PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Insect Fauna of the Organic Deposits at Sugworth and Its Environmental and Stratigraphic Implications

P. J. Osborne

Phil. Trans. R. Soc. Lond. B 1980 **289**, 119-133
doi: 10.1098/rstb.1980.0031

THE INSECT FAUNA OF THE ORGANIC DEPOSITS AT SUGWORTH AND ITS ENVIRONMENTAL AND STRATIGRAPHIC IMPLICATIONS

By P. J. OSBORNE
Department of Geological Sciences, University of Birmingham, Birmingham B15 2TT, U.K.

(*Communicated by F. W. Shotton, F.R.S. – Received* 16 *May* 1979)

[Plate 1]

CONTENTS

		PAGE
1.	Introduction	120
2.	Faunal list	122
3.	Taxonomic notes on incompletely identified species of special interest	126
4.	Environmental implications of the fauna	127
5.	Climate	130
6.	The age of the deposits and their comparison with other fossil faunas	131
	References	133

Forty serial samples, taken at 10 cm intervals throughout the organic part of the deposit, were investigated entomologically, and considerable numbers of insects, predominantly beetles, were found. These were not evenly distributed through the deposit, but their numbers tended to form two very distinct peaks, with some evidence of a third, separated by intervals that were virtually devoid of insect remains. This spasmodic deposition of beetle fragments was attributed to periodic flooding, and this idea was given support by the habitat requirements of the insects themselves, with the greatest numbers belonging to species that live in rapidly flowing water and, in decreasing numbers, species of still water and reed beds, and species that might have been scoured from stream banks. The same faunal assemblage is repeated in each peak and there is no suggestion that the environment changed at all during the period of deposition. A number of beetle species were recorded that are no longer found living in Britain, and these, as well as the much larger number that are still native to this country, indicate a climate at least as warm as, or possibly slightly warmer than, that of the present day. Comparison with other interglacial faunas revealed no close match, but this was not surprising in view of the small number of sites so far studied. It was concluded that, although our knowledge of beetles from interglacial deposits is still inadequate to allow dating by this means, they do not contraindicate a Cromerian age for the Sugworth material and, if their evidence is taken in conjunction with that of the stratigraphy, this age seems to be the most likely.

1. Introduction

In all, 40 samples were collected from the deposit to be examined for insect fossils. These were taken serially, in 10 cm units, from profile D (Shotton *et al.* 1980), from base-line, at 85.2 m above O.D., to 4 m higher, i.e. 2.8 m below ground level. The numbering of these samples is the same as that adopted in Gilbertson (1980) and by Robinson (1980), except that, to save space in the faunal list, the final nought is omitted from each figure. Thus, the lowest sample is D0, the next D1 and so on up to D39 at the top. The size of the samples was fairly uniform, ranging between 4.5 and 7.5 kg and averaging 6.25 kg. These sample weights are shown in table 1.

The samples consisted principally of coarse sand with a greater or lesser admixture of organic material. This organic component was made up of fine, unidentified plant debris, with,

Table 1. Sampling depths, sample numbers and weights, relative organic content and numbers of named individuals per sample

depth/cm	sample no.	weight/kg	organic content	number of individuals
80				
90	39	5	–	0
100	38	5½	–	1
110	37	5½	–	0
120	36	5	–	9
130	35	4½	+	21
140	34	5½	++	21
150	33	6	++	50
160	32	4½	++	19
170	31	5½	++	25
180	30	7	++	24
190	29	6½	++	122
200	28	5½	++	46
210	27	5½	++	77
220	26	6	+	19
230	25	7	+	5
240	24	7	+	0
250	23	7	+	1
260	22	6	+	0
270	21	5½	+	0
280	20	5	–	1
290	19	5½	+	0
300	18	6½	+	0
310	17	6½	+	0
320	16	6½	+	3
330	15	7	++	16
340	14	7	++	22
350	13	7	++	9
360	12	6½	+	35
370	11	7	+++	65
380	10	7	+++	49
390	9	7½	++	44
400	8	7	++	31
410	7	7½	++	35
420	6	6½	++	44
430	5	7	+	12
440	4	7½	+	1
450	3	7	–	1
460	2	6½	–	0
470	1	7	+	2
480	0	7	+	28

sometimes, accumulations of what appeared to be leaves and, occasionally, sticks and comminuted wood. During disaggregation of the samples prior to extraction of the insect remains, a comparative assessment was made of the amounts of organic material in each layer and this is given in table 1. Organic content is symbolized by either –, i.e. little or none noted, or a varying number of + signs, the greater number of signs signifying greater organic content.

The final column in table 1 shows the numbers per sample of individuals of all the named taxa. It will be seen that, as a broad generalization, the numbers of individuals are highest in the samples with the greatest organic content.

To retrieve the insect remains, the samples were first broken down in warm water. The few layers in which lumps of clay were present were soaked in hot sodium carbonate solution, but otherwise, little violence, either chemical or mechanical, was required to reduce the matrix to a slurry. Fine inorganic material was removed by washing through a 300 μm sieve and the residue was sorted directly under a binocular microscope. When a large volume of residue was left on the sieve, paraffin flotation was used to concentrate the fossils before sorting.

The fragments of insect cuticle recovered were mounted on card mounts with gum tragacanth. This has led to considerable shrivelling and deterioration in the condition of many of the specimens, but was considered to be safer than keeping them in spirit, with the risk that they might inadvertently dry up in an uncontrolled manner, which would have been far more destructive. It was also necessary, in many instances, to examine the fragments dry during identification, and the consequent repeated drying and wetting of the specimens was felt to be particularly undesirable in view of their presumed antiquity.

The identification of the Sugworth insect remains presented a considerable problem. Many were only fragments of the original sclerites and were frequently shrivelled or distorted. As it was obvious, also, that a considerable proportion of the fauna was made up of species no longer found in the British Isles and that might be living today at some remote distance from Britain or, perhaps, be extinct altogether, it was decided that over-caution should be the rule in these identifications. Specific names have not been applied, therefore, unless the fossils were well enough endowed with characters that the possibility that another species, indistinguishable on the basis of the available skeletal parts, and that is either extinct or now living far away, was remote. This ultra-cautious approach has resulted in the inclusion in the faunal list of a large number of entries that have not been taken beyond generic level or that have trivial names qualified by a query mark. The more important of these taxa with imperfect identifications are discussed in detail at the end of the species list.

