
| <i>Dascillus cervinus</i> (L.) | 11/1 | — | — |
| Helodidae | | | |
| gen. et sp. indet. | 12/1, 11/1 | A/6, B/3, C/4, D/1, F/16, G/3 | 6/2, 7/1, 8/7, 13/2, 14/1 |
| Dryopidae | | | |
| <i>Dryops</i> sp. | 10/2, 9/2, 7/2, 6/4, 4/4 3/1 | A/1, D/1 | — |
| <i>Elmis maugei</i> Bedel | 11/2 | — | — |
| <i>Limnius tuberculatus</i> Muell. | 11/1 | — | — |
| <i>Esolus parallelopedus</i> (Muell.) | 2/1 | — | 6/1 |
| <i>Latelmis volckmarii</i> (Pz.) | 11/1 | — | — |
| Byrrhidae | | | |
| <i>Byrrhus pilula</i> L. | 4/1 | — | — |
| <i>Byrrhus</i> sp. | — | E/1 | — |
| Nitidulidae | | | |
| <i>Meligethes</i> sp. | 11/1 | — | — |
| <i>Librodor ?quadriguttatus</i> (F.) | — | E/1 | — |
| Rhizophagidae | | | |
| <i>Rhizophagus</i> sp. | — | E/1, F/2, G/5 | — |
| Cucujidae | | | |
| <i>Pediacus dermestoides</i> (F.) | 6/1 | — | — |
| <i>Laemophloeus spartii</i> (Curtis) | — | F/1 | — |
| <i>Laemophloeus</i> sp. | — | — | 3/1 |
| Cryptophagidae | | | |
| <i>Hennoticus serratus</i> (Gyll.) | — | D/1 | — |
| Phalacridae | | | |
| <i>Phalacrus nigrinus</i> (Marsh.) | — | A/1 | 4/1, 5/2, 6/10, 8/1, 13/4 |
| <i>Phalacrus</i> sp. | — | — | 9/1, 11/1 |
| Lathridiidae | | | |
| <i>Enicmus</i> sp. | — | — | 10/1 |
| Colydiidae | | | |
| <i>Cerylon histeroides</i> (F.) | 5/1 | — | — |
| <i>Cerylon</i> sp. | — | D/1, F/1 | — |
| Anobiidae | | | |
| <i>Grynobius</i> sp. | 12/1, 10/1, 8/1, 6/1 | F/2 | 5/1, 6/6, 7/2, 9/1, 12/1, 13/1 |
| <i>Anobium ?fulvicorne</i> Sturm | — | F/1 | — |
| Pythidae | | | |
| <i>Lissodema quadripustulata</i> (Marsh.) | — | C/1 | — |
| Scarabaeidae | | | |
| <i>Onthophagus fracticornis</i> (Preyss.) | 4/1 | — | — |
| <i>O. similis</i> Scriba | 4/1 | — | — |
| <i>Onthophagus</i> sp. | 12/1, 7/1 | — | — |
| <i>Geotrupes</i> sp. | — | — | 14/1 |
| <i>Aphodius fimetarius</i> (L.) | — | — | 11/1 |
| <i>Aphodius</i> sp. | 12/2, 11/4, 10/5, 9/2, 6/1, 4/1, 3/1, 2/2, 1/1 | — | 6/1, 14/1 |
| <i>Phyllopertha horticola</i> (L.) | 12/1, 10/1 | — | — |
| Cerambycidae | | | |
| <i>Rhagium bifasciatum</i> F. | 2/1 | — | — |
| <i>Alosterna tabacicolor</i> (Deg.) | — | — | 8/1 |