Assessment of numbers of individuals was rarely a problem, as the majority were only represented by one specimen per sample. When more examples were present, however the number given in the list is the minimum that must have been present to account for the skeletal parts recovered.

Although occasional examples of insects other than beetles, chiefly Hemiptera, were found, these constituted such a small minority that their inclusion in the list did not seem to be worth while and they have been omitted. Thus, the following list consists entirely of Coleoptera. Nomenclature follows Kloet & Hincks (1973), and species not now found living in Britain are fitted into this classification in the appropriate places and are marked with an asterisk.

2. Faunal list

name	39	38	37	36	35	34	33	32	31	30	29	28	27	26	25	24	23	22	21	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0
Notiophilus sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.
Dyschirius globosus (Hbst.)	.	.	.	.	1	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	1	.	.	.	.	.	.
Dyschirius sp.	.	.	.	.	.	1	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Trechus secalis (Pk.)	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trechus sp.	.	.	.	.	.	1	1	1	.	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.	1	1	1	.	1	1	1	.	.	1	.	.	1	.	.	.
Asaphidion flavipes (L.)	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bembidion gilvipes Stm.	.	.	.	.	.	.	.	1	.	1	.	1	1	.	1	.	.	.	.	.	.	.	.	.	.	3	.	2	2	4	3	.	.	1	1	.	.	.	.	1
Bembidion guttula (F.) or *unicolor* Chaud.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Bembidion sp.	.	.	.	.	.	.	1	.	.	.	1	.	2	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	1	1	.	.	.	.	.	.
Tachys sp.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.
Stomis pumicatus (Pz.)	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Pterostichus diligens (Stm.)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.
Pterostichus strenuus (Pz.)	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Calathus sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Panagaeus cruxmajor (L.)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Chlaenius sp.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Odacantha melanura (L.)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	1	.	.	.	.	.	.
Dromius sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Gyrinus sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	1	.	.	.	.	.	.	.	.
Georrissus crenulatus (Rossi)	.	.	.	.	1	.	1	1	.	.	1	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Hydrochus sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Helophorus sp.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cercyon spp.	.	.	.	.	.	1	1	.	.	.	.	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	2	1	2	2	.	1	.	.	.	.	.	1
Chaetarthria seminulum (Hbst.)	.	.	.	.	.	.	.	.	1	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	1	.	.	.	.	1
Ochthebius bicolon Germ.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ochthebius minimus (F.)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Ochthebius sp. ‘n’	.	.	.	.	1	1	1	.	1	.	2	5	3	1	.	.	.	.	.	.	.	.	.	.	1	1	.	.	1	1	.	.	1	4	1	.	.	.	.	.
Ochthebius sp.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	1
Hydraena riparia Kug.	.	.	.	.	.	.	.	2	1	1	6	4	5	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	2	2	2	1	.	.	.	.	.	1
Limnebius sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Acrotrichis sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	1	.	.	.	.	.	.	.	.	.

	39	38	37	36	35	34	33	32	31	30	29	28	27	26	25	24	23	22	21	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0
Silpha atrata L.	.	.	.	.	.	.	1	.	.	.	1	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
**Neuraphes* sp.	.	.	.	.	.	.	.	.	1	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.
Micropeplus caelatus Er.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Micropeplus porcatus (Pk.)	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Metopsia ?retusa (Steph.)	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Carpelimus sp.	.	.	.	.	1	2	1	.	.	.	5	1	3	2	.	.	.	.	.	.	.	.	.	.	1	1	.	6	6	6	6	1	2	2	1	.	.	.	.	2
Platystethus nitens (Sahlb.)	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Anotylus nitidulus (Gr.)	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
**Anotylus opacus* Kr.	.	.	.	.	2	1	.	1	1	.	2	.	1	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Anotylus rugosus (F.)	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	1	1	.	.	.	.	.	.	.	.	.
Oxytelus fulvipes Er.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stenus spp.	.	.	.	.	1	1	1	.	1	.	3	.	2	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	5	2	2	1	1	1	.	.	.	.	.	2
Euaesthetus ruficapillus Bois. & Lac.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Paederus sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
Lathrobium longulum Gr.	.	.	.	.	2	.	1	.	.	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lathrobium sp.	.	.	.	.	.	.	1	.	1	.	.	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1
Ochthephilum fracticorne (Pk.)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.
Astenus sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
Rugilus sp.	.	.	.	.	.	.	.	.	.	.	1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Xantholinus linearis (Ol.) or *longiventris* Heer	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Erichsonius sp.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Philonthus sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Tachinus sp.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Deinopsis erosa (Steph.)	.	.	.	.	.	1	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	3	2	1	1	1	.	.	.	.	.	.	.
Aleocharinae indet.	.	.	.	1	.	1	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	1	.	.	.	.	.	.	.	.
Bryaxis sp.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Tychus ?niger (Pk.)	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.
Brachygluta sp.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aphodius spp.	.	.	.	.	.	1	1	.	.	1	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
**Rhyssemus algiricus* Luc.	.	.	.	2	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Onthophagus sp.	.	.	.	.	1	.	4	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.
**Valgus hemipterus* L.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

	39	38	37	36	35	34	33	32	31	30	29	28	27	26	25	24	23	22	21	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0
Limnichus sp.	.	.	.	.	.	.	1	1	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	3	.	.	.	.	.	.	.	.	.	.
**Pelochares versicolor* Waltl.	.	.	.	.	.	.	1	.	.	1	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Helichus substriatus (Mull.)	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dryops sp.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Esolus parallelepipedus (Mull.)	.	.	.	1	.	.	.	1	.	.	6	.	4	1	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.
**Esolus pygmaeus* (Mull.)	.	.	.	.	1	.	.	.	.	.	22	.	4	.	.	.	.	.	.	.	.	.	.	.	2	3	.	8	.	.	2	2	8	8	.	.	.	.	.	.
Esolus parallelepipedus or **pygmaeus*	.	.	.	.	.	1	1	.	2	4	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	1	.	.	.	.	3
Limnius volckmari (Pz.) or *germari* Er.	.	.	.	.	.	.	1	.	.	.	5	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Normandia nitens (Mull.)	.	.	.	.	.	.	.	.	.	.	2	2	3	2	.	.	.	.	.	.	.	.	.	.	.	1	1	2	3	1	2	.	3	6	1	.	.	.	.	1
Oulimnius troglodytes (Gyll.)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.
Oulimnius tuberculatus (Mull.)	.	.	.	.	.	.	3	1	1	2	19	7	11	2	1	.	.	.	.	.	.	.	.	.	4	1	.	3	14	11	7	4	3	5	1	.	.	.	.	2
Stenelmis canaliculata (Gyll.)	.	.	.	.	.	.	1	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Riolus sp.	.	.	.	.	.	.	.	.	.	1	6	.	1	1	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	1	.	1	1	1	.	.	.	.	.	.
**Dupophilus brevis* Kuw.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Trachys ?troglodytes Gyll.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Agrypnus murinus (L.)	.	.	.	.	.	.	1	.	1	1	1	1	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1
Throscus sp.	.	1	.	1	1	.	1	1	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	1	.	.	1	1	.	.	.	.	.	1	.	1	1	.	.	.
Grynobius planus (F.)	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Anobium sp.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hadrobregmus denticollis (Creutz.)		.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ptilinus pectinicornis (L.)	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Dasytes sp.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Epuraea sp.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Sphindus dubius (Gyll.)	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cerylon sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Corylophus cassidioides (Marsh.)	.	.	.	.	.	.	.	.	.	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	3	1	2	1	2	1	1	.	.	.	.	.
Scymnus sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
Stephostellus ?angusticollis (Gyll.)	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypulus quercinus (Quensl.)	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

	39	38	37	36	35	34	33	32	31	30	29	28	27	26	25	24	23	22	21	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	0
Donacia crassipes F.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.
Donacia thalassina Germ.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	1	.	.	.	.	.	1
Donacia spp.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	.	1	.	.	.	.	.	.	.	1
Altica sp.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Epitrix pubescens (Koch)	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	.	.	.	.	.	.	.	.	.
Chaetocnema sp.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Psylliodes sp.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Apion spp.	.	.	.	1	1	1	6	2	1	3	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	2	1	2	.	.	.	.	.	.	.	6
Otiorhynchus ?desertus Rosen.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sciaphilus asperatus (Bonsd.)	.	.	.	.	1	.	1	.	1	.	3	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	1
Leiosoma sp.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Magdalis armigera (Fourc.)	.	.	.	.	.	.	.	.	.	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.
Tanysphyrus lemnae (Pk.)	.	.	.	.	.	.	1	1	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	1	1	2	1	1	1	.	.	.	.	.
Rhyncholus lignarius (Marsh.)	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Dryophthorus corticalis (Pk.)	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Bagous ?nodulosus Gyll.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Bagous sp.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Notaris acridulus (L.)	.	.	.	.	.	1	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Notaris scirpi (F.)	.	.	.	.	.	.	1	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Micrelus ericae	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Ceutorhynchus sp.	.	.	.	.	.	.	.	.	3	.	1	1	2	2	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.
Limnobaris sp.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Anthonomus ?pomorum (L.)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Curculio sp.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rhynchaenus spp.	.	.	.	.	.	1	.	.	.	.	3	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.
Ramphus pulicarius (Hbst.)	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Scolytus multistriatus (Marsh.)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Scolytus scolytus (F.)	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Scolytus sp.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.
Acrantus vittatus (F.)	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
**unknown* sp. 'A'	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

3. Taxonomic notes on incompletely identified species of special interest (see p. 121)

Ochthebius *sp.* '*n*'

Elytra representing at least 25 examples of a very small *Ochthebius* were recovered from a number of samples spread through the deposit. These elytra strongly resembled those both of the British species *O. exaratus* Muls. and of the southern European *O. narentinus* Rtt., but, because of the distortion and shrivelling that had occurred on drying, it was not possible to say which. This being so, they would have been placed on the list as '*Ochthebius exaratus* or *O. narentinus*' if other distinguishing skeletal parts, especially pronota, had been present to support this diagnosis, but, unfortunately, none of these were found. On the other hand, among the small number of *Ochthebius* pronota that were recovered, a few were found that matched the elytra in size, but that were clearly neither *O. exaratus* nor *O. narentinus*. Although it is not impossible, it seems unlikely that the elytra of at least 25 specimens of a beetle should become incorporated into a deposit without a single pronotum. If, however, the elytra and the correspondingly sized pronota do belong together, the species is not one found living in Britain today, nor, so far as can be ascertained, in western Europe. It seems, therefore, unavoidable that this insect, among the most abundant in the Sugworth deposits, must be recorded as '*Ochthebius* sp.', at least for the time being.

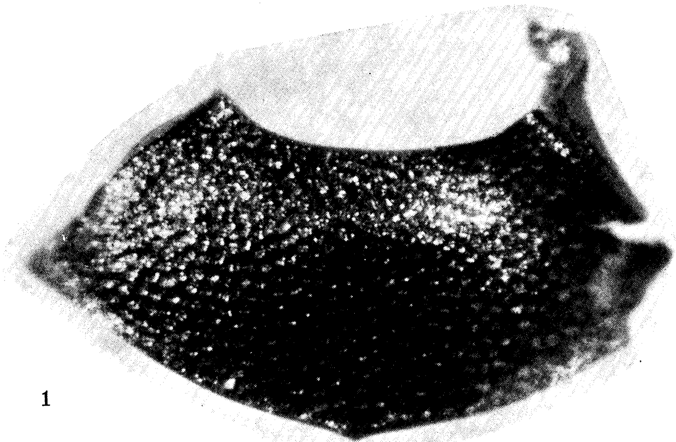
Neuraphes *sp.* (figure 3, plate 1)

Scattered throughout the deposit were examples of a Scydmaenid, of which only the pronota were recognized, belonging to the genus *Neuraphes* but not to a species currently found in Britain. The pronotum is roughly the size and shape of that of the British *N. carinatus* (Muls.) but, perhaps, a trifle broader and with a rather shorter basal carina. The principal distinguishing feature, however, is the sculpture of the upper surface, for, whereas *N. carinatus* is smooth and shining, the Sugworth specimens have at least the first three-quarters of the dorsal surface of the pronotum shagreened and matt. Freude *et al.* (1971), in their key to the genus *Neuraphes*, say of the very rare species *N. imitator* Blattny, next in the key to *N. carinatus*, 'die O.S. des Korpers chagriniert, nur schwach glanzend', so that it is possible that the Sugworth specimens may belong to this species. It has not so far been possible to examine a specimen of *N. imitator* for comparison. In the key by Freude *et al.*, little use is made of characters found on the pronotum, so that, in the absence of other skeletal parts, the key can be of little further use, and progress beyond '*Neuraphes* sp.' is not possible at this stage.