FAUNAL LIST (*cont.*)

| | RS ₂ | Worldsend | Little Stretton |
|--|---|-----------|----------------------------------|
| Chrysomelidae | | | |
| <i>Donacia</i> sp. | — | — | 14/1 |
| <i>Plateumaris discolor</i> (Pz.) | 6/2, 4/1 | — | — |
| <i>P. sericea</i> (L.) | 4/1 | — | 4/1, 11/1, 13/4, 14/3 |
| <i>Plateumaris</i> sp. | 11/1, 10/1, 7/2 | — | — |
| <i>Hydrothassa aucta</i> (F.) | 11/1 | — | — |
| <i>H. marginella</i> (L.) | 3/2, 2/1 | — | — |
| <i>Phytodecta decemnotata</i> (Marsh.) | — | A/1 | — |
| <i>Galerucella</i> sp. | 11/2 | — | — |
| <i>Longitarsus</i> sp. | 2/2 | — | — |
| <i>Haltica</i> sp. | 11/1 | — | — |
| <i>Chaetocnema</i> sp. | 6/1 | — | — |
| <i>Cassida flaveola</i> Thunb. | 11/1, 5/1, 3/1 | — | — |
| Curculionidae | | | |
| <i>Apion</i> sp. | 12/1, 11/1, 7/1, 3/1, 2/1 | — | 6/1 |
| <i>Otiorrhynchus ligustici</i> (L.) | 10/1 | — | — |
| <i>Caenopsis waltoni</i> (Boh.) | 2/1 | — | — |
| <i>Phyllobius</i> sp. | 10/1 | — | — |
| <i>Strophosomus</i> sp. | 10/1, 3/1 | — | — |
| <i>Barynotus moerens</i> (F.) | 2/1 | — | — |
| <i>Sitona cambricus</i> Steph. | 9/1, 6/1 | — | — |
| <i>Sitona</i> sp. | 11/1, 7/1, 4/1 | — | — |
| <i>Dryophthorus corticalis</i> (Payk.) | — | F/1 | — |
| <i>Eremotes ater</i> (L.) | — | F/2 | — |
| * <i>E. elongatus</i> (Gyll.) | — | F/2, G/1 | — |
| * <i>E. strangulatus</i> Perris | — | F/5, G/2 | — |
| <i>Bagous</i> sp. | 9/1, 7/1, 4/1, 2/1 | A/1 | 5/1, 6/2, 14/1 |
| <i>Tanysphyrus lemnae</i> (Payk.) | — | — | 5/1, 6/7, 7/5, 8/2, 9/3, 11/3 |
| <i>Notaris scirpi</i> (F.) | 4/1 | — | 3/2 |
| <i>Notaris acridulus</i> (L.) | 12/2, 11/2, 10/4, 9/3, 8/1, 7/5, 6/4, 4/7, 3/3, 2/1 | — | — |
| <i>Thryogenes scirrhosus</i> (Gyll.) | 4/1 | — | — |
| <i>Thryogenes</i> sp. | 7/1 | — | — |
| <i>Anthonomus?</i> <i>pedicularius</i> (L.) | — | G/1 | — |
| <i>Anthonomus</i> sp. | — | — | 7/1 |
| <i>Curculio nucum</i> L. | — | A/1 | — |
| <i>C. nucum</i> L. or <i>glandium</i> Marsh. | — | — | 6/1 |
| <i>Liosoma deflexum</i> (Pz.) | 10/1, 9/1 | — | — |
| <i>Liosoma</i> sp. | 3/1 | — | — |
| <i>Alophus triguttatus</i> (F.) | 12/1, 11/1 | — | — |
| <i>Acalles ptinoides</i> (Marsh.) | — | — | 12/1 |
| <i>Ceuthorhynchus</i> sp. | 10/1, 7/1, 4/1 | — | 11/1 |
| <i>Rhinoncus pericarpus</i> L. | 11/1, 4/2 | — | — |
| <i>Phytobius</i> sp. | 12/2 | — | — |
| <i>Orobitis cyaneus</i> (L.) | 6/1 | — | — |
| <i>Anoplus roboris</i> Suff. | 4/1 | — | — |
| <i>Rhynchaenus quercus</i> (L.) | — | F/2 | 3/21, 5/3, 6/5, 9/1 |
| <i>Rhynchaenus</i> sp. | — | — | 6/1 |
| Scolytidae | | | |
| <i>Scolytus rugulosus</i> (Ratz.) | — | F/1 | — |
| <i>Hylesinus fraxini</i> (Pz.) or <i>orni</i> Fuchs | 2/1 | — | 5/1, 13/1 |
| <i>Myelophilus minor</i> (Hart.) | 1/1 | — | — |
| <i>Hylastes ater</i> (Pk.) | — | — | 5/1 |
| <i>H. brunneus</i> Er. | — | G/3 | — |
| <i>H. attenuatus</i> Er. | — | F/1 | — |
| <i>Dryocoetes villosus</i> (F.) | — | G/1 | 5/1, 7/1, 9/1, 12/1 |
| <i>Pityogenes bidentatus</i> (Hbst.) | — | G/3 | — |
| <i>Anisandrus</i> sp. | — | — | 5/1 |