Rhyncolus (*sens. lat.*) *spp.*

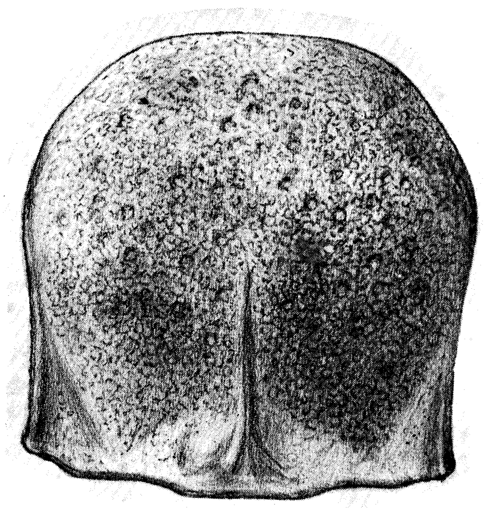
A number of heads, of pronota and of elytra belonging to members of this group were collected from different levels through the deposit, but have, so far, mostly remained unidentified. It is certain that at least three, and possibly four, non-British species are included, and it is hoped that much more work on the group will result in some, or all, of these being named more specifically. In the meantime, however, their presence is noted but they are omitted from the faunal list, with the possibility that they will form part of a supplementary list of Coleoptera from Sugworth to be published at a later date.

All members of this group live in dead wood, some in conifers, some in hardwoods and some in either. All three types might be represented here.



1

2



3

FIGURE 1. Unknown 'sp. A', pronotum, magn. × 90.
FIGURE 2. Unknown 'sp. A', left elytron, magn. × 90.
FIGURE 3. *Neuraphes* sp. pronotum, magn. × 200 (drawing).

(*Facing p.* 126)

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Unknown 'sp. A' (figure 1 and 2, plate 1)

A single left elytron and a pronotum were found which, because they came from the same sample (no. 34) and are comparable in size, sculpture and colour and appear capable of being fitted together, are assumed to belong to the same animal. They have so far defied identification, even to family level.

The elytron is roughly 1.25 mm long and, if we assume little or no distortion to have taken place, about 0.5 mm wide. The pronotum is about 0.5 mm from the front margin to the back and its maximum width is 1.25 mm. The front margin is about half the width of the base. The beetle was clearly convex and short and probably approximated in size, shape and colour, but in no other respect, to the histerid *Onthophilus striatus* (Forst.). Both parts were black when found.

The elytron is devoid of striae and is confusedly punctured, the spaces between the punctures being about the same width as the punctures themselves. Most of the punctures were of more or less uniform size, but there were a few much smaller and some larger scattered among them. As there was no obvious cutaway at the corner of the elytron, it is likely that the scutellum was either very small or absent altogether. Puncturation of the pronotum was dense, almost rugose, the punctures practically touching each other. The base was slightly sinuate, more or less corresponding to the shape of the base of the elytron, and came to a small point in the centre. The hind angles were very acute, but did not give the impression of having, in life, projected beyond the margin of the elytron.

4. Environmental implications of the fauna

Although all the samples were of approximately the same size and the crude macroscopic assessment of their lithologies did not disclose any very marked differences throughout the deposit, other than variations in the proportion of included organic matter, beetle fossils were not uniformly distributed but were concentrated in two distinct bands. These were in samples 5 to 16 and 25 to 36, with the intervening samples, numbers 17 to 24, containing few or no beetle remains. What may have been the tail end of another, earlier, band of productivity can also be seen in sample 0 (see table 1 and figure 4). The actual taxa making up these two episodes of activity are remarkably similar and there is no suggestion that two different environmental régimes were represented. In fact, the fauna do not show any sign of environmental variation at all and, with its lithology of coarse sand with sticks and leaves, it may well be that the entire deposit represents only a short period of time. If not, then conditions must have remained stable for a long while.

Several generalized, but easily defined, habitat types are shown by the beetle assemblage to have been present in the vicinity of Sugworth at the time of deposition. The most obvious of these are grassland; trees; still or slowly flowing water; in association with reed beds; and rapidly running water. In figure 4, the number of individuals recorded from each sample indicative of these five biotopes is shown graphically, together with a graph including all the named taxa. There is obviously a difference between this last graph and the sum of the other five, and this represents those beetles that are so catholic in their requirements that they are found more or less everywhere and those few from habitats so specialized or uncommon that they are not a significant part of the environment. The taxa upon which each graph is based are as follows.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Grassland

The taxa associated with grassland are chiefly forms such as *Onthophagus* sp. and *Aphodius* sp., which live in the dung of grazing animals. The staphylinids *Anotylus opacus*, *Anotylus rugosus* and *Oxytelus fulvipes* are also included as, although they may be found in rotting vegetation of various kinds, dung is their most usual habitat, too. The larvae of *Agrypnus murinus* live on grass roots and the adult is found among long grass, while the predator *Stomis pumicatus* is almost always found in grassland and so is included.

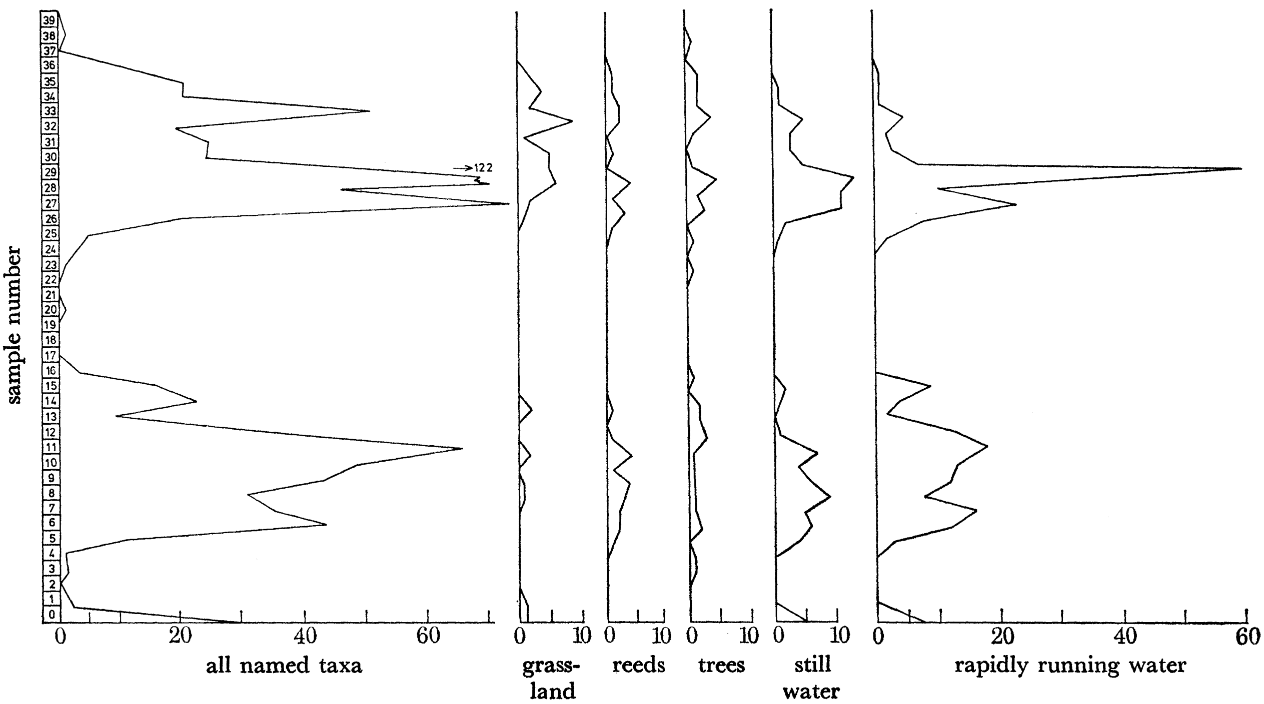


FIGURE 4. Number of named individuals per sample representing the various habitat groups.

Trees

Only deciduous trees are essential for the tree feeding beetles recorded, although the hosts of a small number may also include conifers. Insects living on *Salix* are not counted as tree dependent, as these could have been on very small bushes or even *Salix herbacea*. Taxa that are included are nearly all woodborers or bark beetles, although there are some exceptions. Those whose occurrences are shown on the graph are *Throscus* sp., *Grynobius planus*, *Ptilinus pectinicornis*, *Anobium* sp., *Hadrobregmus denticollis*, *Magdalis armigera*, *Rhyncolus lignarius*, *Dryophthorus corticalis*, *Cerylon* sp., *Hypulus quercinus*, *Anthonomus ?pomorum*, *Curculio* sp., *Scolytus multistriatus*, *Scolytus scolytus*, *Scolytus* sp. and *Acrantus vittatus*. In addition to these, it will be remembered that a number of *Rhyncolus* (*sens lat.*) spp. were present but do not appear on the list (see p. 126).

Reed beds

The weevils *Notaris acridulus*, *Notaris scirpi*, *Limnobaris* sp. and *Bagous* spp. all live on waterside vegetation such as *Carex*, *Phragmites*, *Scirpus* and other reeds. Many members of the genus *Donacia*, too, live on these plants, but, as *Donacia crassipes* is found principally on waterlilies and

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Donacia sp. cannot be assigned to any host plant with certainty, the only member of the group to count for the purposes of the graph is *Donacia thalassina*. The carabid *Odacantha melanura* lives among reeds as a predator, while the little corylophid *Corylophus cassidioides* is found under fallen reeds.

Still or slowly flowing water

Included in this group are *Hydrochus* sp., *Helophorus* sp., *Chaetarthria seminulum*, *Ochthebius bicolon*, *Ochthebius minimus*, *Ochthebius* spp. and *Hydraena riparia*, all of which live in still water, either clambering among vegetation, hanging beneath the surface film or inhabiting the mud at the edge. *Gyrinus*, the whirligig beetle, which swims mainly on the surface, and the weevil *Tanysphyrus lemnae*, whose host plant is the floating duckweed, *Lemna*, are taken into account, and also *Donacia crassipes*, *Donacia thalassina* and *Donacia* spp. *Donacia crassipes* lives on waterlilies, and most of the other *Donacia* species, on various forms of emergent aquatic vegetation rooted in a muddy bottom.

Rapidly flowing water

The family Elmidae has contributed all the species in this section. These insects live in well aerated water, where they cling to submerged stones. Taxa included here are *Esolus parallelopipedus*, *Esolus pygmaeus*, *Limnius volckmarii* or *germari*, *Normandia nitens*, *Oulimnius troglodytes*, *Oulimnius tuberculatus*, *Riolus* sp. and *Dupophilus brevis*. The dryopid *Helichus substriatus*, which usually lives in rivers, and the elmid *Stenelmis canaliculata*, usually a lake species, were both considered to be borderline cases and so have not been included in either of the categories of aquatic beetles.

Although there are very obvious differences in the numbers represented by each of these graphs, their form in each case is very much the same. The high peaks are found in the same levels for every habitat group, so that there is no question of one biotope expanding at the expense of another.

Easily the best represented group is the one whose members live in rapidly running water. Next in importance is the quiet water assemblage with its corollary the reed bed fauna. It is most likely, therefore, that the deposit consisted of material, carried by a stream, that was dropped as the water lost its momentum on entering a larger body of water. The coarse, sandy matrix, with its occasional more organic horizons, has the appearance of deposits from flood waters. It is probable, then, that the high peaks in beetle numbers, coinciding as they do with increases in organic content, represent periods of flooding. Water with high velocity was able to dislodge the elmids from their stones and rose up the banks far enough to collect terrestrial beetles, representing the countryside through which the stream was passing. On reaching a lake or larger river this flood refuse was dropped, incorporating a selection of the fauna of the quieter water. The lake or river was near enough to being stationary to permit a growth of duckweed on its surface and also to become colonized by the floating fern *Azolla*. Although no insect evidence for the presence of this plant was found, its massulae were recovered from a number of samples during sorting for beetles. The water margins were fringed with reed beds and the water was deep enough to permit the growth of waterlilies.

In between times of flooding the stream probably flowed less violently and dropped down from its banks. Little organic material and few terrestrial insects were picked up and the well adapted elmids were able to live undisturbed. Sediment brought down at these times was therefore comparatively sterile.