(b) Notes on selected species

As was the case in part I, far more interesting species were found than considerations of space permit to be described in full. This section is, therefore, restricted to species which are no longer found living in Britain and to some of those British species whose distributions in this country are very restricted today.

Agabus wasastjerna

This species, of which heads, pronota, elytra and underside sclerites, representing at least six individuals were recorded has been previously discovered in interstadial deposits at Chelford, Cheshire (Coope 1959). These deposits, ¹⁴C dated 60 800 ± 1500 years B.P. (GrN. 1475) represented an acid water pool and marshy area surrounded by coniferous woodland, a fairly typical habitat for *A. wasastjerna*. The beetle is confined to northern Europe today, being only found as far south as north Germany. It is no longer found in Britain but is widespread in Fennoscandia.

Batrisodes venustus

Although this species is found living in Britain today and is accounted the commonest of our members of the genus it is still regarded as a considerable rarity. It is found sporadically as far north as Cumberland (Pearce 1957) and is confined to the southern half of Scandinavia. The habitat of *B. venustus* is the rotten interior of deciduous trees, particularly oaks, where it is usually found with the ant *Lasius brunneus* Lat.

Porthmadius austriacus

Heads, pronota, prosterna and probably elytra belonging to at least three examples of *P. austriacus* were recovered. It is not found today in either Britain or Fennoscandia and on the continent it is a southern species and its usual habitat is rotten wood in deciduous woodland.

Onthophagus fracticornis and *similis*

Only a single specimen of each of these two species was recovered. They were, until recently, confused under the name *fracticornis* and were finally distinguished by Landin (1959). After examining many examples in British collections Allen (1967) came to the conclusion that he had seen only seven genuine specimens of *fracticornis*, all without data, all others being *similis*. Thus it would seem that today, though *similis* is fairly widespread in southern England, *fracticornis* is very rare or, more probably, now extinct in this country. That this ratio between the two species has not always prevailed is shown by the recovery of nearly 300 individuals of *fracticornis* unaccompanied by any *similis* from a Bronze Age site at Wilsford, Wiltshire (Osborne 1969) bearing a radiocarbon date of 3330 ± 90 years B.P. (N.P.L. 74). Both species are found in the south of Scandinavia and in that area, according to Hansen *et al.* (1960) *fracticornis* is a little more widespread than *similis*. Farther south on the Continent both are widely distributed and are largely sympatric. Both live in the dung of large graminivorous mammals, usually these days, of cattle, and no obvious difference in their habitat requirements is known. In fact Landin (1959) says that he has taken both species in the same pile of dung.

Dryophthorus corticalis

This species was not recognized as British until 1925 when it was discovered living in Windsor Forest, Berkshire, by Donisthorpe. Like *Batrisodes venustus* (p. 361) it lives in rotten trees, most

frequently but not exclusively, oaks. It is very often found with the ant *Lasius brunneus*, but Donisthorpe (1927*b*) considers that it is not a regular myrmecophile, but is a tolerated lodger in the ant's nest. *D. corticalis* has been recorded by Osborne (in Kelly & Osborne 1963) from a Flandrian site dated 4830 ± 100 years B.P. (N.P.L. 39) and has been found in other deposits of approximately the same age which have not yet been precisely dated.

Eremotes elongatus

This weevil, of which at least three individuals were recorded, is a wood borer. Although it has been known to attack *Abies*, the chief host of *E. elongatus* is *Pinus*. In Fennoscandia it has been recorded from only a few scattered localities in the south and it is absent from Britain altogether. Farther south in France and Germany it becomes more widespread, and Hoffmann (1959) records it from Algeria living on *Abies numidica*.