The majority of the taxa not covered by the five main habitat categories are animals that

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

do not have an obvious preference and are chiefly to be found amongst leaf litter and other accumulations of vegetable debris. A small number, mainly phytophagous species, do have fairly well defined habitats. Thus, *Sphindus dubius* lives on Mycetozoa growing on dead wood, and the adults are also found occasionally among moss. The flea beetle, *Epitrix pubescens* lives on *Solanum*, while the species of *Chaetocnema* are found mostly on *Polygonum* and related plants. The weevil *Sciaphilus asperatus* passes its immature stages in the roots of *Primula officinalis* and again the adult is found in moss. *Micrelus ericae* is found on various Ericaceae and *Ramphus pulicarius* lives on species of *Salix*. All of these are compatible with the foregoing picture of a rapidly running stream flowing through a mixed landscape of grassland with trees, picking up a collection of beetles from both its own bed and its banks during times of flood, to deposit them later when the stream entered a larger body of water, where they joined representatives of the indigenous fauna there.

5. Climate

From a faunal list that includes so many 'genus only' identifications, climatic deductions cannot be very precise. It is clear, however, that there is no suggestion in the insect evidence of temperatures lower than those of Sugworth at the present day.

Of the species present at Sugworth that no longer live in Britain, all, with the possible exceptions of '*Neuraphes* sp.' and the unrecognized 'sp. A', today occur further to the south. The scarabaeids *Valgus hemipterus* and *Rhyssemus algiricus* and the limnichid *Pelochares versicolor* are all found in France at the present time, *Rhyssemus* rather further to the south than the other two. The elmid *Dupophilus brevis* is a southern European insect and *Anotylus opacus* is found in southeast Europe, its distribution being centred around the Danube basin. None of these species is found in mainland Scandinavia, although one or two occur in Denmark.

The species that are found in Britain today but that have very restricted ranges here are not very informative. Until recently, *Stenelmis canaliculata* was known as British from specimens from only one locality, Lake Windermere. As it has now been recorded from the River Nene, and, according to fossil evidence, was much more widespread here during the late Flandrian, its lack of present day records may owe more to its habitat, which is rather inaccessible and so tends to be neglected by collectors, than to genuine rarity. *Dryophthorus corticalis* is a weevil that lives in rotten wood, particularly old oaks, usually in company with the ant *Lasius brunneus* (Lat.). This species, too, is one which, though known from only a single present locality, Windsor Forest, Berkshire, was widespread earlier in the Flandrian before forest clearance in favour of man's agriculture eliminated most of its habitat. Thus, although it appears to have retreated to the south, its present restricted range owes more to man's activities than to climatic change. The presence of *Micropeplus caelatus* may be of greater climatic significance, however, as there is no obvious reason for its retreat from a number of localities from which it is known as a Flandrian fossil (Osborne 1974; M. A. Girling, personal communication) to its single known modern station in southwest Ireland, a spot noted for the mildness of its climate. The species has a very sporadic distribution on the continent, which does not appear to owe anything to human activities and could well be due to a number of relict occurrences in favoured sites surviving from a time when climatic conditions were more suitable. In Scandinavia *M. caelatus* is confined to the southernmost tip of Sweden, another suggestion of its need for a temperate climate, probably milder than southern England today.

On the evidence from the insect remains, therefore, it is possible to say that the climate was at

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

least as warm as that of Sugworth today and was most likely to have been somewhat warmer. A more positive indication of higher temperatures may be obtained if '*Neuraphes* sp.', 'sp. A' and the various Rhyncolines become identified.

6. The age of the deposits and their comparison with other fossil faunas

That the Sugworth deposits were laid down under interglacial conditions is clear from the insect evidence alone, as beetle assemblages were found that indicate summer temperatures at least as high as and possibly higher than those of the present day, and a number of species were present that are dependent on deciduous trees. It is unfortunate that so few insect faunas from interglacial times have been described that dating or even stratigraphic correlation by their use is not yet possible. Certain similarities with, and differences from, the Sugworth fauna may be seen in other interglacial assemblages, however, that may be used to support dating evidence from other lines of research.

The present interglacial, the Flandrian, has been better studied entomologically than the preceding ones. From early in the period, around 9600 a B.P., a fauna has been described that consists of beetles that inhabit marshland or water and also of a number associated with deciduous trees (Osborne 1974). Later in the interglacial, around 5000 a B.P., the insects from a number of sites give evidence of dense woodland, and many species not now on the British List are recorded from sites of this age (Osborne 1964, 1972; Buckland & Kenward 1973). After this, the activities of man, a factor not operating in the earlier interglacials, began to make themselves felt, and a Bronze Age (3330 a B.P.) fauna from Wilsford, Wiltshire, has been examined in which the insects were all of open grassland, with no evidence whatever for trees (Osborne 1969). Despite the wide range of environments represented by these Flandrian insect assemblages, no deposit has yet been found from this period that contains a fauna with a marked similarity to that of Sugworth. The radiocarbon 'date' from Sugworth, beyond 47000 a B.P., would, in any event, rule out the possibility of a Flandrian age for this deposit, and there is some slight evidence for higher temperatures than those indicated by the known Flandrian faunas.

From earlier times, the Hoxnian interglacial has provided some well documented insect faunas. To date, the most completely studied of these is the one from Nechells, Birmingham (Shotton & Osborne 1965). Here again, a temperate fauna was found, but the few exotic species it included suggested a somewhat cooler climatic régime than at Sugworth. The most notable species, *Platypus oxyurus* Duf., though a woodboring insect living on *Abies* and now found considerably further south than England, tends to inhabit high ground, chiefly in the Pyrenees. Another lignicolous beetle, *Brachytemnus submuricatus* Schonh., was found in some numbers and this species, too, is found in southern France, but again tending towards higher ground. Neither beetle was recorded from Sugworth. Other deposits at Quinton, Birmingham, and at Brandon Wood near Coventry that are considered, on stratigraphic and palynological grounds, to be contemporary with Nechells contain similar faunas, including *Platypus oxyurus* (H. K. Kenward, personal communication).

Another site in the Brandon area, referred to as 'Brandon Channel', appears to belong to either the late Hoxnian or early Wolstonian. A fauna from this locality indicated much cooler conditions than those from Nechells and Quinton, however, and it is probably more correctly assigned to a time early on in the Wolstonian glaciation, although a small but not insignificant element in the fauna carried the suggestion of warmer conditions and may have been a relict population surviving for a short time in specialized habitats (Osborne & Shotton 1968).

The only other comprehensive interglacial insect fauna that has been investigated to date is that from the Ipswichian site at Trafalgar Square, London (G. R. Coope, personal communication). This material contained a very rich beetle assemblage as well as a mammal fauna and many molluscs. A large proportion of the Sugworth insects, including most of the exotic species, such as *Pelochares versicolor* and *Valgus hemipterus*, and species still living in Britain but with very restricted distributions, like *Stenelmis canaliculata* and *Dryophthorus corticalis*, and even the unknown 'sp. A', are present in the Trafalgar Square fauna. The great disparity in size between the two faunas precludes a more direct comparison, but it appears that very similar environments are represented. In view of the fact that an Ipswichian age for Sugworth does not seem to be compatible with the stratigraphic evidence (Shotton *et al.* 1980), it is most likely that the resemblance between the two faunas is due to the deposits being laid down under very similar climatic conditions.

A summary of this section must necessarily be inconclusive because of the paucity of previous work on insects from the earlier interglacials and, in fact, none at all on beetles from the Cromerian. Direct comparison with this period is not, therefore, possible but if, as is supposed, the Cromerian climatic régime was akin to that of the Ipswichian, the resemblance of the Sugworth fauna to that of Trafalgar Square may be considered as slender additional evidence of a Cromerian age for the Sugworth deposits.

My thanks are due to two specialists, Dr P. Nohel and Mr P. Hammond, who have confirmed my tentative identifications of *Micropeplus caelatus* and *Anotylus opacus* respectively. I would also like to thank Professor F. W. Shotton for explaining the stratigraphy of the Sugworth deposits to me and for drawing the pronotum of *Neuraphes* sp. (plate 1, figure 3) and Dr G. R. Coope for his cooperation in allowing me access to the beetle material from the Ipswichian site at Trafalgar Square. Finally, I should like to thank Mr R. C. Swift of the Geography Department, Birmingham University, for his photographs of 'unknown sp. A' (plate 1, figures 1 and 2).

References

Buckland, P. C. & Kenward, H. K. 1973 Thorne Moor: A paleoecological study of a Bronze Age site. *Nature, Lond.* **241**, 405–406.

Freude, H., Harde, K. W. & Lohse, G. A. 1971 *Die Kafer Mitteleuropas*, vol. 3. Krefeld: Goecke & Evers.

Gilbertson, D. D. 1980 The palaeoecology of Middle Pleistocene mollusca from Sugworth, Oxfordshire. *Phil. Trans. R. Soc. Lond.* B **289**, 107–118.

Kelly, M. R. & Osborne, P. J. 1964 Two faunas and floras from the alluvium at Shustoke, Warwickshire. *Proc. Linn. Soc. Lond.* **176**, 37–65.

Kloet, G. S. & Hincks, W. D. 1973 A check list of British Insects, pt. 3, Coleoptera and Strepsiptera; rev. R. D. Pope. *Handb. Ident. Brit Insects*, **XI**. pt. 3, *R. Ent. Soc. Lond.*

Osborne, P. J. 1969 An insect fauna of late Bronze Age date from Wilsford, Wiltshire. *J. Anim. Ecol.* **38**, 555–566.

Osborne, P. J. 1972 Insect faunas of Late Devensian and Flandrian age from Church Stretton, Shropshire. *Phil. Trans. R. Soc. Lond.* B **236**, 327–367.

Osborne, P. J. 1974 An insect assemblage of Early Flandrian age from Lea Marston, Warwickshire, and its bearing on the contemporary climate and ecology. *Quat. Res.* **4**, 471–486.

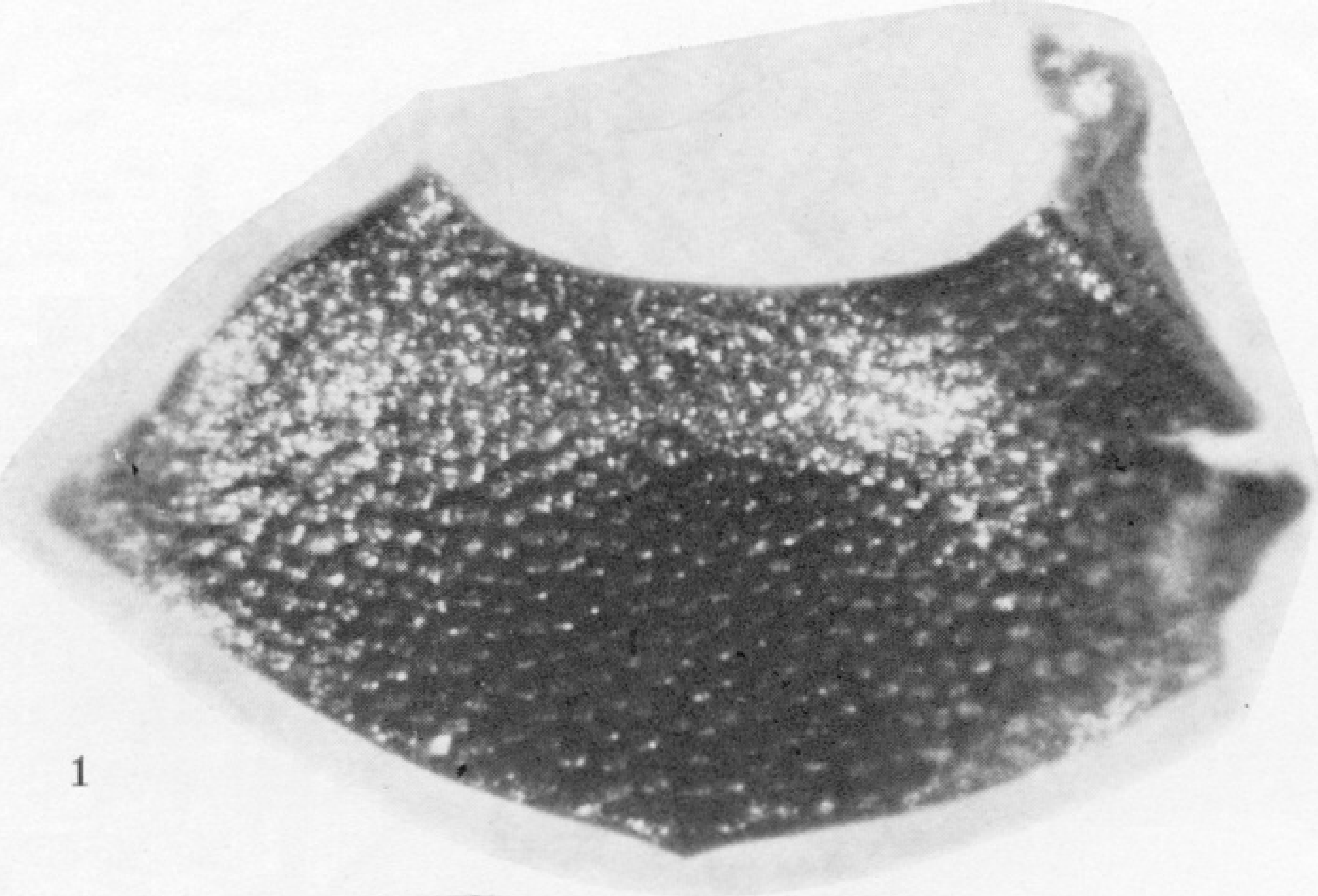
Osborne, P. J. & Shotton, F. W. 1968 The fauna of the Channel Deposit of Early Saalian age at Brandon, Warwickshire. *Phil. Trans. R. Soc. Lond.* B **254**, 417–424.