Eremotes strangulatus

A minimum of seven individuals of this species were recovered. *E. strangulatus* appears to have a very restricted distribution today for it has not been recorded in either Britain or Scandinavia and Hoffmann (1959) says that it is peculiar to mid-France and Corsica. The French localities he cites are Landes, Charente Maritime, Gironde, Var and Alpes Maritimes. Like the preceding species *E. strangulatus* lives in wood, various species of *Pinus* in a weakened or moribund condition being selected as hosts.

8. INTERPRETATION OF THE FAUNAL EVIDENCE

This section is divided into two parts. The first (*a*) deals with the local ecology of the three sites demonstrated by their insect faunas, but without reference to the climate. This, or more strictly the thermal environment, is discussed in the second section (*b*).

(*a*) *Ecology*

The faunal sequences from these three sites do not suggest any environmental changes to correspond with the vegetational changes that mark the boundaries between the pollen zones as shown by Rowlands (1966). A close correlation was not expected, however, because the picture derived from pollen analysis is a broad regional one, while that shown by the insects is much more local. In the following discussion therefore the only use made of the pollen evidence is to correlate the deposits chronologically.

*RS*₂

The lower samples from this site contain only sparse faunas from which no clear picture of the contemporary environment can be drawn. In sample 12, however, a marked increase in the numbers of species takes place and, though fluctuations do occur, on the whole high numbers are continued up to sample 1. From sample 12 upwards the environment indicated by the insects is fairly uniform with no obvious changes in the local ecology. This sequence is discussed, therefore as a single unit.

Aquatic species, particularly those which inhabit still or slowly flowing water, are common. Amongst these are *Agabus bipustulatus*, *Dytiscus semisulcatus*, *Ochthebius minimus*, *Hydraena britteni*, *H. riparia*, *H. gracilis*, *Helophorus brevipalpis* and *H. flavipes*. As well as these still water forms a number of Dryopidae were found, including *Elmis aeneus*, *Esolus parallelopipedus*, *Limnius*

tuberculatus and *Latelmis volckmarii*, all associated with running water. The staphylinid *Dianous coeruleus* was also recorded and this species, though not aquatic, is always found at the margins of rapidly running streams, often behind waterfalls. This assemblage suggests a pool, probably formed by the gravel fan impeding the local drainage, which was fed by water running off the adjacent high ground down the Carding Mill valley. Immediately around the pool a somewhat marshy area seems to have existed, where *Bembidion doris*, *Notaris acridulus* and *N. scirpi* were living. *Plateumaris discolor*, too, was present, a species which suggests rather acid bog conditions. Away from this aquatic and wet ground environment the locality at this time appears to have been occupied by open grassland. *Adelocera murina* and *Phyllopertha horticola*, both of which live as larvae at the roots of grass, were found. Two species of *Hydrothassa*, *aucta* and *marginella*, were recovered, both of which are found in damp meadowland on species of Ranunculaceae. *Onthophagus fracticornis* and *O. similis* (see p. 361) and the majority of the species of the genus *Aphodius* live in dung, chiefly that of large, graminivorous mammals. As well as these a number of species were found which are most frequently, but not exclusively found in this habitat, amongst which are *Oxytelus rugosus*, *O. complanatus* and *Aploderus caelatus*, while the hydrophilids *Cercyon*, *Megasternum* and *Cryptopleurum* and the histereid *Onthophilus striatus* are found in accumulations of decaying vegetable matter, including dung. Large herbivores must have been present and it is suggested that this locality was occupied by pasture land. A small number of beetles associated with trees was found, each species represented by only a single individual. These were *Pediacus dermestoides*, *Cerylon histeroides*, *Campylus linearis* and *Rhagium bifasciatum*, all of which live in dead wood in a fairly advanced state of decay, *Anoplus roboris* which is found on living *Alnus* and a *Hylesinus*, either *fraxini* or *orni* both of which attack ash.

Worldsend

This section is chronologically the shortest of the three, falling almost entirely into zone VIIb according to its pollen. Despite this it is only in this deposit that an obvious change in the local environment can be detected. This change occurs at the junction of samples E and F. Above and below this the faunas fall into two uniform groups so that this deposit is discussed in two parts, the first containing samples A to E and the second samples F and G. In the lower part of the sequence the insects are mostly inhabitants of open water or moss and vegetable debris. Aquatic beetles include *Hydroporus scalesianus*, *Hydroporus* sp., *Agabus* sp., *Ilybius* sp., *Ochthebius minimus* and *Hydraena* sp. All these indicate still water. Terrestrial plants whose presence is shown by the insects are *Salix*, the host plant of *Phytodecta decemnotata* and *Corylus* upon which the nut-weevil, *Curculio nucum*, lives. *Phalacrus nigrinus* which lives on smutted *Carex* was also found. Thus the Worldsend locality at this time consisted of a body of still water bordered by marshy ground. No beetles indicating the presence of trees other than *Corylus* were recovered and this tends to suggest that if trees were present in the neighbourhood they were fairly remote from the site. At the base of sample F the environment shows a sudden change. So marked is this effect that a hiatus in deposition might well be suspected, although the pollen spectrum shows no evidence of this. In the lithology at this time there is a change to a darker colour but this is all that is apparent to the naked eye, the texture and general appearance of the muddy peat being otherwise unaltered. If, however, a hiatus did occur it could not have been of very long duration as these events all took place well within pollen zone VIIb. The open water fauna disappears and is replaced by *Agabus wasastjerna* (see p. 361) an acid-water pool species, together with some unidentified Hydroporines. *A. wasastjerna* is frequently associated with coniferous woodland

and its appearance at this time is in accord with the presence of *Eremotes strangulatus* (see p. 362), *Hylastes attenuatus* and *H. brunneus*, all of which live on pine and of *Eremotes elongatus* (see p. 362), *Myelophilus minor* and *Pityogenes bidentatus* whose host plants are *Pinus* and other coniferous trees. As well as these conifers deciduous woodland in which the dominant tree was probably oak is indicated. Beetles which live on broad-leaved trees include *Melasis bubrestoides*, *Eremotes ater*, *Scolytus rugulosus* and *Dryocoetes villosus*, all woodborers or bark beetles. *Rhynchaenus quercus* lives on oak whilst *Batrisodes venustus* (see p. 361) and *Dryophthorus corticalis* (see p. 361) are generally associated with this tree. *Laemophloeus spartii*, the species of *Cerylon* and *Rhizophagus*, are all found under the bark of decaying logs, and the non-British *Porthmadius austriacus* (see p. 361) inhabits rotten wood. The great increase in numbers of individual beetles after sample E is, to a large extent, due to *Bryaxis* sp. Unfortunately it was not found possible to identify these further than to their genus, of which some members live in moss on the floor of deciduous woodland, others in deep moss in marshy places and others again in grass tussocks. Deep moss is also the habitat of *Rybaxis laminata/longicornis* and accumulated vegetable debris is the home of such species as *Micropeplus tesseraula* and *Stenichnus* sp.

During the time of deposition of samples F and G therefore, dense woodland existed at Worldsend with a rather acid water pool near the trees.

It is highly interesting that so exotic a fauna should be living in midland Britain at this late date, though not without precedent. Osborne (in Kelly & Osborne 1963) has described a fauna from Shustoke, Warwickshire dated at 4830 ± 100 years B.P. (N.P.L. 39) which implied a similar environment. Here, too, *Dryophthorus corticalis* was found, accompanied by *Rhysodes sulcatus*, now extinct in Britain and *Ernoporus caucasicus* Lind. which is known from only one British locality (Allen 1969). *Sphaerites glabratus* was also recorded from Shustoke and this species is found today in northern and montane coniferous forests, an analogy with *Agabus wasastjernaee* at Church Stretton. The non-British *Pycnomerus terebrans*, another inhabitant of dead deciduous wood, was recovered from a deposit at Minsterly, about 20 km north of Church Stretton (P. J. Osborne, unpublished). This site was also placed in pollen zone VII b (P. H. Rowlands, personal communication). Another similar find was that of a specimen of *Cerambyx cerdo* L. in a piece of bog oak ^{14}C dated 4000 ± 60 years B.P. (Birm. 1), from Cambridgeshire (Duffey 1968). All these species, either extinct or extremely limited in their distribution in Britain today, belong to an environment of forest from which dead and fallen timber is never removed, a situation which has become very uncommon in these islands today due to the activities of man.

Neither need the presence of what appears to be a pine wood be altogether surprising. Godwin (1956) cites a number of instances of late Flandrian deposits containing abundant macro-remains of *Pinus* but without a corresponding abundance of pine pollen. He suggests that this phenomenon was due to the stands of *Pinus* being very localized and so not affecting the general forest composition as indicated by the pollen rain, an explanation which could clearly be accepted at Worldsend. This frequency of macro-remains of *Pinus* in late Flandrian deposits Godwin attributes to either the extension of ombrogenous peat formation or to general water-logging of hitherto dry forest land. In either case it seems likely that the Worldsend stands of *Pinus* would have occupied the wet valley floor with *Quercus*-dominated deciduous woodland growing on the drier ground of the nearby hillsides.

Little Stretton

This site lies approximately a kilometre south west of Worldsend and contained a fauna which exhibited certain affinities with that of the upper part of the Worldsend deposit. In the lower samples, unrepresented at Worldsend, the faunas are rather sparse and serve only to suggest an open marshy habitat, probably with *Carex*. An expansion of the insect fauna takes place from sample 5 upwards. Species inhabiting open water such as *Agabus undulatus*, *A. bipustulatus*, *Ilybius* sp., *Dytiscus* sp., *Hydraena riparia*, *Ochthebius* sp., and also *Tanysphyrus lemnae*, whose foodplant is Duckweed, all make their appearance in samples 5 and 6. *Bembidion doris* and *Phalacrus nigrinus* are present, suggesting a *Carex* marsh environment nearby whilst deep damp moss is indicated by *Euaesthetus ruficapillus* and *Rybaxis laminata/longicornis*. Deciduous woodland is suggested by the terrestrial part of the fauna. *Rhynchaenus quercus*, *Hylastes ater*, *Dryocoetes villosus* and *Anisandrus* sp. all live on broad-leaved trees, amongst which the most important is *Quercus*. These species are reinforced in the next three samples by the addition of *Melasis buprestoides*, *Syntomium aeneum*, *Batrissodes venustus* (see p. 361) and *Alosterna tabacicolor*, all of which are indicative of deciduous forest, while the aquatic fauna, too, becomes more extensive with the addition of *Hydraena testacea*, *Ochthebius minimus*, *Hydrochus brevis*, *Limnebius truncatellus*, *Hydaticus ? transversalis*, *Rantus* sp. *Agabus sturmi*, *Hydroporus dorsalis* and a number of other unidentified Hydroporines. This aquatic element becomes even more important towards the top of the section. After sample 9 *Hyphydrus ovatus*, *Hydroporus bilineatus*, *Copelatus haemorrhoidalis*, *Hydraena britteni* and *Hydrobius fuscipes* are added to the open water fauna. In the terrestrial part of the assemblage of the higher samples such species as *Dryocoetes villosus* and *Acalles ptinoides* still testify to the presence of deciduous trees but there is some evidence also of an opening up of the environment. The dung beetles *Aphodius fmetarius* and *Geotrupes* sp. both make their appearance in these layers, with their suggestion of grazing mammals. *Plateumaris sericea* and *Phalacrus nigrinus*, which both live on waterside reeds, reappear after an absence from the middle layers. This suggests that trees had advanced practically to the water's edge during the mid-part of this time, inhibiting the growth of littoral reeds and that in the upper layers they had receded from the edge of the pool. Throughout the Little Stretton sequence the insects provide no evidence of coniferous woodland, suggesting that these trees were extremely localized in the Church Stretton valley (see p. 364).

Summary of the ecological evidence

These brief analyses of the environments indicated by the insect faunas show that, even within the small area of the Church Stretton valley, completely different habitats existed synchronously. At RS₂ which was at some distance from the steeply rising hillsides, open grassland occupied the flat valley floor throughout this time. This area may have been cleared of forest by man in the interest of agriculture. The few beetles recorded which are associated with trees all inhabit decaying logs, suggesting that trees had been growing in the vicinity in the recent past. If this was a man-made cleared area, however, it is too protracted a period to be a 'landnam' type of clearance (see Iversen 1941) and must imply settled rather than nomadic occupation. Farther down the valley at Little Stretton, evidence of clearance is much more tenuous and appears later in the sequence. Between these two localities, in the narrowest part of the valley at Worldsend, dense woodland persisted until well into zone VII b. Even here, however, it may be possible to visualize some trace of man's activities. It is noteworthy that almost all the beetles

which are indicative of woodland in this deposit attack trees which are either dead or dying. It seems at least possible, therefore, that the end of this sequence represents man's attempt to reclaim this area by felling the trees and probably burning the trash. This could account for the high numbers of lignicolous beetles at the site and the sudden darkening of the lithology. The covering of gravels which overlie the organic deposits here would then have been released from the adjacent hillside as a consequence of the removal of the protective vegetation cover.

(b) *Climate*

Although the insects show that a variety of habitats existed in the Church Stretton valley during the late Flandrian the climate prevailing can hardly have varied much from site to site at any one time. It is reasonable, therefore, to discuss the thermal environment of the three sites together. All three are unequivocally temperate. If, as in part I, a Scandinavian distribution south of the 15 °C isotherm is taken as the criterion of a 'thermophile' then a large number of the species from each site merit this description. In fact, if to these 'thermophiles' are added those species whose distributions are almost all south of the isotherm but which have one or two odd stations just to the north of it, their percentage representation in the total of specifically named beetles from each site is: RS₂ 31 %, Worldsend 44 % and Little Stretton 48 %. There seems little doubt that summer temperatures were at least as high as those of midland Britain today. *Porthmidius austriacus* and *Eremotes strangulatus* are no longer found in either this country or Fennoscandia, having withdrawn well to the south on the continent, while the non-British *E. elongatus* is only found in the south of Scandinavia. From the presence of these species in Worldsend it might be inferred that summer temperatures were even higher than those of today. All these insects, however, are dependent on dead wood and it is possible that it is the drastic reduction of their habitat due to man's activities rather than a decline in temperature that has eliminated them from this country. A similar case is that of *Ernoporus caucasicus* whose occurrence in the late Flandrian of Shustoke, Warwickshire (¹⁴C date 4830 B.P.) and other midland sites of about this age, could easily have been taken as evidence of a decline in temperature except that Allen (1969) has found it living in Herefordshire today. In fact the species lives on *Tilia*, a tree which, though common here 5000 years ago, has all but disappeared from Britain in the natural state, again probably due to man's agency. Although these southern woodboring species are temptingly suggestive of higher temperatures it is not permissible to accept their uncorroborated evidence. The presence of *Onthophagus fracticornis* and *O. similis* is suggestive but not conclusive of a warmer thermal environment. Unhappily, as mentioned above, only seven authentic British specimens of *fracticornis* were known to Allen (1967) and none of these bore any data. Although it seems probable that all came from the south of England proof is again wanting. However, *Agabus wasastjerna*e has also disappeared from our fauna but has retired towards the north, again more probably on account of the disappearance of its habitat than of a rise in temperature!

Until more conclusive evidence is available from the late Flandrian, therefore, the insect faunas indicate that during zones VIc and VII the summer temperatures were as high as those of today, or may even have been somewhat higher.

I have received much generous assistance with the identifications of certain groups of insects and would like to record my gratitude for this to the following: Professor F. W. Shotton, F.R.S. and Mr H. Kenward (Hemiptera), Dr R. B. Angus (*Helophorus*), Herr Volker Puthz (*Stenus*) and

Dr A. J. Pontin (Formicidae). Both Professor Shotton and Dr G. R. Coope have critically read the manuscript and my thanks are due to them for many helpful suggestions. I would also like to thank Dr Coope with whom I have enjoyed much stimulating discussion on the implications of the insect faunas of the late-Glacial period.

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