Robinson, J. E. 1980 The ostracod fauna of the interglacial deposits at Sugworth, Oxfordshire. *Phil. Trans. R. Soc. Lond.* B **289**, 99–106.

Shotton, F. W. & Osborne, P. J. 1965 The fauna of the Hoxnian Interglacial Deposits of Nechells, Birmingham. *Phil. Trans. R. Soc. Lond.* B **284**, 353–378.

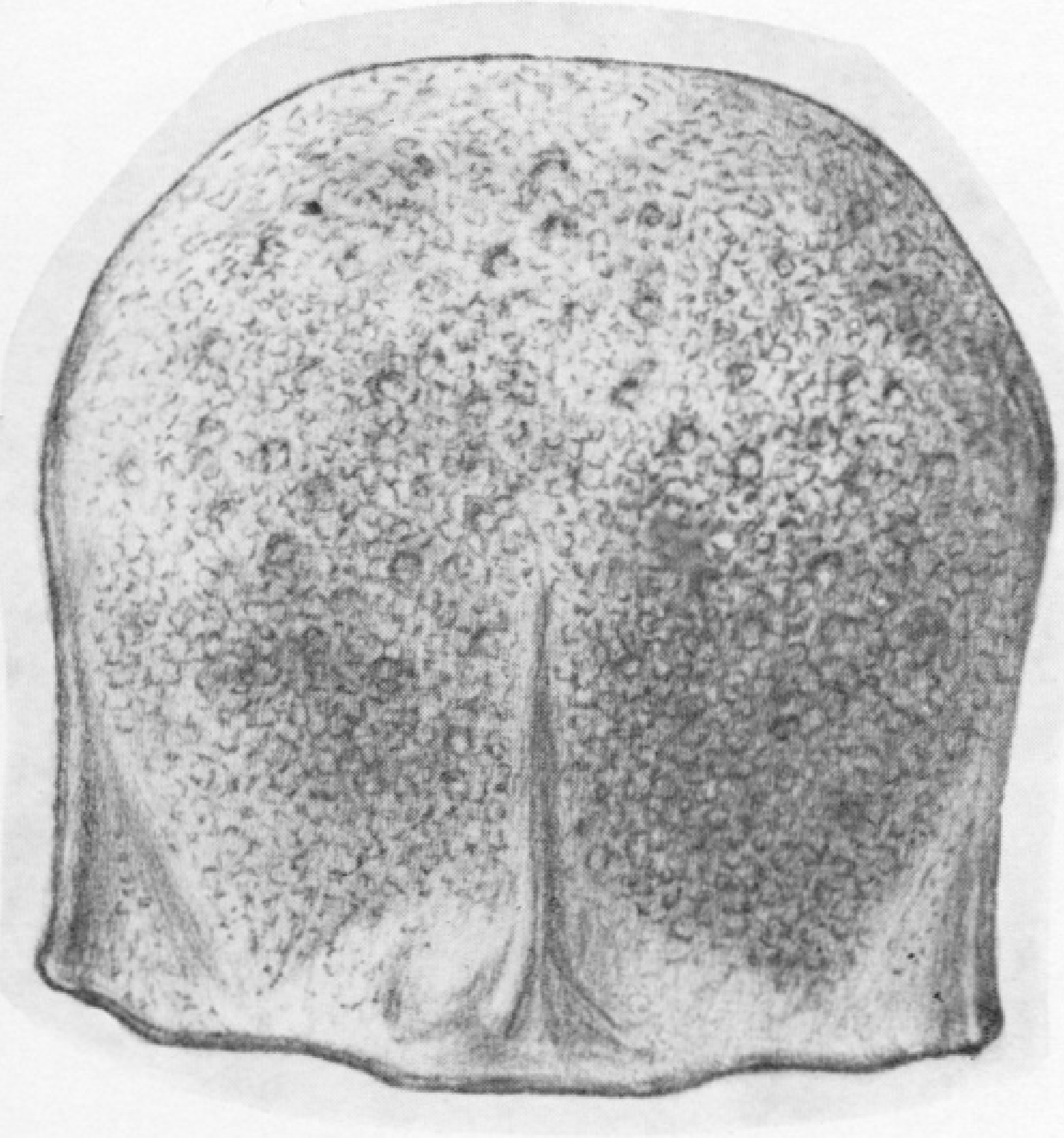
Shotton, F. W., Goudie, A. S., Briggs, D. J. & Osmaston, H. A. 1980 Cromerian interglacial deposits at Sugworth, near Oxford, England, and their relation to the Plateau Drift of the Cotswolds and the terrace sequence of the Upper and Middle Thames. *Phil. Trans. R. Soc. Lond.* B **289**, 55–86.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES



1

2



3

FIGURE 1. Unknown 'sp. A', pronotum, magn. ×90.

FIGURE 2. Unknown 'sp. A', left elytron, magn. ×90.

FIGURE 3. *Neuraphes* sp. pronotum, magn. ×200 (drawing).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES