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A Late Pleistocene Fauna and Flora from Upton Warren, Worcestershire

G. R. Coope, F. W. Shotton, I. Strachan and S. P. Dance

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A LATE PLEISTOCENE FAUNA AND FLORA FROM UPTON WARREN, WORCESTERSHIRE

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With an appendix on the genus *Pisidium* at Upton Warren

By S. P. DANCE

(*Received* 3 *February* 1961)

[Plates 19 to 22]

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A large fauna and a large flora are described from terrace deposits of the River Salwarpe at Upton Warren, Worcestershire. The fossils occur in several extensive lenticular bands of silt in the lower half of a gravel succession. From the stratigraphy and a radiocarbon age of 42 000 years, the deposits are ascribed to the beginning of the Gottweig Interstadial, immediately following the maximum of the Midland Irish Sea Glaciation. The latter is thus considered to belong to the last and most severe episode of the Early Würm.

The silt bands represent a succession of ancient pools which contained an extensive fauna of vertebrates, molluscs, ostracods, insects and spiders and a large flora which call for explanation in ecological and climatological terms. The beetles include a substantial component not now British; there is a strong northern element but others are more southern in their present-day distribution, one or two are continental and at least three appear to be extinct. The flora is akin to that of present-day south Sweden except for a great scarcity of trees.

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There is evidence from several directions of the existence of brine springs, causing the water of one pool to be mildly brackish and affecting its fauna and flora. Some of the drier land plants also suggest a salty environment. Apart from this complication, the fauna shows an unexpected mixture of northern and less northern forms which nowadays would be mutually incompatible. This is explained as due to a very rapid amelioration of climate following the glacial maximum, with Arctic species still persisting against the inroads of the more thermophilous species coming from the south. The scarcity of trees is not ascribed to true tundra conditions but it is suggested that the grazing of large herds of bison may have had a controlling influence on tree growth.

I. The geology of the site

(*a*) *Location*

The Upton Warren site was a large gravel pit worked until 1958 by the Queslett Sand and Gravel Company Limited. It lies in the county of Worcester, on the east side of the main Birmingham–Worcester road midway between Bromsgrove and Droitwich at latitude 52° 18′ 15″ N, longitude 2° 5′ 40″ W, National Grid reference SO/935673.

(*b*) *Stratigraphical position of the Upton Warren deposits*

The gravel occurs under a terrace feature, only a few feet above alluvium level, fringing the River Salwarpe, a tributary of the Severn. Wills (1938, pp. 201–3 and Pl. XIV) described how this terrace becomes more widely separated from the alluvium as it is followed downstream, until at the mouth of the Salwarpe it is 45 ft. above alluvium and coincident with the Main Terrace of the Severn. With this he therefore correlated it, though at the time of his paper the Upton Warren gravels were not known to be fossiliferous. The subsequent finding of a mammalian fauna (described below) which includes *Mammuthus primigenius*, *Coelodonta antiquitatus*, *Bison priscus* and *Rangifer tarandus*, strongly supports the correlation, since the same cold fauna is found in the Main Terrace of the Severn (Wills 1938, pp. 186, 190, 205) and in its equivalent, Avon no. 2 (Tomlinson 1925, p. 150).

The position of these terraces in the Pleistocene sequence of the Midlands is well established. Definitely older must be both the morphological features and the deposits underlying them, which constitute Avon Terraces 3 and 4 and the Kidderminster Terrace of the Severn. Terrace no. 3 contains *Hippopotamus amphibius* and *Elephas antiquus*. *Corbicula fluminalis* occurs in the lower part of no. 4, and at the top of no. 4 are late Acheulian implements (Shotton 1953, pp. 230, 231). These deposits are clearly younger than the Wolston Series and Chalky Boulder Clay of east Warwickshire (Shotton 1953) which are now generally accepted as due to the Saale (Riss or Penultimate) Glaciation. It follows, therefore, that Terraces 3 and 4 must cover the Eemian (Riss/Würm or Last) Interglacial. The Severn Main Terrace, with its cold fauna, thus falls into the Last Glaciation. Wills (1924) has shown the relationship between the Irish Sea Glacier which advanced as far south as Burton–Lichfield–Wolverhampton–Church Stretton, the ponding of Lake Lapworth against the watershed which then existed at Ironbridge, the cutting of the Ironbridge Gorge by overflow waters, and the deposition of the Main Terrace when the gorge was only partly cut. Thus the Main Terrace, and hence the Upton Warren gravels, may be related to a stage in the retreat of the Irish Sea Glacier some time after it had reached its farthest south position only 20 miles north of Upton Warren.

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Progressively later than the Main Terrace are the Worcester (Upper Danesford), Lower Danesford and Power House (Atcham) terraces (Wills 1938, p. 230) in the upper part of the Severn, to be correlated with later stadia of the Last Glaciation. Wills has equated the Worcester Terrace with what he calls the Little Welsh or Welsh Readvance Glaciation.

(*c*) *Radiocarbon dating of Upton Warren and its bearing on correlation with the European Pleistocene succession*

From Band no. 2 (see later), pieces of the dark layers that were visibly plant-containing, were cut out with a clean knife and dropped into a glass jar. The band here was under about 18 ft. of gravel in a newly exposed vertical face, so that modern contamination of the samples was unlikely. The material was washed through a sieve with distilled water and the retained residue dried. From this were then picked out fragments of plant matter until more than enough was available for a determination of age by radiocarbon. It proved impracticable to obtain an adequate sample from the organic layer which sometimes occurred 5 ft. lower at the base of the gravels, for where seen, this made up the floor of the pit, disturbed by the action of the grab and under shallow water, and contamination was therefore very probable.

The sample was sent to the Yale Geochronological Laboratory, which reported that its age was in excess of the sensitivity limit of their measuring apparatus (38 350 years), but was not likely to be greatly beyond this (Barendsen, Deevey & Gralenski 1957, sample Y 311 A). It was then sent to Professor de Vries at Gröningen who was able to give a positive figure. His ultimate interpretation (de Vries 1958*a*, *b*) for a sample only subjected to acid pretreatment, was 41 500 $\pm$ 1200 (GRO 595).

At this time it was thought that the age of certain deposits of the Eemian Interglacial had been determined, within the range of 50 000 to 43 000 years. These 'determinations' were later shown (Tauber & de Vries 1958) to have been made on contaminated samples, but as this was then not known, the Upton Warren date seemed out of place. In order to check and, if possible, correct it, a new determination was made on more of the same sample, giving it a pre-treatment designed to remove modern humic contamination. The result this time (GRO 1245) was 41 900 $\pm$ 800. Moreover, the extracted humus (GRO 1063) which should have shown the influence of any contamination, gave a figure in excess of 40 000 (de Vries 1958*a*). The age of the organic layer 2 could therefore be said to be very firmly substantiated at, in round figures, 42 000 years.

As a final check, we sent to Gröningen a small sample of peat which had been dredged from the lower part of the gravels of Avon no. 2 Terrace in a pit at Fladbury, Worcestershire. Though on a different river, this had long been correlated with the Severn Main Terrace and therefore with Upton Warren (Tomlinson 1925; Wills 1938; Shotton 1953). Though the exact position of the peat within the terrace deposits was unknown, its age would be expected to be close to that of Upton Warren if the correlation were correct. Support for the correlation had also been provided by an assemblage of beetle remains from the Fladbury specimen which, though more limited than that of Upton Warren owing to the small size of the sample, had enough in common with it to suggest that the age was similar.

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The Fladbury date was determined as 38 000 ± 700 (GRO 1269), a useful confirmation of the validity of the Upton Warren figure.

The absolute age of the Upton Warren fauna and flora can then be regarded as established. Its position in the complicated sequence of climatic and ecological changes that affected Britain and Europe during the Würm Glaciation is important and is made much clearer by the accumulation of radiocarbon dates for various parts of the European sequence. The modern position has been fully discussed by Gross (1958), following the general lines of Woldstedt. Table 1 is based on part of Gross's table, p. 182, but includes three early dates not printed in Gross's paper, made possible by the refinement of thermal diffusion concentration in radiocarbon measurements. These are 57 000 for the peaty layer in the Middle Sands of Cheshire at Chelford (Simpson & West 1958, p. 249, footnote; Coope 1959); a figure of 59 000 in the Brörup–Loopstedt Interstadial (in fact, two separate determinations on Brörup material agreeing closely); and the oldest date yet measured, 64 000 ± 1100 (GRO 1397), in the Amersfoort Interstadial (de Vries 1958*a*; Andersen, de Vries & Zagwijn 1960). The position of the dividing lines is also modified following the dating of a layer in the Hörmating (Bavaria) drumlin (Ebers 1960; Gross 1960).

Dominating the succession is the long Gottweig Interstadial complex which separates the Older Würm from the Main Würm. Defined by the thick soil zone at the top of Younger Loess I, it has been shown to post-date the Mousterian culture and of course to antedate Younger Loess II (Main Würm). It is associated in time with the long evolution of the Aurignacian culture. When Andersen (1957) first redescribed the Brörup section and recognized there a substantial Post-Eemian Interstadial, he equated this with the Gottweig Interstadial. In a more recent paper (Andersen *et al.* 1960) no mention is made of this correlation; and even though the Gottweig Interstadial cannot be recognized yet in either Denmark or Holland, it is clear both from geological reasons and the accumulation of radiocarbon dates that it is much later than the Brörup–Loopstedt Interstadial.

Using Gross's chronology (table 1), it appears that the Irish Sea Glaciation of the Midlands is Wv_3, for it was during its retreat that the Upton Warren (and Fladbury) gravels were deposited. It is of interest that this glaciation which marks the greatest extent of ice in England during the Würm corresponds with the maximum of the Older Würm, but not with the greatest extent of Würm Glaciation of the continent, which is Wh_2. Also, although on stratigraphical grounds it is clear that the Upton Warren deposits shortly post-date the Irish Sea maximum, it is also clear that the abundant Chelford flora and fauna, which has previously been described as interstadial (Simpson & West 1958; Coope 1959), is older than the Irish Sea Glaciation and lies in the important Brörup–Loopstedt Interstadial.

(*d*) *Detailed geology of the site*

The Terrace deposits consist dominantly of coarse gravel with many pebbles up to 3 in. in size and occasional ones exceeding 1 ft. Interbedded irregularly with the gravels are bands of brown sand. The maximum thickness of deposit seen in the workings was 31 ft. Entirely within the lower half of the gravels occurred a number of dark bands, never more than 3 ft. thick and usually less. Typically each consisted of a lower layer of grey sand, often pebbly and with all ferruginous coloration destroyed, containing molluscs but not much carbonaceous matter; a middle layer, highly carbonaceous, of silt and fine sand;

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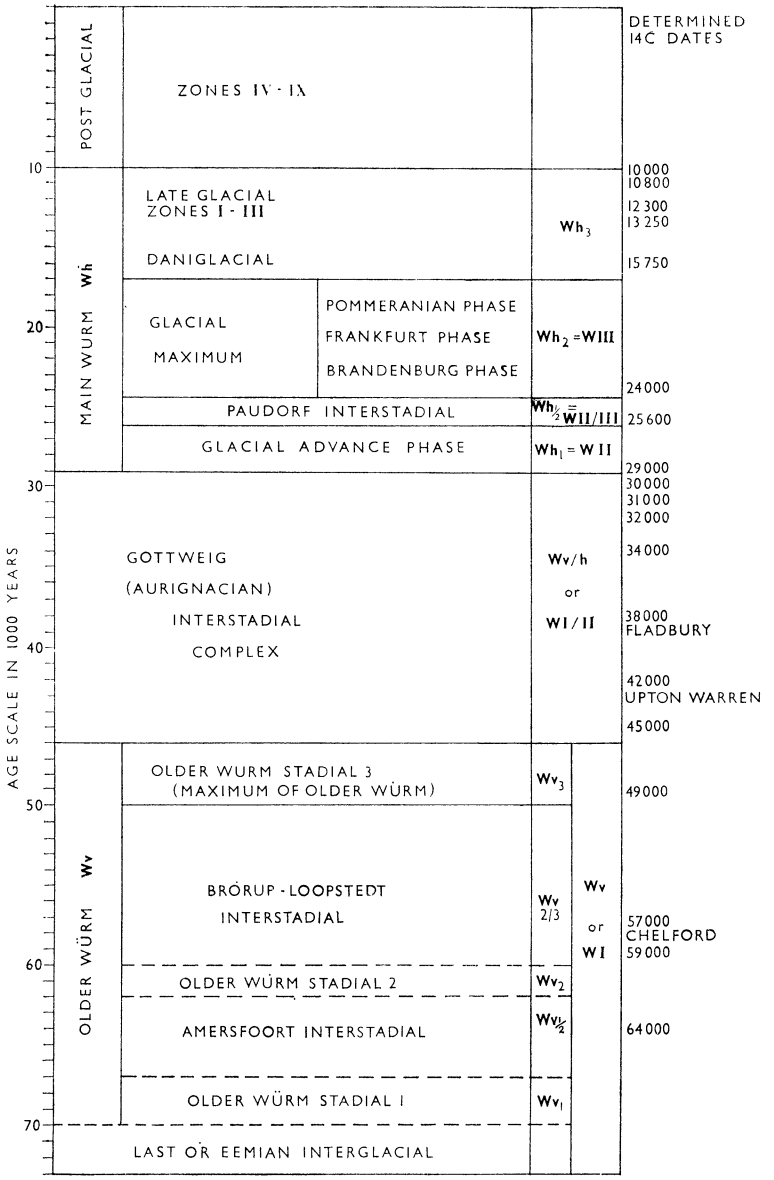
and an upper layer of greenish grey silt. Organisms were most abundant in the dark zone. This threefold zonation could usually be seen even when the band was strongly disturbed by cryoturbation.

The number, thickness and extent of these dark bands varied as the pit face advanced. At the end of the pit's period of working when the face had approached towards Hen

TABLE 1



Brook, they had disappeared. From the nature of the sediment they could be interpreted as very shallow ponds, an interpretation confirmed beyond question by their content of pond-dwelling plants, molluscs, ostracods, fish and water beetles. We therefore visualize that, as the valley filled up spasmodically with gravelly alluvium there were periods of quiescence and during some of these, in the earlier stages of aggradation, large shallow pools existed on the floodplain long enough to allow colonization by plants and animals. In due course these were silted up and covered by newly arriving sand and gravel.

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There is the general impression that accumulation of these coarse gravels was rapid in a geological sense, but it is not possible to express in years the time represented by each dark band or by the separating sands and gravels. Nor, since the upper dark layer was not organically rich enough to give an adequate sample, and the basal layer was almost certainly contaminated, was it possible to get a series of radiocarbon dates which might have indicated whether the black band sequence covered much time.

These dark layers, representing very shallow water, should be horizontal. It is clear from figure 1 that they are more or less parallel to each other, but by no means level. Band 2 drops 9 ft. in a face distance of 240 ft. and Band 1 falls 10 ft. in the same length. What might appear a puzzling feature receives a simple explanation in the presence of the Stoke Prior Salt Works little more than half a mile beyond point *A* in figure 1. The pumping of brine from the Keuper Marl has produced a large subsidence with a lake just north of the

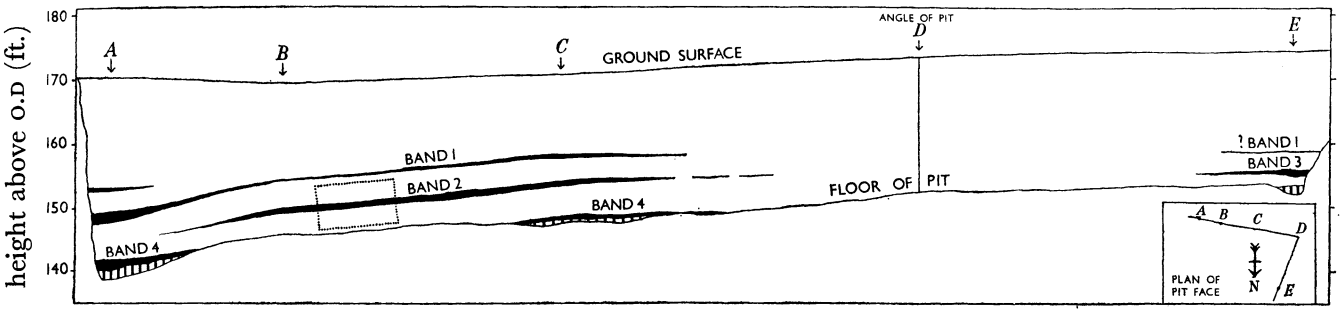

FIGURE 1. Distribution of organic bands in the working face on 21 June 1955. Ground level and details of the section were accurately determined at points *A* to *E*, but minor irregularities of the organic bands are not shown. The dotted rectangle covers the area illustrated in detail in figure 2. ■ = Organic layers; ▥ = Keuper Marl. Vertical scale $2\frac{1}{2}\times$ horizontal.

River Salwarpe near 'the Moors' and the downwarping of the dark bands is another manifestation of this same cause. The only important bearing of this subsidence on the interpretation of Upton Warren is that the base and top of the terrace at point *A* must be regarded as originally not lower than 150 and 181 ft. O.D., respectively.*

The bands were given numbers according to figure 1. Band 4 occurred irregularly on the uneven surface of Keuper Marl and was often absent—as it was in an exploratory section at *E*. Band 3 was only seen over a small length of the western face, but Band 2 was sectioned in its entirety and progressive working showed it to thin out and disappear southwards as well as to the west and east. Although Bands 2 and 3 are approximately on the same level and might be contemporary, they were never seen to join and their fauna is sufficiently distinct (see p. 387) to make it certain that they were separate pools in space, if not necessarily in time. Band 1 was usually thinner than 2 and not so richly organic. A thin black streak above Band 3 may be on the same level as Band 1.

After these numbers had been allocated and used in correspondence, a still higher band appeared in the corner of the pit (point *A*) but it was never proved to extend far and no collecting was done from it. It was therefore not given a number.

* Levelling was based on a bench mark on the bridge on the main road over the river. This may itself be suspect of having subsided but it is clear from the engineering of the road and the position of the Salwarpe in its channel that the effect cannot be large.

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(*e*) *Cryoturbation within the gravels*

The simplicity of structure shown in figure 1 is fallacious. The dark bands were undulating and frequently broken by festoons, an effect which showed most strikingly in Band 2. Figure 2 shows the detail of a length of the layer which is involved in intense disturbance and cut by at least one frost wedge. The festooning affects the sands and gravels down to $2\frac{1}{2}$ ft. below the organic band and also for the same distance above, but does not extend into the higher coarse gravels which sharply truncate the disturbances. The significance of these in relation to climate is discussed later.

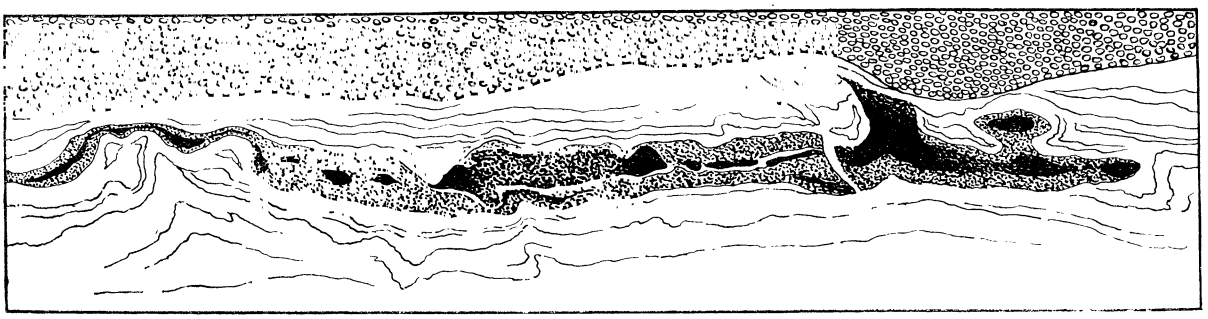

FIGURE 2. Detail of a length of Band 2 (black and close stipple) showing cryoturbation prior to the overlying coarse gravel. Length of section 30 ft. True scale. (From a photograph and sketches by R. Pickering.)

(*f*) *Evidence for sea level at the time of the Upton Warren deposition*

It is well known that throughout the Pleistocene there was a world-wide fall of sea level, evidenced by a succession of beaches and river terraces, from a figure of about +300 ft. in the Early Pleistocene down to the present-day sea level (Zeuner 1959, Chapter IX). This fall was, however, by no means steady. There were periods when the glaciations were building up to their maxima and water was being locked up in the ice caps, when the lowering of sea level was accelerated and even taken below that of the present day; there were intervening times when the rate of fall was decreased or even reversed, so that the sea rose in level. It is not possible to postulate where the sea lay at the time when the Upton Warren gravels were deposited by reference to any general principle but we can draw valid conclusions from a study of the space relationships of the Main Terrace of the Severn (M. 1 of Wills) and of its correlatives in other rivers, including the Salwarpe.

The benches which are the relics of the old alluvial plain, now dissected and left as steps above the river, extend from above the Ironbridge Gorge down to the tidal estuary at least as far as Woolaston. Their position has been plotted by Wills (1938, Pls. XIV and XV). The surfaces lie approximately on a smooth curve, but depart from the best curve that can be drawn by as much as 10 ft. These discrepancies are normal and arise from three causes—original error in estimating the exact height, the fact that the front part of a terrace may have been lowered by subsequent erosion, and the fact that the back of a terrace may be raised by solifluxion creep of material from the adjacent higher land. If the curve of the old alluvial course is drawn to give the best fit to all the observations, it is seen to become almost flat in the present-day tidal reach and to asymptote to a height of about 32 ft. above O.D. The modern alluvium of the same stretch of river lies at about 20 ft.

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above O.D. It can therefore be assumed that when the Main Terrace gravels had been completely deposited, along with those in its tributary valleys, the alluvial plain of that time led down to a sea between 10 and 15 ft. above present-day level.

The maximum thickness of the gravels at Upton Warren was 31 ft. and this order of thickness has been recorded along the Severn above the Salwarpe confluence, in the lower part of the Severn at least down to Gloucester and along the tributary Avon. The bottom of the channel which was filled with Main Terrace gravels thus forms a curve about 30 ft. lower than the top of the terrace. Being a surface of erosion rather than of deposition, it need not bear the same relation to contemporary sea level as did the top of the terrace, but it must grade to a sea level which at its lowest could only be 15 to 20 ft. below O.D. and could be expected to be a little higher, say 5 to 10 ft. below O.D. (This argument makes no allowance for the possible existence of a knickpoint joining on to a lower profile graded to a lower sea level, the whole being now submerged—of which there is, however, no evidence.)

If therefore we assume that alluviation of the Severn and its tributaries started with a sea level 5 to 10 ft. below O.D. and finished when the sea had risen 20 ft., the deposition of the dark bands at Upton Warren, in the lower 10 ft. of the section, must correlate with a sea level almost identical with that of the present day.

We have felt it necessary to establish as closely as possible the level of the sea because had this been very different from the present day, it might have explained some of the unusual features of the Upton Warren flora and fauna. As it is, we can say that the plants and animals to be described below lived in and around ponds on a gravelly flood plain about 150 ft. above sea level and just about as far inland as Upton Warren is now. Any changes in the biota cannot be ascribed to important changes in topography.

II. The fauna and flora

(*g*) *Collection, separation and preservation of the fossils*

The bones and teeth of the larger mammals were chiefly recovered by the quarry workmen, though occasionally also by the authors. Some, by their staining, were obviously from the organic-rich layers, but many others came from the general body of the gravels.

All other organisms were restricted to the dark bands. The larger molluscs were obvious on inspection but all the other remains were virtually invisible and rather thinly scattered in the deposit and it was not until a great concentration had been achieved that they became apparent.

The technique of separation was simple though time-consuming. After any visible pebbles had been removed, the sample was washed through two sieves—the upper of about 6 mm mesh to retain pebbles, some plant fragments and the larger molluscs, the lower of about 0·6 mm aperture. With the silt and clay removed, the concentrate consisted of sand grains and small pebbles with much miscellaneous vegetable material, seeds, molluscs, ostracods, insect parts and any remains of small vertebrates such as fish or rodents. Occasional checks were made on the fine material passing through the sieve to ensure that it carried no organisms. The material retained on the 0·6 mm sieve was usually roughly dried before being sorted under a binocular microscope. This part of the operation

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was particularly time-consuming, especially since a second or even third inspection usually revealed further organic material. Large numbers of specimens were obtained purely because a great amount of suitable material was washed through the sieves—we would estimate about 600 kg.

Preservation of everything but insect and arachnid remains presented no problem, but the latter on drying tended to buckle and sometimes crack. It was found best to stick these on cards. As they dried, iridescent colours common in the beetles disappeared in most cases in favour of a uniform black and although this could to some extent and for a few times be regenerated by damping, it was advisable to note the exact colour of the metallic tints whilst the specimens were damp, if it was to be used as a character in identification.

(*h*) *Comprehensive list of fauna and flora*

VERTEBRATA

MAMMALIA

Mammuthus primigenius (Blum.).
Coelodonta antiquitatus (Blum.).
Bison priscus (Boj.).
Rangifer tarandus (L.)
Equus caballus L.
Dicrostonyx henseli Hinton. Band 3.
Microtus sp. Band 3.

AMPHIBIA

Rana temporaria L. Band 3.

PISCES

Gasterosteus aculeatus L. Band 2 (rare), Band 3 (abundant).

MOLLUSCA

	Band 2	Band 3	Band 4
Lymnaea peregra (Müller)	501 (55 %)	167 (28·4 %)	2 (6 %)
L. truncatula (Müller)	1 (0·1 %)	3 (0·5 %)	17 (47 %)
L. palustris (Müller)	10 (1·1 %)	—	—
Planorbis laevis Alder	227 (25 %)	137 (23·3 %)	—
P. crista (Linn.)	—	2 (0·4 %)	—
P. leucostoma Millet	—	2 (0·4 %)	—
Succinea pfeifferi (Rossmässler)	48 (5·3 %)	—	8 (22 %)
Succinea cf. *schumacheri* (Andrae)	2 (0·2 %)	—	—
Ancylus fluviatilis Müller	—	—	8 (22 %)
Pupilla muscorum (Linn.)	4 (0·4 %)	1 (0·2 %)	1 (3 %)
Pisidium casertanum (Poli)	2 (0·1 %)	5 (0·4 %)	—
P. subtruncatum Malm.	1 (0·05 %)	45 (3·8 %)	—
P. nitidum Jenyns	—	> 500 (43 %)	—
P. obtusale Lamarck var. *lapponicum* Clessin	30 (1·6 %)	—	—
P. vincentianum Woodward	192 (10·5 %)	—	—

(Each mollusc species is shown as a percentage of the total collected from each band, two shells of a bivalve counting as one individual.)

ARTHROPODA

CRUSTACEA—Ostracoda

	Band 2	Band 3
Candona candida (Müller)	common	common
C. neglecta Sars	occasional	occasional
Ilyocypris bradyi Sars	fairly common	rare
I. gibba (Ramdohr)	rare	rare
Cypris pubera Müller	very rare	very rare
Cyprinotus salinus (Brady)	very common	—
Erpetocypris reptans (Baird)	occasional	rare

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INSECTA

ODONATA

Three mandibles of a small species.

HEMIPTERA

SALDIDAE

Salda littoralis (L.). Band 3. 12 left hemelytra, 11 right hemelytra.
Saldula saltatoria (L.). Band 3. 1 (possibly 2) right hemelytron.

JASSIDAE

Aphrodes bifasciatus (L.). Band 3. 3 left wings, 3 right wings.
Strongylocephalus agrestis (Fall.). Band 3. 1 left wing.
Deltocephalus ocellaris (Fall.). Band 3. 1 right wing.

MEGALOPTERA

SIALIDAE

Sialis sp. Band 3. 32 heads, 2 larval mandibles.

TRICHOPTERA. All Band 3.

PHRYGANEIDAE

Phryganea obsoleta Hagen. 6 inferior appendages to ♂ genitalia.

LIMNEPHILIDAE

Fragments of wings.

Miscellaneous remains of unidentified caddis flies including 20 adult heads, many larval sclerites and cases.

COLEOPTERA	band	head	pro-notum	left elytron	right elytron	remarks
CARABIDAE						
Carabus hortensis L.	3	0	1	0	0	—
Carabus sp.	3	0	0	0	f	2 mandibles
Nebria gyllenhali (Schoen.)	3	0	1	0	0	—
Pelophila borealis (Payk.)	3	0	1	1	0	—
Notiophilus aquaticus (L.)	1	1	0	0	0	—
	3	17	2	16	16	—
Helobium multipunctatum (L.)	3	1	2	1	2	—
Elaphrus lapponicus Gyll.	3	1	0	1	0	—
E. cupreus Dufts.	2	3	1	1	3	—
	3	5	7	8	6	sternites
E. riparius (L.)	3	18	11	18	19	—
Loricera pilicornis (Fab.)	3	5	4	8	5	—
Dyschirius arenosus Steph.	3	0	3	3	5	1 pair joined elytra
D. septentrionum Munst.	3	1	2	3	6	head with mandibles
D. globosus (Hbst.)	3	0	2	2	1	—
Dyschirius spp.	2	0	1	0	0	—
	3	0	1	0	0	—
Bembidion lampros (Hbst.)	3	0	0	0	1	—
B. bipunctatum (L.)	2	0	0	1	1	—
	3	10	12	53	48	2 heads with mandibles
B. obliquum Sturm	3	0	2	11	11	—
B. virens Gyll.	3	0	0	1	0	—
B. femoratum Sturm	3	0	1	4	1	—
B. lunatum (Dufts.)	3	0	3	4	3	—
B. aeneum Germ.	3	0	5	12	13	—
Bembidion spp.	3	2	2	3	4	—
Patrobus septentrionis Dej.	3	2	1	1	0	—
P. assimilis Chaud.	3	0	1	0	1	—
Harpalus cordatus (Dufts.)	3	0	1	0	0	—
Harpalus sp.	3	0	1	0	0	—
Amara municipalis Dufts.	3	0	2	0	0	—
A. erratica Dufts.	3	0	1	0	0	—
A. interstitialis Dej.	3	0	1	1	0	—

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INSECTA (*cont.*)

	band	head	pro-notum	left elytron	right elytron	remarks
COLEOPTERA (*cont.*)						
CARABIDAE (*cont.*)						
A. quenseli (Schoen.)	3	0	9	0	0	—
Amara spp.	3	4	0	4	4	some of these are probably from above spp.
A. (*Cyrtonotus*) *torrida* Ill.	2	0	1	1	0	—
	3	14	19	19	16	—
Feronia adstricta (Eschs.)	3	0	1	0	1	—
F. nigrita (Fab.)	3	0	1	1	1	—
F. diligens Sturm.	3	0	0	1	0	—
Calathus melanocephalus (L.)	3	0	0	1	1	—
Agonum sexpunctatum (L.)	3	0	1	1	1	—
A. sahlbergi (Chaud.)	3	0	1	2	4	(see p. 395)
A. versutum (Gyll.)	3	0	1	0	0	—
Cymindis angularis Gyll.	3	0	0	1	0	—
HALIPLIDAE						
Haliplus obliquus (Fab.)	3	0	0	4	1	—
H. ruficollis agg.	3	0	0	2	2	—
DYTISCIDAE						
Hygrotus cf. *novemlineatus* (Steph.)	3	0	2	2	0	—
H. impressopunctatus (Schall.)	3	1	0	0	0	1 meso-metasternum
Deronectes depressus-elegans agg.	3	0	1	6	3	—
D. griseostriatus (De G.)	3	1	0	?	2	—
Hydroporus arcticus Thoms.	3	0	6	0	0	5 meso-metasterna
H. palustris (L.)	3	0	0	2	1	1 meso-metasternum
H. planus (Fab.)	3	10	38	ff	ff	52 meso-metasterna
Hydroporus spp.	3	0	2	ff	ff	1 meso-metasternum
Agabus congener (Thunb.)	3	1	2	0	0	—
A. nebulosus (Forst.)	3	1	2	2	1	1 assoc. ind. with underside
A. articus (Payk.)	3	0	5	ff	ff	3 meso-metasterna
A. sturmii (Gyll.)	3	3	3	0	0	—
A. bipustulatus (L.)	3	0	3	2	3	—
Ilybius subaeneus Er.	3	0	0	0	0	1 last sternite
Ilybius sp.	3	0	0	0	0	1 last sternite like *I. similis*
Ilybius sp.	3	0	1	1	3	—
Rantus exsoletus (Forst.)	3	5	1	ff	ff	—
Rantus sp.	3	1	0	0	0	—
Colymbetes paykulli (Er.)	3	5	9	ff	ff	8 abdominal sternites
C. fuscus (L.)	3	36	34	ff	ff	36 abdominal sternites
Dytiscus marginalis L.	3	2	?	ff	ff	isolated limb fragments
GYRINIDAE						
Gyrinus minutus Fab.	3	1	0	0	0	—
HYDROPHILIDAE						
Ochthebius dilatatus Steph.	3	0	0	1	1	associated
Limnebius truncatellus (Thunb.)	3	0	0	1	1	—
Helophorus nubilis Fab.	3	0	1	0	0	—
H. aquaticus (L.)	3	163	192	17	14	2 heads and pronota joined, many heads with mandibles
H. brevipalpis Bedel	3	31	53	20	24	—
Sphaeridium scarabaeoides (L.) or *lunatum* Fab.	3	1	0	0	0	—
Cercyon melanocephalus (L.)	3	0	0	9	10	—
C. ustulatus (Preyss.)	3	0	0	?	1	—
C. tristis (Ill.)	3	0	0	15	6	—

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INSECTA (*cont.*)	band	head	pro-notum	left elytron	right elytron	remarks
COLEOPTERA (*cont.*)						
HYDROPHILIDAE (*cont.*)						
Cercyon spp.	3	0	2	9	4	—
Cryptopleurum minutum (Fab.)	3	0	0	1	2	—
Hydrobius fuscipes (L.)	2	2	0	0	0	—
	3	18	9	10	7	—
Laccobius minutus (L.)	3	0	0	3	0	—
Enochrus quadripunctatus (Hbst.) var. *fuscipennis* (Thoms.)	2	1	0	0	0	—
SILPHIDAE						
Thanatophilus dispar (Hbst.)	3	19	24	23	22	+aedeagus
Aclypea opaca (L.)	3	2	0	5	5	1 pair last abd. segs.
Catops sp.	3	0	0	0	1	—
LEIODIDAE						
Hydnobius punctatus (Sturm.)	3	0	0	2	2	—
Leiodes spp.	3	0	5	7	14	—
STAPHYLINIDAE						
Omalium sp.	3	1	0	0	0	—
Olophrum sp.	3	0	0	1	1	similar to *O. boreale* (Payk.)
Olophrum spp.	3	0	0	1	7	—
Arpedium sp.	3	0	2	0	0	—
Acidota crenata (F.)	3	1	0	2	0	—
Geodromicus plagiatus (F.)	2	0	0	1	0	—
	3	3	1	9	14	—
cf. *Oxytelus* sp.	3	1	0	0	0	(see p. 396 and plate 21)
Platystethus nitens Sahlb.	3	0	2	0	0	—
Platystethus spp.	3	11	0	0	0	—
Bledius littoralis Heer	3	0	8	0	0	—
Bledius spp.	3	1	1	1	5	—
Xantholinus linearis Ol.	3	5	1	0	0	—
Philonthus rotundicollis Mén.	3	4	14	0	0	—
P. linki Solsky	3	1	0	0	0	—
Philonthus spp.	3	13	6	9	10	Probably including elytra of *P. rotundicollis* and pronota close to *P. varius* Gyll., *P. varians* Payk. and *P. longicornis* Steph.
Staphylinus pubescens DeG.	3	1	0	0	0	—
S. olens (Müll.)	3	0	0	1	0	—
S. aeneocephalus DeG. or *fortunatorum* (Wol.) (= *cupreus* Rossi)	3	9	20	4	6	—
Quedius spp.	3	8	17	?	?	several species like *Q. boops* (Grav.)
Tachinus sp.A.	3	20	95	83	98	numerous last hind-body segments and 3 aedeagi (see p. 396 and figure 3)
Tachinus spp.	3	0	8	8	4	hind-body segments
CANTHARIDAE						
Cantharis figurata Mann	3	0	1	0	0	—
C. rufa L. (*liturata* Fall.)	3	26	21	?	0	—
Cantharis cf. *paludosa*	3	1	0	0	0	—
ELATERIDAE						
Hypnoidus riparius (Fab.)	3	0	6	3	2	1 prosternum
Corymbites melancholicus Fab.	3	0	1	0	0	1 prosternum

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INSECTA (*cont.*)

	band	head	pro-notum	left elytron	right elytron	remarks
COLEOPTERA (*cont.*)						
DRYOPIDAE						
Dryops ernesti Des Gosiz	3	3	3	6	9	—
GEORISSIDAE						
Georissus crenulatus (Rossi)	3	0	0	6	1	—
HETEROCERIDAE						
Heterocerus hispidulus Kies.	3	7	17	22	26	several associated prosterna
H. fusculus Kies.	3	1	1	1	1	—
H. fenestratus (Thunb.)	3	1	1	1	1	—
BYRRHIDAE						
Simplocaria semistriata (Fab.)	3	2	6	47	44	—
Morychus aeneus (Fab.)	2	0	0	1	0	—
	3	0	0	0	1	—
Cytilus sericeus (Forst.)	3	7	15	13	8	—
Byrrhus fasciatus (Forst.) or *arietinus* Steff.	3	5	6	6	5	—
B. pilula L.	3	3	2			
B. pustulatus (Forst.)	2	0	0	0	1	—
Syncalypta sp.	3	0	0	0	2	—
NITIDULIDAE						
Kateretes rufilabris Lat.	3	1	1	0	0	joined
CRYPTOPHAGIDAE						
Antherophagus pallens (Fab.)	3	0	1	0	0	—
COCCINELLIDAE						
Hippodamia tredecimpunctata (L.) or *septemmaculata* DeG.	3	2	0	0	0	—
Coccinella septempunctata L.	3	1	0	0	0	—
C. undecimpunctata L.	3	4	2	ff	ff	two heads joined to pronota
ANOBIIDAE						
Caenocara bovistae (Hoff.)	3	0	1	0	1	—
ANTHICIDAE						
Anthicus sp.	3	0	0	0	2	—
TENEBRIONIDAE						
Crypticus quisquilius (L.)	3	15	14	14	14	—
SCARABAEIDAE						
Geotrupes sp.	3	0	0	0	1	fragmentary
Aphodius fossor (L.)	3	0	1	0	0	—
A. rufipes (L.)	3	10	2	4	5	—
A. cf. *distinctus* (Müll.)	3	281	107	23	29	22 small *Aphodius* heads from Band 2
A. cf. *prodromus* (Brahm) or *sphacelatus* (Pz.)	3			25	21	5 small *Aphodius* pronota from Band 2
A. plagiatus (L.)	3			3	6	
A. fimetarius (L.)	3	5	3	?	?	—
Aphodius sp.A.	3	47	25	ff	ff	see p. 396
Aphodius spp.	3	0	0	4	3	—
Aegialia sabuleti (Pz.)	3	4	9	14	11	—
	4	1	0	0	0	—
CHRYSOMELIDAE						
Donacia thalassina Germ.	3	0	1	2	3	undersides and hind tibia
Donacia sp.	2	0	0	?	?	fragmentary elytron
Chrysolina limbata (Fab.)	3	0	0	1	0	—
C. staphylea (L.)	3	14	14	6	2	—
C. marginata (L.)	3	1	1	3	0	—
Chrysolina spp.	3	3	3	0	0	—

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INSECTA (*cont.*)

	band	head	pro-notum	left elytron	right elytron	remarks
COLEOPTERA (*cont.*)						
CHRYSOMELIDAE (*cont.*)						
Gastrophysa viridula DeG.	3	3	1	0	0	—
Phaedon armoraciae (L.)	3	4	3	11	6	3 heads assoc. with pronota
P. pyritosus Ol.	3	0	3	7	6	see p. 396 and plate 21
Entomoscelis adonidis Pell.	3	1	0	0	1	—
Galeruca tanaceti (L.)	3	27	11	9	5	—
Crepidodera interpunctata Lotsch.	3	1	5	7	10	—
Chaetocnema spp.	3	0	0	6	3	—
BRUCHIDAE						
Bruchus/Bruchidius spp.	3	0	0	2	0	—
CURCULIONIDAE						
Apion spp.	3	0	0	1	5	—
Otiorrhynchus arcticus (Fab.)	2	2	0	0	0	—
	3	30	18	ff	ff	—
O. ligneus (Ol.)	2	1	0	0	0	
	3	22	24	8	8	—
O. rugifrons (Gyll.)	3	5	0	0	0	—
Phyllobius spp.	3	2	0	0	0	—
Sitona lepidus Gyll.	2	1	0	0	0	
	3	46	24	5	8	—
Sitona spp.	2	1	0	0	0	—
	3	3	1	0	0	—
Bagous tempestivus (Hbst.)	3	0	0	0	1	—
Notaris aethiops (Fab.)	3	12	3	5	8	—
	4	5	4	3	3	—
Notaris acridulus (L.)	3	0	2	1	1	—
N. bimaculatus (Fab.)	3	0	1	ff	ff	—
Grypus equiseti (Fab.)	3	2	1	6	5	—
Phytonomus dauci (Ol.)	3	1	0	0	0	—
P. nigrirostris (Fab.)	2	0	0	1	0	—
Ceuthorhynchus spp.	3	0	1	0	2	—
Rhinoncus castor (Fab.)	3	1	1	0	0	—
Litodactylus leucogaster (Marsh.)	3	13	20	35	34	—
Orobitis cyaneus (L.)	3	0	1	3	1	—
Mecinus collaris Germ.	3	0	0	0	1	—
Rhynchaenus foliorum (Müll.)	3	0	0	1	0	—

Note: f, ff = fragment(s).

HYMENOPTERA. All Band 3.

TENTHREDINIDAE

Dolerus sp. 2 mesonota.

DIAPRIIDAE

Galesus sp. 2 heads.

FORMICIDAE spp. 2 heads.

Miscellaneous Hymenoptera. 84 heads, 141 thoracic fragments, 1 abdomen.

DIPTERA

NEMATOCERA

TIPULIDAE. Band 3. 6 heads, 30 larval heads.

CHIRONOMIDAE. Band 3.

Chironomus sp. 78 larval heads.
Cryptochironomus defectus agg. 2 larval heads.
Glyptotendipes sp. 20 larval heads.

BIBIONIDAE

Dilophus sp. Band 2. 2 thoraxes.
Band 3. 1027 thoraxes, 83 heads.

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INSECTA (*cont.*)

DIPTERA (*cont.*)

SYRPHIDAE

Melanostoma/Platycheirus spp. Band 3. 9 tergites.

Miscellaneous Diptera. Band 3. 81 heads and numerous thoracic fragments.

ARACHNIDA. All Band 3.

ARANEAE

LINYPHIIDAE

Erigone sp. 41 cephalothoraxes.

LYCOSIDAE. 2 cephalothoraxes.

ACARI

Pelops sp. 1 individual.

Miscellaneous. 21 individuals.

PLANTS

	Band 2	Band 3
Armeria maritima (Mill.)	—	*p*, *cal* common
Artemisia sp.	*p*	*p*
Atriplex sp.	—	*s*
Betula sp.	*p*	*p*
Blysmus rufus (Huds.)	—	*n* fairly common
Campanula cf. *rotundifolia* Linn.	—	*s* very rare
Campanula sp.	*p*	—
Campylium sp.	—	*sh*
Capsella bursa-pastoris (Linn.) (?)	—	*s* rare
Carex dioica Linn.	—	*n*+*u* very rare
C. flava Linn.	—	*n* fairly common
C. rostrata Stokes	—	*n* common
Carex spp.	*n*	*n* very common
Caryophyllaceae	*p*	*p*
Cerastium arvense Linn.	—	*s* rare
Characeae	*o*	*o* abundant
Coenococcum geophilum	—	spore body, common
Compositae Liguliflorae	*p*	*p*
Compositae Tubuliflorae	*p*	*p*
Cruciferae	*p*	*p*
Cyperaceae	*p*	*p*
Dianthus cf. *carthusianorum* Linn.	*s*	*s* common
Draba incana Linn.	—	*fv* very rare
Eleocharis palustris (Linn.)	—	*n* very rare
E. quinqueflora (Hartm.)	*n*	*n* fairly common
E. uniglumis (Link.)	*n*	*n* common
Empetrum nigrum Linn.	—	*st* rare
Glaux maritima Linn.	—	*f*, *s* common
Gramineae	*p*	*p*
Helianthemum chamaecistus Mill.	—	*p*
Hippuris vulgaris Linn.	*st*	*st* abundant
Isoetes cf. *hystrix* Durieu	—	*sp* very rare
Lathyrus (?) or *Vicia* (?) sp.	—	*fv*, *s* very rare
Leontodon autumnalis Linn.	—	*a* common
Linum praecursor Reid	—	*s* fairly common
Luzula spicata (Linn.)	—	*s* rare
Montia fontana agg.	*s*	*s* very common
moss capsule	—	bryoid, rare
Myriophyllum alternifolium DC	—	*n* common
M. spicatum Linn.	—	*n* abundant
Myriophyllum sp.	—	*p*
Parnassia palustris Linn.	—	*s* very rare
Pedicularis palustris Linn.	—	*s* fairly common
Pinus sylvestris Linn.	*p*	*p*
Plantago maritima Linn.	—	*f*, *s* fairly common

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PLANTS (*cont.*)

	Band 2	Band 3
Polygonum aviculare agg.	—	*n* very common
P. amphibium Linn.	—	*n* common
Potamogeton alpinus Balb.	—	*st* very rare
P. densus Linn.	—	*st* abundant
P. filiformis Pers.	*st*	*st* abundant
Potentilla anserina Linn.	*a*	*a* very common
P. palustris (Linn.)	—	*a* very rare
P. reptans Linn.	—	*a* rare
P. sterilis (Linn.)	—	*a* fairly common
Potentilla spp.	*a*	*a* fairly common
Primula cf. *farinosa* Linn.	—	*s* rare
Primula sp.	—	*s* rare
Ranunculus acris Linn.	*a*	*a* fairly common
R. repens Linn.	—	*a* fairly common
R. sceleratus Linn.	—	*a* common
R. (*Batrachium*) spp.	*a*	*a* common
cf. *Rhinanthus* sp.	—	*s* rare
Rumex acetosella Linn.	—	*n* common
Salix herbacea Linn.	—	*l* very rare
Salix cf. *phylicifolia* Linn.	—	*l* very rare
Scabiosa columbaria Linn.	—	*cal* very rare
Schoenoplectus lacustris Linn.	*n*	*n* fairly common
Scleranthus annuus Linn.	—	*cal* common
Selaginella selaginoides (Linn.)	*mis*	*mes* rare
Stellaria palustris Retz.	—	*s* fairly common
Taraxacum officinale agg.	*a*	*a* common
Thalictrum alpinum Linn.	—	*a* very rare
T. minus Linn.	—	*a* very common
Thalictrum sp.	*p*	*p*
Triglochin maritima Linn.	—	*f* fairly common
Tripleurospermum maritima Linn. v. *inodora* Linn.	—	*a* very rare
Viola sp.	—	*s* very rare
Viscaria alpina (Linn.)	—	*s* common
Zannichellia palustris agg.	*a*	*a* very common

(*a*, achene; *cal*, calyx; *f*, fruit; *fv*, fruit valve; *l*, leaf; *mes*, megaspore; *mis*, microspore; *n*, nut or nutlet; *o*, oospore; *p*, pollen; *s*, seed; *sh*, shoot; *sp*, spore; *st*, fruit stone; *u*, utricle.)

Explanation of plate 19

All magnifications × 12

Figure 19. *Elaphrus cupreus*, head.

Figure 20. *E. cupreus*, pronotum.

Figure 21. *E. cupreus*, right elytron.

Figure 22. *E. lapponicus*, head.

Figure 23. *E. lapponicus*, left elytron.

Figure 24. *E. riparius*, head.

Figure 25. *E. riparius*, pronotum.

Figure 26. *Dyschirius thoracicus*, right elytron.

Figure 27. *Amara torrida*, pronotum.

Figure 28. *Feronia nigrita*, left elytron.

Figure 29. *F. diligens*, left elytron.

Figure 30. *Agonum sexpunctatum*, pronotum.

Figure 31. *A. sahlbergi*, pronotum.

Figure 32. *A. versutum*, pronotum.

Figure 33. *Helobium multipunctatum*, head.

Figure 34. *H. multipunctatum*, pronotum.

Figure 35. *Notiophilus aquaticus*, head.

Figure 36. *N. aquaticus*, left elytron.

Figure 37. *Cymindis angularis*, left elytron.

Figure 38. *Bembidion bipunctatum*, left elytron.

Figure 39. *Nebria gyllenhalli*, pronotum.

Figure 40. *Pelophila borealis*, pronotum.

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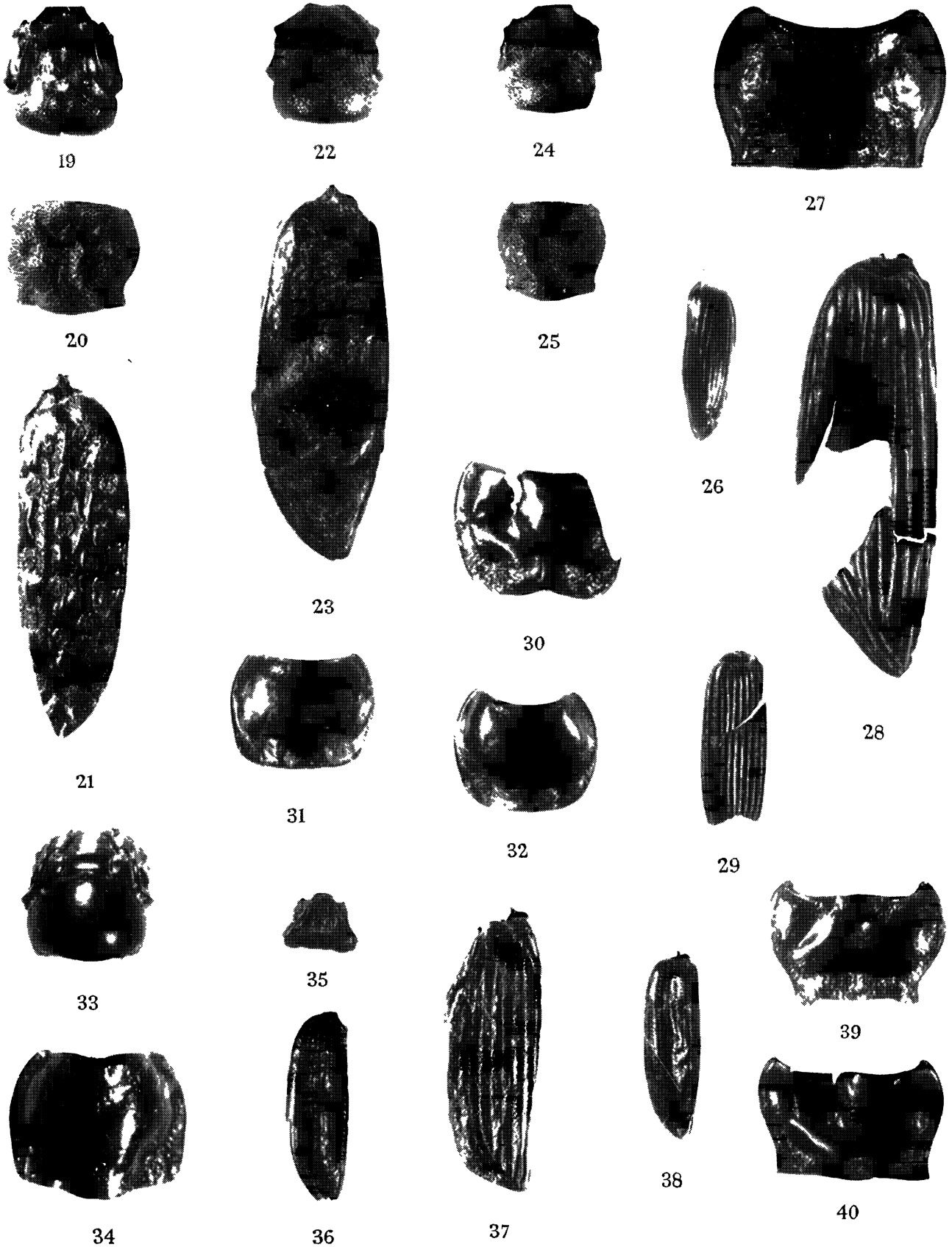

FIGURES 19 TO 40

(*Facing p.* 394)

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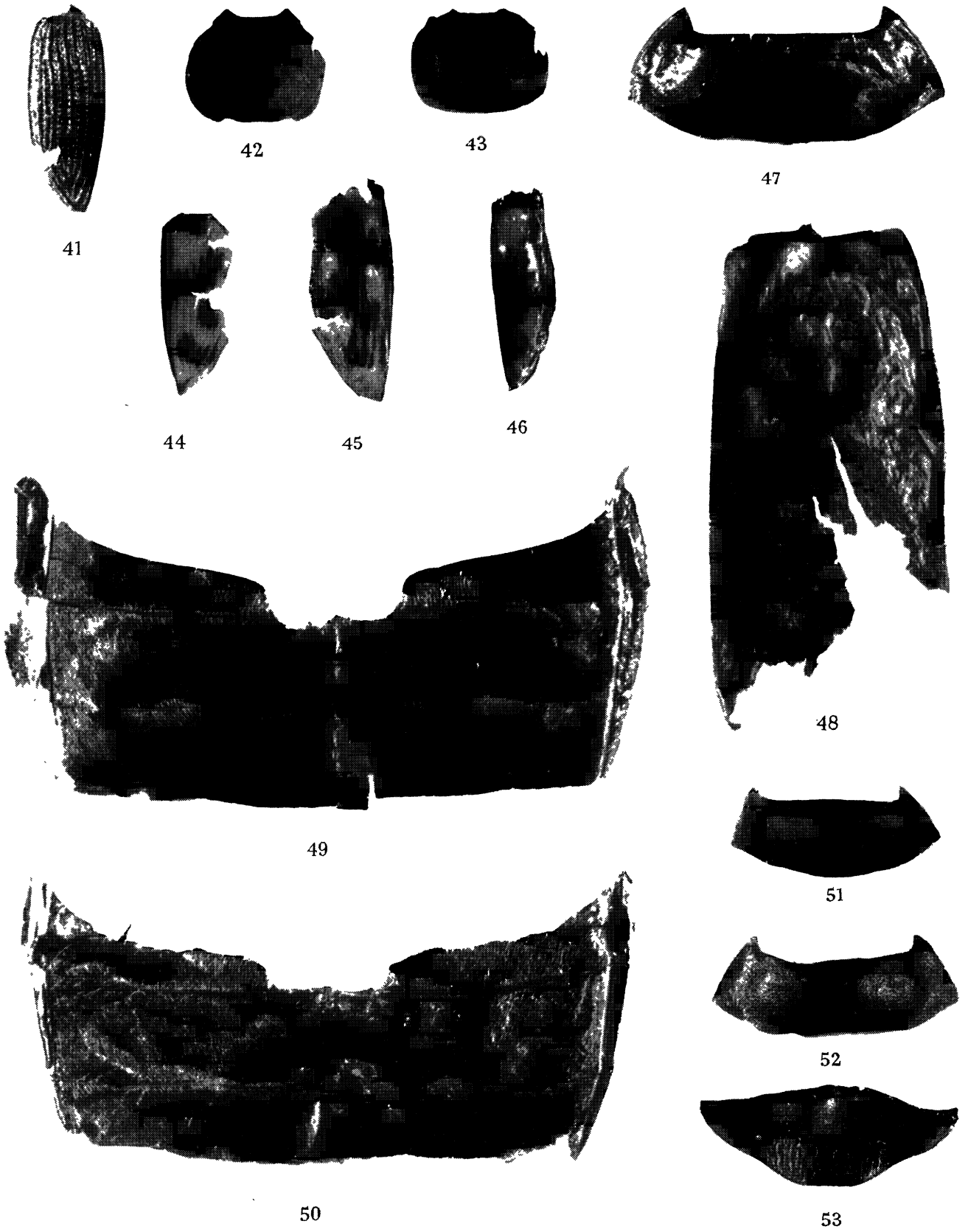

FIGURES 41 TO 53

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TABLE 2. NUMBER OF POLLEN GRAINS AND SPORES COUNTED IN BANDS 2 AND 3.

Each type expressed as a number and (in brackets) as a percentage of total counts of terrestrial plants.

	Band 2	Band 3
Betula	1 (0·4)	1 (0·25)
Pinus	7 (3)	1 (0·25)
Salix	2 (1)	1 (0·25)
Gramineae	3 (1)	43 (11)
Cyperaceae	200 (80)	154 (40)
Artemisia	3 (1)	10 (2·5)
Thalictrum	3 (1)	40 (10)
Caryophyllaceae	7 (2)	28 (7)
Compositae		
Tubuliflorae	4 (1·5)	13 (3·5)
Liguliflorae	15 (6)	26 (6·5)
Armeria	—	6 (1·5)
Helianthemum	—	1 (0·25)
Plantago	—	55 (14)
Polygonum	—	3 (1)
Ranunculus	—	3 (1)
Selaginella	11 (4)	1 (0·25)
Myriophyllum	—	135
totals counted	256	521

(*i*) *Notes on certain listed species*

Agonum sahlbergi *Chaud.*

Several fragments of *Agonum*, provisionally named *A. mulleri* Hbst., were submitted to Professor Lindroth, who identified them with *A. archangelicum* J. Sahlb., a species found living today only round the White Sea. However, in a subsequent revision of this species, Lindroth (1960) has pointed out that *A. archangelicum* is a pure synonym of *A. sahlbergi* Chaud. Under this name the beetle's modern distribution was given as eastern Siberia and a locality on the banks of the Clyde near Glasgow from which, however, no specimens

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EXPLANATION OF PLATE 20

All magnifications × 12

FIGURE 41. *Aegialia sabuleti*, left elytron.

FIGURE 42. *Byrrhus pilula*, head.

FIGURE 43. *B. fasciatus* or *arietinus*, head.

FIGURE 44. *Haliplus obliquus*, right elytron.

FIGURE 45. *Deronectes depressus-elegans* agg., left elytron.

FIGURE 46. *Hydroporus palustris*, right elytron.

FIGURE 47. *Agabus bipustulatus*, pronotum.

FIGURE 48. *A. bipustulatus*, right elytron.

FIGURE 49. *Colymbetes fuscus*, abdominal sternites 1, 2 and 3, showing the so-called stridulatory file between segments 2 and 3.

FIGURE 50. *C. paykulli*, abdominal sternites 1, 2 and 3, showing absence of stridulatory file.

FIGURE 51. *Agabus arcticus*, pronotum.

FIGURE 52. *A. sturmii*, pronotum.

FIGURE 53. *Ilybius subaeneus*, last abdominal sternite of male.

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have been obtained recently. With the equation of *A. archangelicum* and *A. sahlbergi* and the fossil occurrence of the species at Upton Warren its puzzling modern distribution is more easily understood as remnants of a much wider distribution during Würm Glaciation times. The possibility must remain, however, that the Scottish specimens may represent individuals or their offspring that had been brought passively, in ballast or cargo, from ports on the White Sea to Glasgow.

Tachinus *sp.A.*

Under this heading we include a large number of fragments of a *Tachinus* which in many respects resembles *rufipes* (L.). Associated with these remains are abdominal segments which we believe to be conspecific, but the last segments of both male and female have shapes which, though typical of *Tachinus* in general, clearly do not belong to *rufipes* or any other British species nor to any foreign species familiar to the Rev C. E. Tottenham. These diagnostic segments are illustrated in figure 3 in the hope that, if the species is still living today, it may be recognized.

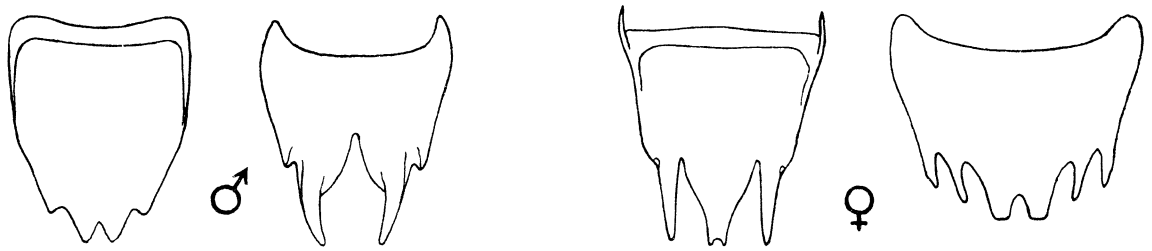

FIGURE 3. *Tachinus*, sp.A. Terminal tergite and sternite of male and female. (Magn. × 25.)

Cf. Oxytelus *sp.*

A single distinctive head has so far proved unidentifiable. It matches best the genus *Oxytelus* but is quite unlike any species of that genus familiar to us. It is illustrated (figure 61, plate 21) again in the hope that it may be recognized as a present-day species.

Aphodius *sp.A.*

Under this designation we group a number of heads of *Aphodius* which possess a large bifid central tubercle slightly posterior to a line joining the backs of the eyes. This extremely distinctive head has so far defied our attempts to match it with a modern species and we think it is probably extinct. Fortunately one of the heads was attached to a pronotum and it has thus been possible to recognize numerous pronota of the same species. Unfortunately the elytra of *Aphodius* are usually very frail as fossils and thus rarely found complete. There are, however, five almost complete and many fragments of elytra that do not match any modern species known to us. Since the size of these elytra is suitable for the heads and pronota, it is reasonable to assume that they represent the same species. We draw attention to this unusual insect in the hope that we may receive information about it, if the species still exists anywhere today.

Phaedon pyritosus

A number of elytra and pronota of *Phaedon* from Band 3 could not be matched with any known British species. The elytra, however, had a sharp lateral ridge that extended only

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half way from the base towards the apex (figure 63, plate 21), a feature used to distinguish the subgenus *Neophaedon* from *Phaedon* (*sensu stricto*) which has the ridge for the full length of the elytron. *Neophaedon* is, however, monotypic, with the European *pyritosus* Rossi as the only species. The fossil specimens differ from modern representatives of the species in their much more numerous transverse grooves between the striae which gives the elytron a very distinctive appearance (figure 64, plate 21). This at first sight encouraged us to believe that we had a new species of *Neophaedon*. However, it was similar rugosity on the elytron of *Notiophilus* that persuaded Henricksen (1933, p. 111) to erect a new species, *N. coriaceus*, but as Lindroth points out (1948, p. 5) these rugosities can be produced by chemical action on dead specimens of *N. aquaticus* and were probably therefore post-mortem changes. With this possibility in mind we have included the fossil specimens of *Neophaedon* in the species *pyritosus*. The distribution of *pyritosus*, being southern and central European, is quite out of harmony with the rest of the Upton Warren fauna, and this suggests that perhaps the fossil remains represent an extinct northern form of the species.

Dianthus *cf.* carthusianorum (figure 76, plate 22)

About twenty seeds of a *Dianthus* have been found. Of the three native species in Britain, only *D. gratianopolitanus* has seeds which are at all similar to the fossil ones. Comparison with similar continental species has been made and from size considerations it appears that they are most likely referable to *D. carthusianorum*. This appears to be the first record of *Dianthus* from British glacial deposits.

Glaux maritima (figures 78–81, plate 22)

About a dozen capsules and numerous seeds can be assigned to this species. The identification of Primulaceae seeds appears to be difficult but the capsules, often complete with seeds, are here diagnostic. Godwin (1956) gives only one record for *Glaux*.

Linum praecursor *Reid* (figures 84, 85, plate 22)

Godwin (1956, 1959) following Mrs E. M. Reid, regards C. Reid's fossil species as probably synonymous with *L. anglicum* although 'the fossil seeds are consistently smaller'. Clapham, Tutin & Warburg (1952) state that seeds of *L. anglicum* (*L. perenne* auct. angl.) are 4 to 5 mm long. Ross-Craig (1952) illustrates a seed which is about 5·2 mm long. Continental authors (Beijerinck 1947; Bertsch 1941), however, give *L. perenne* seeds a length of only 3 mm. The present fossil seeds are about 4 mm long. In view of the discrepancies in these recorded sizes, it seems best at present to retain Clement Reid's fossil name until a detailed survey of the problem can be made, thus avoiding the making of inferences on climate from doubtful comparisons with recent species.

Lathyrus *or* Vicia *sp.* (figure 83, plate 22)

A seed and a fragment of pod are probably leguminous. The valve is 8 mm long (but incomplete) and 2·5 mm broad. The seed is about 1·5 mm in diameter, has a finely wrinkled surface and a long hilum. None of the British species examined appears to have this combination of characters. *Vicia hirsuta* has the long hilum but is apparently smooth while *Lathyrus nissolia* which is rough has a short hilum. Until a further range of species can be examined, this specimen must remain unidentified.

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III. Discussion of the ecology of the site

We have tried as far as possible to discuss the evidence for climate in a section independent of this consideration of general ecology, but it has not always been possible to dissociate the two factors.

(*j*) *Geological considerations*

The petrology of the organic bands (unlike the main mass of gravel) indicates a régime of still or gently flowing water, in pools that were floored by humous silt or fine sand. As the elevation of this part of the Salwarpe Valley must have been about 150 ft. above contemporary sea level, the river and its flood-plain pools must have been above any tidal influence and the water would therefore be expected to be 'fresh'. Since a small degree of 'brackishness' has to be invoked to explain certain occurrences of molluscs, ostracods and plants which are discussed more fully under their appropriate headings, it will suffice to point out here that springs of brine from the Keuper Marl are a natural feature of the Droitwich district and that such as these, mingling with the river water, could provide a plausible explanation of maritime species at an inland locality.

(*k*) *Ecological conditions deduced from the fossils*

(*k* 1) *Vertebrate remains*

The exact stratigraphical position of most of the bones of the larger mammals is unknown except in a very few cases, where they were found definitely *in situ* by one of us during one of our many visits to the pit. The position of these bones was almost invariably in the soft sand below the organic layers or more rarely in the organic silt itself. In most cases larger bones were fragmentary and no associated skeletons were found. Very often the bones are marked extensively by rootlets and appear to have lain near the surface for some time before being buried. The method of sampling and the fragmentary nature of the bones make deductions about the relative abundance of the species almost impossible. The most conspicuous remains—tusks and teeth of mammoth and various sorts of limb bones—were the most abundant, whilst vertebrae and skull bones were almost never collected. However, it appears that the bison was by far the most abundant species of larger mammal and the mammoth was also fairly frequent. No less than fourteen large pieces of tusk were treated at Birmingham and there were reports of several more that had disintegrated on drying during the earlier phases of quarrying operations. The assemblage of larger mammals is quite typical of the fauna of the Last Glaciation in Britain, though the occurrence of horse is unlikely in a full glacial context.

Although there is indirect evidence (p. 405, in the discussion of dung- and carcass-beetles) that the larger vertebrates used the alluvial ponds as drinking holes, probably during migratory treks, the haphazard occurrence of the bones in isolation suggests that these represent animals that died elsewhere and whose bones were transported by the river after dissociation.

During the washing and sorting of Band 3, three microtine molar teeth were found. These were submitted to J. N. Carreck of the Geology Department, Queen Mary College, for identification and comment. One of the teeth, an upper molar (m^2) was identified as from the lemming *Dicrostonyx henseli* Hinton which is found extensively in deposits of the

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Last Glaciation but which appears to have become extinct in this country at the close of this glaciation. A second tooth, also m^2, was not specifically determinable, but was comparable with those from the *Microtus nivalis* (Martin) group and *M. arvalis* (Pallas) group. Members of the former group are known in Britain only from deposits of the end of the Last Interglacial and of the latter group only from deposits of that period, the Last Glaciation and Zone V Early Boreal of Nazeing. The third tooth was not identifiable. The microtine teeth therefore suggest an age for these deposits that is in complete agreement with the stratigraphical and other faunal evidence.

(*k* 2) *Mollusca*

Mollusca constitute the only collection of any significance from the basal layer of the gravels (Band 4). Although the fauna is limited, and it is acknowledged that collection from this level was poor, it is clearly significantly different from that of either of the other bands. *Ancylus fluviatilis* present as eight specimens in a total of thirty-six, is unrepresented in the many hundreds of specimens from Bands 2 and 3. Probably also significant, even in such a small collection, is the absence of *Planorbis laevis* and the various species of *Pisidium* which are so abundant in the other bands. *Ancylus fluviatilis* lives attached to stones in running water and this fact coupled with the absence of the pond-dwelling species of *Planorbis* and *Pisidium* indicates that Band 4 was deposited under more turbulent conditions than in the case of Bands 2 and 3.

The much larger collections from Bands 2 and 3 show conclusively that these layers represent different pools, in space at least if not necessarily in time (the ostracods lead to the same conclusion). The faunas are strikingly different. Of fourteen species, only six occur in both bands—*Lymnaea peregra* and *Planorbis laevis* common in both, *Lymnaea truncatula*, *Pupilla muscorum* and *Pisidium casertanum* as rarities, and *P. subtruncatum* very rare in Band 2 but reasonably abundant in Band 3. The astonishing difference between the two layers is shown by the abundance of *P. vincentianum* and the appreciable numbers of *P. obtusale lapponicum* and *Succinea* only in Band 2, whilst *Pisidium nitidum* is not only restricted to Band 3 but constitutes nearly half of its molluscan content.

The distinction between the two faunas is brought out by more than the enumeration of species, for although *Lymnaea peregra* and *Planorbis laevis* occur abundantly in both, they are conspicuously dwarfed in Band 2. It is not easy to find biometric parameters which can be easily measured in the helically spiral *Lymnaea*, but it is much simpler in the near-plane spiral *Planorbis*. In figure 4, the diameter of the snail is plotted against the number of whorls. The only inaccuracy of these measurements arises from the difficulty of being confident of the direction of the axis of the protoconch, which controls the number of whorls credited to each specimen.

The diagram shows clearly that specimens from Band 2 are 10% smaller than those from Band 3 with the same number of whorls and that the largest specimens from Band 3 coil for half a whorl more than do those from Band 2. This latter fauna is thus both stunted and dwarfed. In the case of *Lymnaea peregra* which does not lend itself to easy measurement, these effects are even more apparent to the eye.

The physical factors which caused the dwarfing of these two species in Band 2, were also conducive to the flourishing of *Pisidium vincentianum*, *P. obtusale* var. *lapponicum* and

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Succinea pfeifferi but were inimical to *Pisidium nitidum*. With a different set of physical conditions, *P. vincentianum*, *P. lapponicum* and *Succinea pfeifferi* were unable to exist, *Lymnaea peregra* and *Planorbis laevis* grew to normal size, *Pisidium subtruncatum* became common and *P. nitidum* flourished abundantly. The space relationships of Bands 2 and 3 are such that they must be nearly contemporaneous and it is difficult therefore to suggest that they represent significantly different climates. On the other hand, Mr Dance points out in his

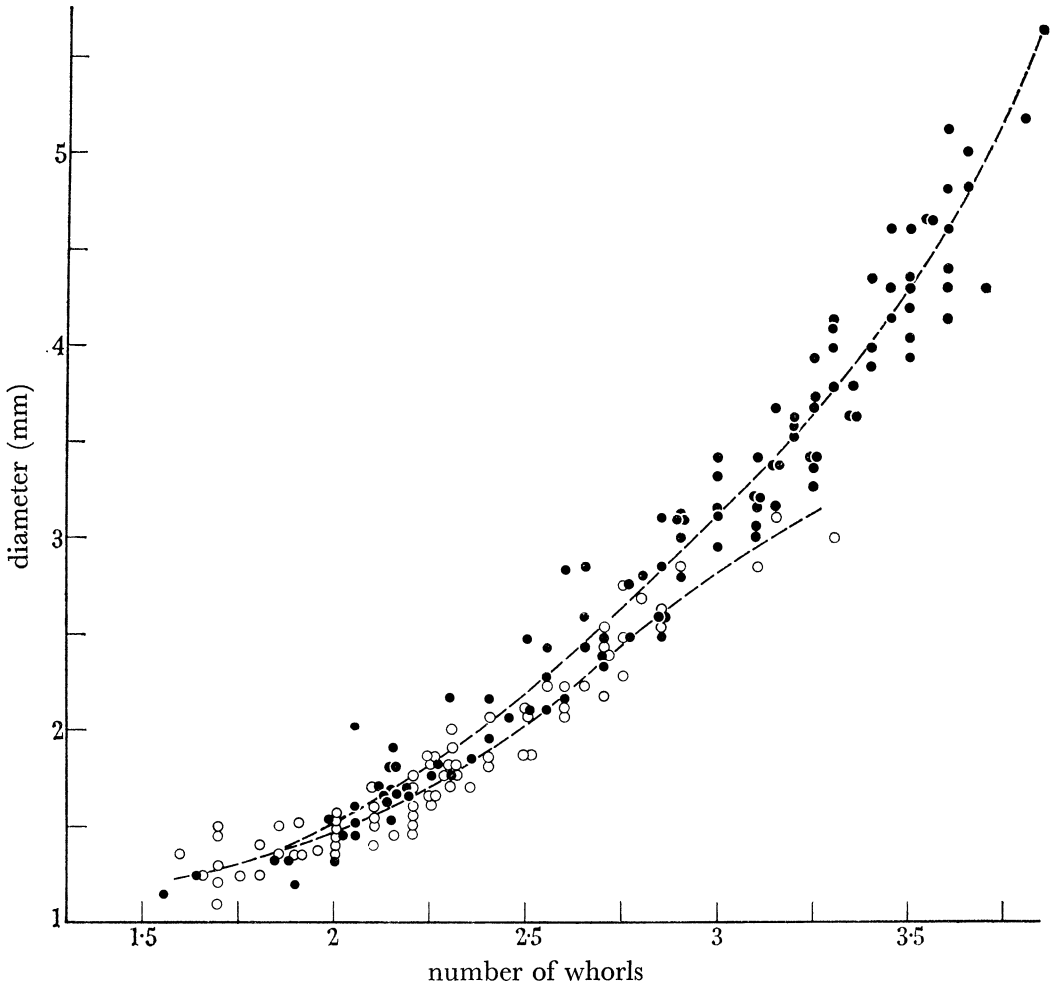

FIGURE 4. Measurements of *Planorbis laevis* from Bands 2 (○) and 3 (●).

appendix on the species of *Pisidium* that *nitidum* and *subtruncatum* are associated together in Britain today in places where there is a constant flow of water and this might be the main distinction between the two pools. It is also suggested (p. 401) that the occurrence of ostracods could be explained if Pool 2 had been slightly brackish due to the escape of 'wild brine' from the Keuper Marl, and the same feature might account for the dwarfing of *Lymnaea peregra* and *Planorbis laevis*. The greater salinity of Pool 2 would correlate with its greater stagnation.

It is not suggested, however, that Pool 3 was anything but calm when its inhabitants lived and died in it, and *Pisidium nitidum* certainly did both. The lack of disturbance in the bottom deposits of the pond is shown by the common preservation of the periostracum on

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the shells, and by the frequency with which the two valves are articulated and tightly closed. Many of these opened for the first time after death when being examined under a binocular microscope with the accompanying heat of an electric lamp, and four still contained a 'litter' of unborn embryos (figure 74, plate 22).

(*k* 3) *Ostracoda*

The seven recorded species of ostracod are all consistent with life in shallow water over a silty or sandy bottom, a situation already apparent from the nature of the deposits in which the fauna occurs. It seems possible, however, that the occurrence of *Cyprinotus salinus* as the outstandingly common form of Band 2 whilst it is absent from Band 3, gives a clue to a physical difference between the pools represented by the two bands. Wagner (1957, p. 109 and fig. 11) has discussed the occurrence of a considerable number of living species, including *Erpetocypris reptans*, *Candona neglecta*, *Ilyocypris gibba* and *Cyprinotus salinus*, in relation to the salinity of the water in which they live. *Erpetocypris reptans* is shown as an inhabitant of 'soft water', *Cyprinotus neglecta* and *Ilyocypris gibba* as living in this environment and also in oligohaline water, whereas *Cyprinotus salinus* is not found unless the water is oligohaline or mesohaline (salinity classification of Välikangas 1933). It would appear that *Erpetocypris* and *Cyprinotus salinus* should not occur together, whereas they both occur in Band 2 (though *Erpetocypris reptans* is uncommon). Nevertheless, the occurrence of *Cyprinotus salinus* abundantly in Band 2, and its absence from Band 3, must mean a difference in salinity of the two pools. Pool 3 was presumably 'soft', i.e. with a salinity under about 0·04 %, whereas Pool 2 was oligohaline. It is important, however, not to overemphasize this salinity difference, because the other species found with *C. salinus* suggest that the water lay in the lower half of the oligohaline range (say between 0·04 and 0·1 %). This water can only be called mildly brackish. Nevertheless, since it appears to have affected the ostracod fauna, it might be considered as a possible explanation of some of the other faunal or floral differences (e.g. the Mollusca, p. 399).

It has already been pointed out that tidal influences are ruled out as an explanation of brackish water and the only alternative source seems to be brine springs from the Keuper Marl on which the gravels lie. Droitwich, only 4 miles from Upton Warren, carries this implication in its name and its salt springs have been known since at least Roman times. Salt is actually worked below the gravel site now and this has been responsible for subsidence and some deformation of the gravels (p. 384). There is no difficulty in postulating some degree of salinity in any of the ponds if the fauna or flora call for it.

(*k* 4) *Trichoptera*

Phryganea obsoleta is a common caddis fly of ponds and lakes in north Britain or at high altitudes (Moseley 1939).

(*k* 5) *Hemiptera*

Salda littoralis and *Saldula saltatoria* are both predators which probably live on insect larvae. They run about on mud under vegetation. Though now often thought of as British coastal species, they are known to occur in suitable habitats inland (Butler 1923).

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(*k* 6) *Coleoptera*

Since beetles were by far the most abundant animal fossils found at Upton Warren and since they have been extensively studied from the ecological point of view, our deductions concerning the conditions under which the organic layers were deposited and the nature of the surrounding country rely greatly upon the present-day requirements of these insects. In making these deductions, however, it must be assumed that for most of the species, their basic ecological requirements have remained the same since the fauna was buried 42000 years ago. This assumption appears to be justified by the resulting ecological homogeneity of the fauna.

Carabidae

Before embarking on an account of the ecological requirements of the Upton Warren carnivorous ground beetles we would like to express our sincere gratitude to Professor Carl Lindroth who has personally supplied much of the information given below and identified some of the more difficult species of this family.

Since these insects are ground dwellers they reflect such conditions as moisture of the habitat, nature of the soil and extent of vegetation cover. The thirty-five species recognized can be grouped according to their demand for moisture as follows:

Hygrophilous—20 species (57 %)
Mesophilous—12 species (34 %)
Xerophilous—3 species (9 %)

This striking preponderance of moisture-loving species is accentuated by the fact that among the eight species most abundantly represented, six are pronounced hygrophiles and

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EXPLANATION OF PLATE 21

All magnifications × 12 unless otherwise stated

FIGURE 54. *Thanatophilus dispar*, head.

FIGURE 55. *T. dispar*, pronotum.

FIGURE 56. *Aclypea opaca*, a pair of elytron.

FIGURE 57. *Notaris aethiops*, joined head and thorax viewed from right ventro-lateral position.

FIGURE 58. *N. aethiops*, right elytron.

FIGURE 59. *Otiorrhynchus arcticus*, associated head and thorax.

FIGURE 60. *Entomoscelis adonidis*, left elytron (× 8). The apex was found several days after the base but probably both parts belong to one elytron.

FIGURE 61. Head with mandibles of an unknown staphylinid similar to *Oxytelus* (× 50).

FIGURE 62. *Cantharis liturata*, pronotum.

FIGURE 63. *Phaedon pyritosus*, right elytron.

FIGURE 64. *P. pyritosus*, detail of sculpture on the central part of an elytron (× 80).

FIGURE 65. Larval case of caddis fly.

FIGURES 66 and 67. *Sialis* sp., two heads showing great variation in size and ornament.

FIGURE 68. *Salda littoralis*, left hemelytron.

FIGURE 69. *Aphrodes bifasciatus*, right wing.

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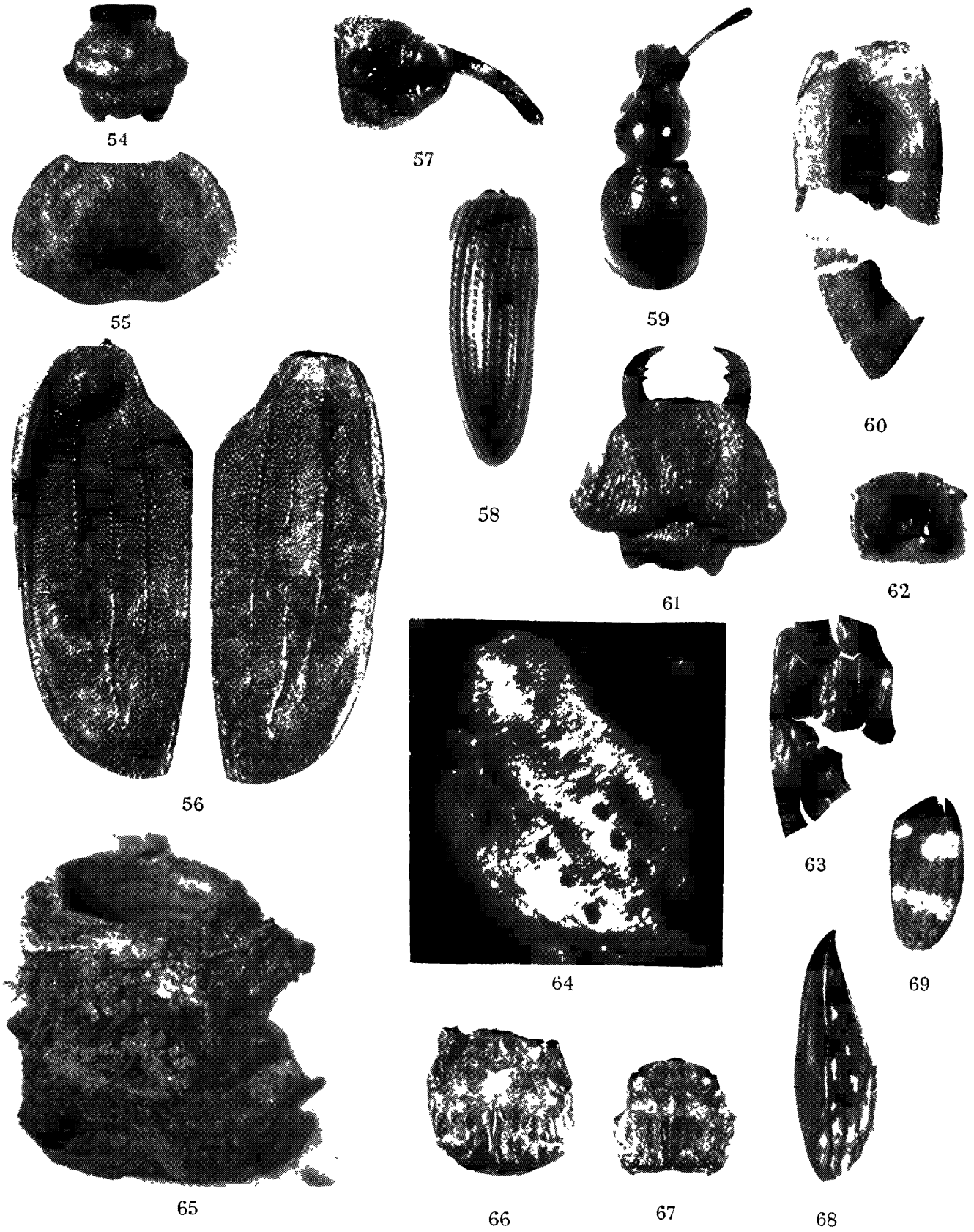

FIGURES 54 TO 69

(*Facing p.* 402)

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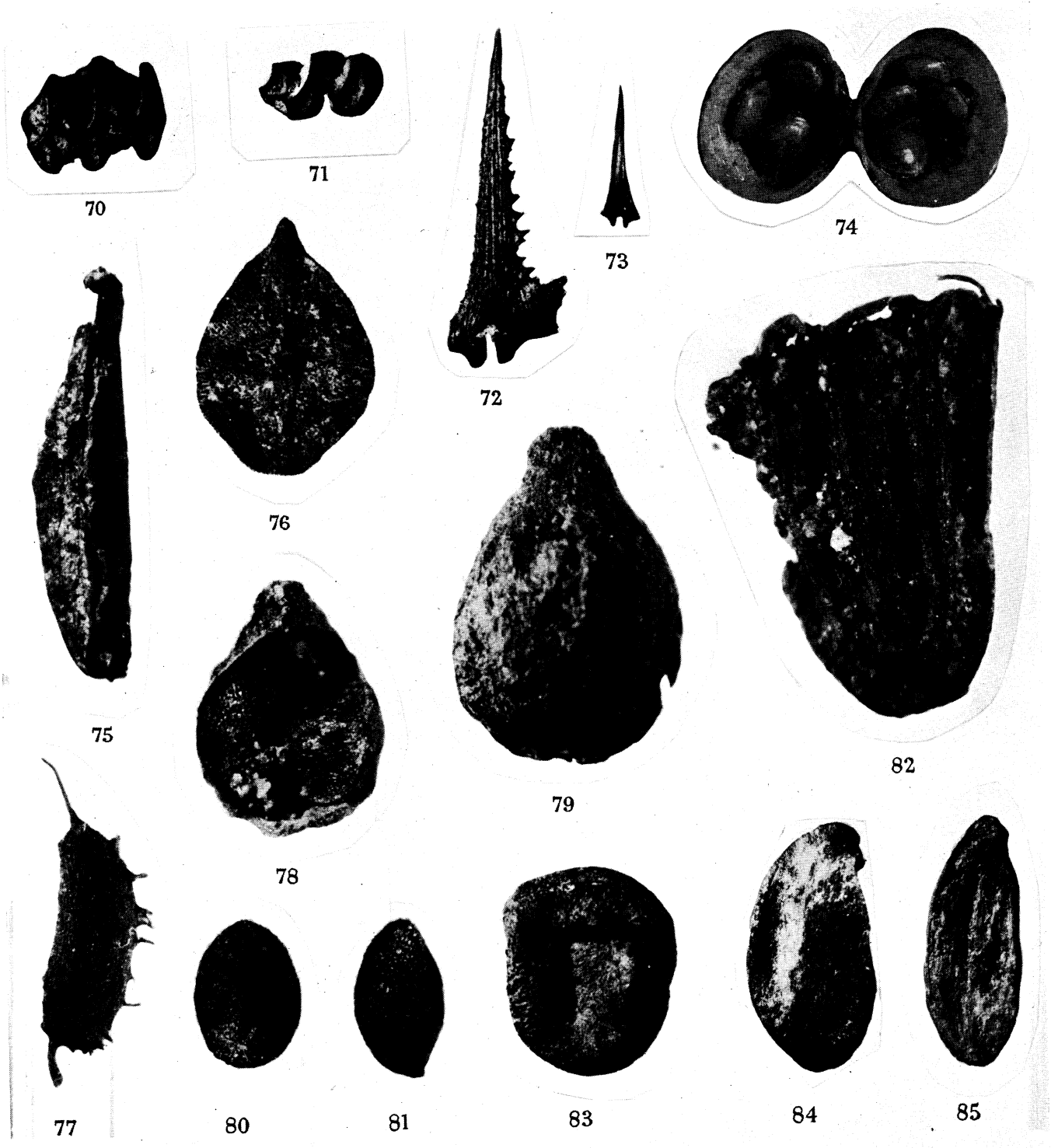

FIGURES 70 TO 85

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only two (*Amara torrida*, *Notiophilus aquaticus*) are mesophiles. Of the three xerophiles only *Amara quenseli* is found in any number (about ten fragments) and the two remaining species (*Harpalus cordatus*, *Cymindis angularis*) are each represented by only one fragment. Almost all the hygrophiles prefer, or are confined to, the margins of standing water and only two (*Nebria gyllenhalli*, *Bembidion virens*) prefer the margins of running water. *Elaphrus lapponicus* requires a rather special habitat being found in the moss tussocks that grow round springs or by cold trickles of water.

In many carabid species a demand for soil moisture is often associated with a photophobic reaction and they are thus confined to habitats with a dense cover of vegetation, often in woods. The reverse of this is found among the Upton Warren carabids. Of thirty-five species recognized, only one, *Carabus hortensis*, is usually found in wooded habitats and it is represented by one fragment only. The remainder are species of open country with only a thin cover of vegetation. Many are pronounced heliophiles and run about in bright sunlight; among the eight most common species only *Amara torrida* does not belong to this group.

Some Carabidae have a marked preference for certain types of soil. Two of the Upton Warren species are restricted to clayey soil (*Bembidion lunatum*, *B. aeneum*) and two species are typical of sandy soil (*Dyschirius thoracicus*, *Amara quenseli*). Since these four species were found in considerable numbers it is most probable that both sandy and clay soil was available in the immediate neighbourhood. Open ground close to the water is indicated by *Elaphrus riparius*, *Dyschirius septentrionum*, *Bembidion bipunctatum* and *B. femoratum*, though these are less fastidious as to particle size of the soil.

It is noteworthy that the Upton Warren carabids include no hygrophilous species associated with an environment either markedly acid or alkaline. *Feronia diligens* is the only species normally associated with acid-water conditions and it is represented here by only one elytron. From this evidence it might be suggested that the pool round which so many of the species lived was neither very acid nor alkaline.

Explanation of plate 22

Figure 70. *Dicrostonyx henseli*, upper molar (m^2) ($\times 12$).

Figure 71. *Microtus* sp. (*nivalis* or *arvalis* group), upper molar (m^2) ($\times 12$).

Figure 72. *Gasterosteus aculeatus*, pelvic spine ($\times 8$).

Figure 73. *G. aculeatus*, small dorsal spine ($\times 8$).

Figure 74. *Pisidium nitidum* with unliberated young ($\times 12$).

Figure 75. *Triglochin maritimum*, fruit ($\times 20$).

Figure 76. *Dianthus* cf. *carthusianorum*, seed ($\times 22$).

Figure 77. *Zannichellia palustris* agg., achene ($\times 15$).

Figure 78. *Glaux maritima*, fruit with seeds ($\times 22$).

Figure 79. *G. maritima*, complete fruit ($\times 22$).

Figures 80 and 81. *G. maritima*, seeds ($\times 22$).

Figure 82. *Scabiosa columbaria*, calyx ($\times 20$).

Figure 83. *Lathyrus* or *Vicia* sp., seed ($\times 20$).

Figures 84 and 85. *Linum praecursor*, seeds ($\times 10$).

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There remains one more point of interest in the ecology of the Carabidae from Upton Warren. *Bembidion aeneum* is frequently associated with salt or brackish water. However, Professor Lindroth has shown (1949, p. 521) that the species requires only a very slight trace of salt in the soil and is found inland in southern Sweden in the areas covered by late Pleistocene marine clays. The occurrence of this species at Upton Warren is of particular interest since there are indications that the pool, represented by Band 2, was slightly brackish (p. 401) and because of the likelihood of brine springs in the area at that time.

Haliplidae

Only one species, *Haliplus obliquus*, has been recognized with certainty. This species is frequently associated with Chara pools though not confined to this habitat.

Dytiscidae

One of the most striking features of the Upton Warren carnivorous water beetles is that, with one exception, they are all characteristic of standing water. *Deronectes depressus-elegans* is the possible exception, since the fossil species is close to the *elegans* end of the complex; a form usually associated with gravelly shallows in running water. Acid-water conditions are suggested by only two species, *Agabus arcticus* and *A. congener*, though since these two are now northern and usually mountain species, this association may be due to the ubiquity of acid habitats in those regions. All the species are normally associated with more or less abundant vegetation in the water. *Rantus exsoletus* and *Agabus nebulosus*, both species represented by more than five individuals, are typical of grassy margins to pools. Many of the larger genera such as *Dytiscus* and *Colymbetes* feed on tadpoles and small fish such as sticklebacks, and bones of these fish and of the common frog were found in the deposits.

Gyrinidae

This family is represented by a single head of *Gyrinus minutus*, a species found in cold, peaty, usually standing water. The absence of larger numbers of Gyrinidae is unexpected and a puzzling problem which must remain open at the moment.

Hydrophilidae

The species of this family fly very well and are often found in enormous swarms. It is not surprising then that *Helophorus aquaticus* was the most abundant beetle at Upton Warren and *H. brevipalpis* was also very common. These are indicative of rich vegetation in or at the margins of pools. *H. nubilis* is associated with sandy margins to ponds and is a root feeder. *Hydrobius fuscipes* is typical of detritus ponds with much vegetation. *Enochrus quadripunctatus* var. *fuscipennis* is usually considered as an acid-water form. *Limnebius truncatellus* is common in stagnant water but more frequent in streams and among the vegetation at the sides of rivers. The species of *Cercyon* are found either in rotting grass or in dung and their frequency may be correlated with the remarkable abundance of the dung beetle *Aphodius*.

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Silphidae

Thanatophilus dispar and *Aclypea opaca* are carcass beetles. The abundance of the former suggests that food was plentiful, a suggestion further supported by the large numbers of staphilinid beetles and the occurrence of bones in the deposit.

Staphilinidae

The species of this family are numerous and very hard to identify. The faunal list therefore under-represents the family since large numbers of fragments were not identified. Most of the species live in rotting vegetation, under stones or in carcasses where they prey on other insects and their larvae. *Bledius littoralis* is found in damp sandy places in company with *Dyschirius septentrionum* (Strand 1946, p. 238).

Leiodidae

Little is known about the ecology of this family. They probably feed on fungi either at the roots of grass or under bark. Many are found in sandy places.

Elateridae

The click beetles are represented by two species only, both of which are grass-root feeders. *Hypnoidus riparius* is found in damp situations and was fairly common in the fauna but *Corymbites melancholicus*, characteristic of dry sandy places, is represented by only one specimen.

Heteroceridae

The species of this family excavate burrows in damp fairly clean sand, and fly very well. *Heteroceras hispidulus* usually requires sand less waterlogged than *H. fenestratus* and *H. fusculus*. They are often associated with species of the carabid *Dyschirius* and the staphilinid *Bledius* though the ecological reasons are not well understood.

Byrrhidae

These beetles are usually found in moss upon which they feed. *Simplocaria semistriata* prefers mossy stones in sandy places and was found in large numbers.

Cryptophagidae

The only species of this family recognized at Upton Warren was *Antherophagus pallens* which is found in the nests of species of *Bombus*. However, no fragments of humble bees were identified in the fauna possibly because these insects frequented the dryer places further away from the pool.

Scarabaeidae

Immense numbers of fragments of *Aphodius* were found though few were specifically identifiable with certainty. Most of the species of this genus feed on dung of large mammals. Bones of these animals, in particular of bison, suggest that the pool may have attracted them as a drinking or wallowing place. *Aphodius plagiatus*, however, is not a dung feeder but lives under stones in damp places. *Aegialia sabuleti* is also not a dung feeder but is found in damp and sandy places by standing or running water.

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Chrysomelidae and Curculionidae

These two families are made up of plant-feeding beetles. Many species have a particular host or preference for a certain plant. The species therefore reflect, to a certain extent, the flora of the times and the following list shows the food plants usually associated with the insects.

Chrysomelidae	
Donacia thalassina	*Scirpus*, *Carex*
Chrysolina limbata	low plants, grass, etc.
C. staphylea	apparently on many low plants, *Achilleum millefolium*, *Rhinanthus crista-galli*
C. marginata	many low plants
Gastrophysa viridula	*Rumex*
Entomoscelis adonidis	*Taraxacum*, *Cochlearia*, *Adonis autumnalis*
Galeruca tanaceti	*Tanacetum vulgare*, *Thymus*, also *Achillea millefolium* and *Cardamine pratensis*
Crepidodera interpunctata	*Urtica*, *Carduus* and dry grass
Phaedon armoraciae	in water, on *Montia fontana* (Fowler)
P. pyritosus	*Ranunculus*
Curculionidae	
Otiorrhynchus arcticus, *O. ligneus*	grass roots
O. rugifrons	*Thymus* probably most important food plant
Sitona lepida	*Trifolium*
Bagous tempestivus	on aquatic plants, particularly *Ranunculus*
Notaris bimaculatus	*Salix* and *Carex*
N. acridulus	*Carex*
N. aethiops	*Sparganium ramosum*, *Carex*
Grypus equiseti	*Equisetum arvense*—rarely on *E. palustre*
Phytonomus nigrirostris	*Trifolium* and *Ononis spinosa*
P. dauci	*Erodium circutarium*, *Geranium molle*
Rhinoncus castor	*Polygonum aviculare* and *Rumex*
Litodactylus leucogaster	aquatic and subaquatic plants.
Orobites cyaneus	*Orobus* and *Viola*
Mecinus collaris	*Plantago maritima*
Rhynchaenus foliorum	*Salix*

Comparison of this list with that of recorded plants is interesting in showing a large number of correlations. Records of such plants as *Plantago maritima*, *Montia fontana* and *Salix* receive confirmation, if such were needed from the occurrence of *Mecinus collaris*, *Phaedon armoraciae* and *Rhynchaenus foliorum*. At the same time there are a few beetles which suggest the presence of plants not shown on the list. Unless the feeding habits of *Grypus equiseti* have radically changed, one must assume the existence of *Equisetum* even though it has not been recognized and the same sort of argument would suggest the likely occurrence of *Thymus*, *Achillea millefolium* and *Trifolium*.

(*k* 7) *Diptera*

The extraordinary large numbers of *Dilophus* give a picture of pools over which this fly swarmed as it does now in the summer in northern latitudes.

The chironomid larvae confirm that the deposits of the pools were richly organic. Where *Chironomus* is the dominant member of the chironomid fauna, as it is here, the bottom conditions may be assumed to be highly eutrophic. *Glyptotendipes* is found in association with fixed aquatic vegetation in still or running water. *Cryptochironomus defectus* is usually a bottom dweller in running water.

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(*k* 8) *Plants*

The evidence for ecology from the plants can be considered from both micro- and macro-remains. The slides prepared from Bands 2 and 3 are virtually devoid of tree pollen and would suggest 'tundra' conditions in the area. The abundant aquatics are to be expected since the deposits are those of pools and probably much of the sedge pollen can be regarded as from waterside plants at least. The commonest terrestrial herbs (*Thalictrum*, *Plantago*, Caryophyllaceae and Compositae) indicate open conditions. The abundant *Myriophyllum* pollen in Band 3 and its absence from Band 2 correlates with the macrofossil occurrence. The differences in pollen counts can be seen in table 2.

More detailed ecology can be derived from the larger plant remains. The greater part of these are seeds or fruits. Occasional isolated fruit valves are found (e.g. *Draba*) and *Glaux* is represented by a dozen or so complete fruits as well as numerous seeds. Leaves are very rare at Upton Warren although they are common in the Fladbury deposit (p. 381). Leafy shoots of mosses, however, do occur. There is a mixture of habitats represented and the flora is presumably that of a wide area around the site which included dry sandy places (*Scleranthus annuus*) as well as lime-rich soils (*Primula farinosa*, *Parnassia palustris*, *Scabiosa columbaria*). The flora of Band 3 is much better known than that of Band 2 but it is noticeable that the abundant *Myriophyllum* and *Potamogeton densus* of Band 3 are completely absent from Band 2. This may well be correlated with a slight difference in salinity (see p. 401).

The aquatics themselves include species characteristic of base-rich (*Myriophyllum spicatum*, *Hippuris*) and acid waters (*M. alterniflorum*) but the former are much commoner and the pool (of Band 3) seems to have been generally alkaline. This suggests that the surrounding land was covered by relatively rich soils, such as unweathered boulder clay, and that the calcifuge element in the flora occurred locally on banks of washed sands.

The occurrence of several land plants characteristic of brackish water and coastal areas is to be noted. While *Armeria maritima* and *Plantago maritima* are well known to have inland forms and to occur in the Late-Glacial floras, *Glaux maritima* and *Triglochin maritima* are reported only from coastal or inland saline waters. The occurrence of these in Band 3 (from other evidence a fresh-water pool) must indicate the local presence of relatively highly saline areas, unless they too indicate merely a boreal climate. *Triglochin maritima* has been reported in Britain from Post-Glacial deposits but apparently only from estuarine sites. The records from the Netherlands may also be from estuarine deposits and Florschütz (1958) does not make it clear whether his 'saltmarsh element' from Full-Glacial deposits (including *T. maritima*) is to be regarded as climatically significant like his 'steppe element' or not.

The virtual absence of trees indicated by pollen counts is confirmed by the lack of macroscopical remains. Of shrubs, a few leaves of *Salix herbacea* and ?*S. phylicifolia* are all that occur.

IV. Evidence bearing upon climate

(*l*) *Geological*

The only feature of significance is the cryoturbation which affected all the organic bands to some extent in certain places, but particularly Bands 2 and 3. As will be seen from figure 2, the disturbances in Band 2 affect also the gravels up to 2 or 3 ft. above the

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organic layer, at which level they are sharply truncated. It can be assumed, therefore, that the climatic conditions were not severe enough to produce cryoturbation of the pool's deposits whilst they were being laid down and whilst plants and animals were living therein, though such conditions must have prevailed at several periods during the deposition of the whole thickness of terrace gravels.

The cryoturbation takes the form of high-angle festooning and at least one small frost wedge. The former presumably expressed itself on the contemporary land surface as soil polygons of a foot or two in diameter, owing their formation to alternations of deep frost and thaw. It can safely be assumed that winters were much more severe than they are now in Worcestershire but they need not have been more rigorous than they now are in the mountains of northern England or Scotland where the formation of soil polygons can still occur. In particular, cryoturbation on this scale does not necessitate the presence of 'permafrost', though it does not preclude it. It is true, of course, that the same county has yielded evidence of polygon structures of large size demanding the presence of permafrost and it has been suggested that this occurred during the maximum of the Irish Sea Glaciation (Shotton 1960). This date would not long precede the deposition of the Upton Warren gravels which might therefore be contemporary with a climate of Arctic severity; but from the geological evidence within the deposit itself, nothing more than a parallel with high-altitude north Britain, or Sweden or Finland can be drawn.

(*m*) *Evidence of climate from the fossils*

It would be expected that the most reliable deductions about climate would come from a study of the present-day distributions of those species enclosed within the deposits and which have survived until today. However, the modern distribution of a species may be governed by factors other than climate (Coope 1959) and caution is therefore necessary in the interpretation of this sort of data. Many species are so cosmopolitan that they can tolerate a wide range of climatic conditions and are thus of little value in climatic deductions. Other species, more limited in their distribution, have greater climatic significance. If a large number of distribution patterns are compared it is often possible to make out a 'fashion' of distribution; the fauna may be dominantly northern or southern, continental or Atlantic. Those species that do not conform with this 'fashion' then require special interpretation.

Ideally it might be expected that the area of most frequent overlap of distribution should be interpreted as the area whose climate most nearly approximates today to the climate at the time of the deposition of the organic layers. The Upton Warren biota, however, presents a more complex picture and the pattern of distributions does not permit so simple a climatic interpretation.

(*m*1) *Vertebrates*

Of the large mammals, the mammoth (*Mammuthus primigenius*) and woolly rhinoceros (*Coelodonta antiquitatus*) are extinct, but are nevertheless commonly thought of as associated with Arctic tundra conditions, particularly since their bodies have been found frozen in northern latitudes. The lemming, *Dicrostonyx henseli*, is also extinct but suggests a comparison with the present-day lemming country of north Scandinavia. Amongst the animals still

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living, the reindeer (*Rangifer tarandus*) is most suggestive of a cold climate with severe winters.

Bones of frog (*Rana temporaria*) were not uncommon in the washings from Band 3 but not from the other organic layers. These bones suggest that the pool did not freeze solid during the winter months and that the frogs were able to hibernate in the mud at the bottom. The frog, however, is found in the far north of Europe though not in full tundra conditions.

Fish bones were very abundant in Band 3 and rare in Band 2. Most were remains of the three-spined stickleback (*Gasterosteus aculeatus*), both adult and young individuals being represented. The bones were sent to Dr E. Trewavas of the British Museum of Natural History and she has kindly commented upon their climatic and ecological significance. According to Heuts (1947*a*, *b*), the three-spined stickleback occurs in Belgium as two types, one in fresh water with few plates and a high vertebral number, and an estuarine type with many plates and a lower vertebral number. Intermediates occur only where these two meet. In the White Sea area, L. S. Berg (1948–49) records *G. aculeatus* as a marine pelagic fish that comes in-shore to spawn in mid-July. There appears to be no evidence of *G. aculeatus* breeding in fresh water under tundra conditions. Where the climate is severe, it is restricted to salt water and it may well be that Heuts' salt-water form is the only one found in the far north. Since the Upton Warren skeletons are dissociated, it has not been possible to determine which of the two types is represented here. The large number of bones and the presence of large and small individuals suggest that the fishes actually bred in the pool represented by Band 3, which was certainly not saline, and if they did this it is indicative of a winter climate that was not unduly severe at the date of deposition of the organic silt. The possibility still remains that the sticklebacks could migrate, via the river, to winter in the Severn Estuary or the sea.

(*m* 2) *Molluscs*

The abundance of *Pisidium vincentianum* and the relatively large numbers of *P. obtusale lapponicum* give this molluscan fauna a special significance which is discussed by Dance in his appendix. The modern distribution of the first species, however, cannot be used as a means of assessing climate. There is a curious anomaly that the modern distribution is Mediterranean, whereas all fossil records come from deposits which, for other reasons, suggest a cold climate—Dance does discuss whether the fossil forms are not at least a separate subspecies. *Pisidium lapponicum*, on the other hand, is a rare present-day form known from very few places—Klin in Russia (latitude 56–57° N), Swedish Lapland, Arctic North America and Lough Neagh (Ireland). Specimens from the last locality are not strongly inflated like those from the first three places of our fossil forms and may well not be comparable. The other three localities, as the only known places where this peculiar variety exists, strongly support a cold climate for the Upton Warren biota.

(*m* 3) *Insects*

Beetles. Of the recorded insect species, coleoptera are by far the most abundant. Since many of them are sensitive indicators of climate, their modern distribution will be considered in some detail.

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One of the most outstanding features of this fauna is the large number of species no longer living in the British Isles (table 3). Three of these may be extinct. Of the remainder, eight are strongly northern, now living in the higher latitudes of Scandinavia (see figures 5 to 7). If to this list we now add table 4, with thirteen species which are north European though still occurring in the north of the British Isles, often as isolated relics (figures 8 to 14), we have what at first sight appears to be an impressive case for a climate considerably more rigorous than that of the present day.

Table 3. Species of Coleoptera absent from Britain

(S = 'southern' species, N = northern species, C = continental species, X = probably extinct species.)
Distribution maps of the species marked with an asterisk are included in figures 5 to 16.

*Carabus hortensis**	*C*	*Philonthus linki*	*C*
Dyschirius septentrionum	*N*	*Tachinus* sp.A.	*X*
Amara municipalis	—	cf. *Oxytelus* sp.	*X*
*A. erratica**	*N*	*Corymbites melancholicus*	*N*
*A. interstitialis**	*N*	*Heterocerus hispidulus*	*S*
*A. torrida**	*N*	*Chrysolina limbata*	*S*
Cymindis angularis	*S*	*Phaedon pyritosus*	*S*
Hydroporus arcticus	*N*	*Entomoscelis adonidis*	*S*
Colymbetes paykulli	*N*	*Crepidodera interpunctata*	—
Bledius littoralis	*N*	*Aphodius* sp.A.	*X*

Table 4. Species of British Coleoptera confined to the north of the British Isles or to isolated mountain tops farther south

Distribution maps of the species marked with an asterisk are included in figures 5 to 16.

*Nebria gyllenhalli**
Pelophila borealis
*Elaphrus lapponicus**
*Bembidion virens**
Patrobus septentrionis
Amara quenseli
*Feronia adstricta**
*Agonum sahlbergi**
Deronectes griseostriatus
Agabus congener
*Agabus arcticus**
Cantharis figuratus var. *scoticus*
*Otiorrhynchus arcticus**

Note: For complete list of northern group add species marked N in table 3

Table 5. Species of Coleoptera living in Britain but whose European distribution is almost entirely south of lat. 60° N.

Northern limits of the species marked with an asterisk are included in figure 15.

Ophonus cordatus
Haliplus obliquus
*Agabus nebulosus**
*Colymbetes fuscus**
*Georissus crenulatus**
Heteroceras fusculus
H. fenestratus
Cateretes rufilabris
Caenocara bovistae
Crypticus quisquilius
*Aphodius plagiatus**
Otiorrhynchus ligneus
Bagous tempestivus
Phytonomus dauci
Mecinus collaris

Note: For complete list of 'southern' group add species marked S in table 3.

However, there is also in the fauna a considerable element whose distribution is relatively southern (table 5 and those of table 3 marked S). It is not suggested by this term that they are species which now live only south of Upton Warren. Most of them are to be found in southern Scandinavia but not north of latitude 60° N. except occasionally in scattered patches (figure 15). They are 'southern' only by comparison with the northerners of tables 3 and 4. If the ranges of the species in these two groups are compared, it is found

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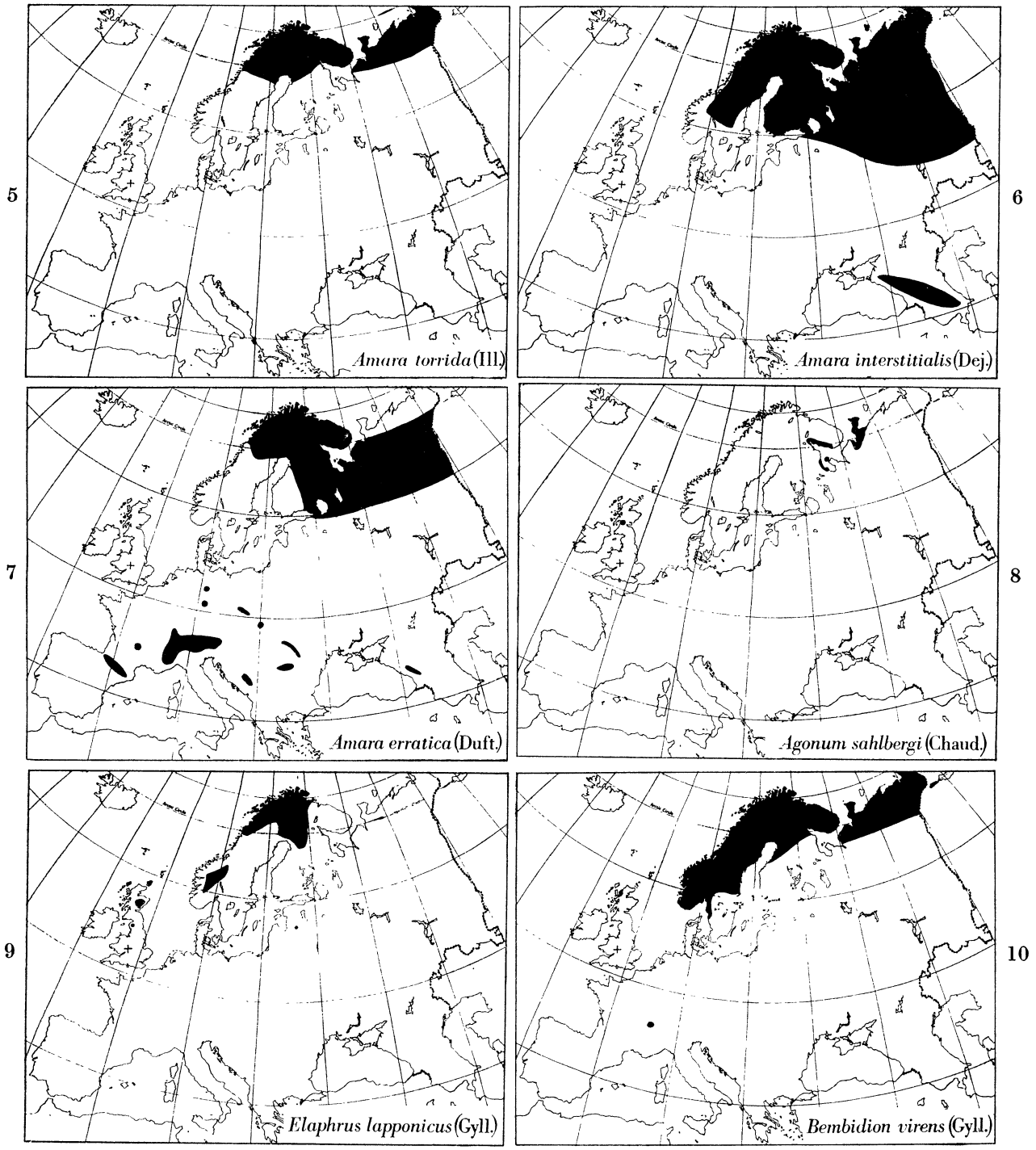
that in many cases they do not overlap at all and some are so far separated today that they appear to be climatically incompatible. Any satisfactory interpretation of climatic conditions must take into account this anomaly.

A third element of the fauna, small but interesting in its unexpectedness, is the 'continental'. *Carabus hortensis* (for distribution see figure 16), while neither northern nor southern, is very clearly non-Atlantic. *Philonthus linki* has an even stranger continental distribution, since it is Asiatic and only known east of the Urals.



FIGURES 5 TO 10

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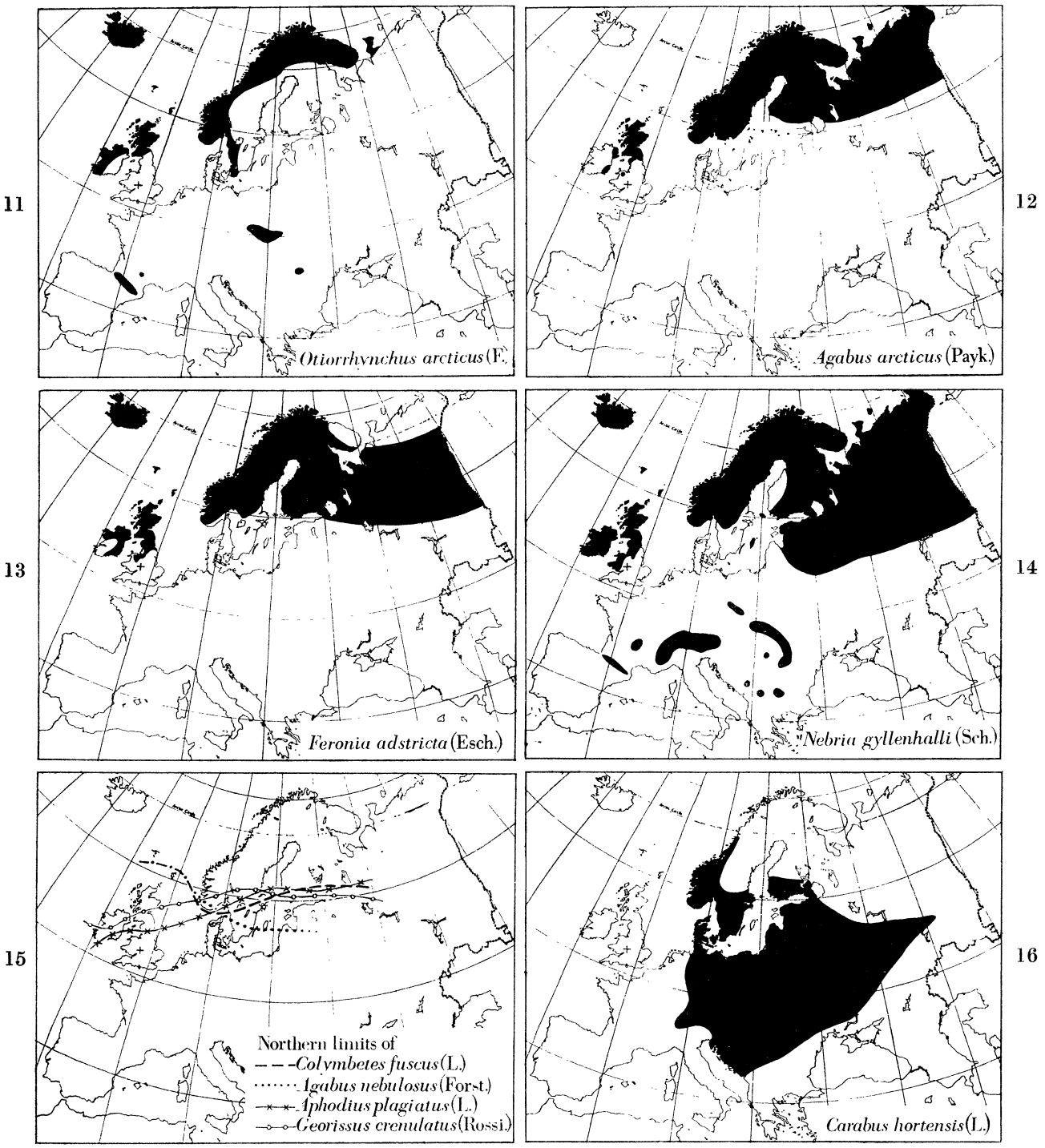
The anomalous occurrence of both 'northern' and 'southern' elements in the fauna might be most simply explained if it is considered that at Upton Warren we have two faunas, representing two periods of contrasting climate, buried together in the same deposit. Since it is unlikely that any significant change in climate occurred during the deposition of the organic mud, any mixed fauna would have to contain a number of species derived from a previous deposit. However, it is thought unlikely that there are



FIGURES 11 TO 16

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derived fossils in the Upton Warren fauna. It has a striking ecological homogeneity and moreover lacks that fraction showing abrasion and fragmentation which would be expected in a fauna compounded of indigenous and derived elements. It is therefore thought most probable that the Upton Warren fauna represents a community of species that actually lived together in the neighbourhood over a relatively short period of time and does not represent a mixed fauna of different ages. The anomaly therefore remains unresolved and an alternative explanation must be sought.

An explanation of the apparent climatic incompatibility of many of the species may be based on the fact that a fauna is not static but fluctuates continuously in response to climatic alterations. During relatively rapid changes of climate and the consequent readjustment of the fauna, certain species are likely to become temporarily out of phase with the climate. There would thus be a mingling of species characteristic of the earlier climate with the incoming species typical of the new conditions. Since the deposits at Upton Warren represent some part of an interstadial during the Last Glaciation such a rapid change of climate might be expected. The mixture of cold-loving species with relatively warmth-loving species in this fauna, might well be accounted for in this manner.

If rapid changes of climate are to be postulated, it is well to ask whether these changes were towards a milder or more severe climate. Before attempting to answer this question, however, it is necessary to examine the effects of changes in temperature on the distribution of insect species. These effects have been summarized by Lindroth (1956).

Alterations in the annual period of biological activity and in the minimum summer temperatures are factors of great importance in the changes of distribution of insect species. These factors affect differently a species at the northern and at the southern extremity of its range. With all cold-blooded animals, low temperatures tend to have an immobilizing effect on individuals. High temperatures have no such effect. An abnormally short, cold summer at the northern limit of toleration of a species, may thus immobilize individuals for a relatively long period and prevent them from reaching a stage of development suitable for hibernation. The effect of this would be to cause a temporary retreat of its area of distribution. At the southern limit of a species the effect of a summer of this type would be negligible. On the other hand, an abnormally hot summer at the southern extremity of its range would not be very disastrous since under these conditions the insect can frequently move to cooler microclimates. Again at its northern limit a hot summer would only serve to extend, temporarily, the range of the species. Thus it is the northern limit of a species that is of greatest climatic significance, whilst the southern limit grades patchily into isolated relic areas associated with cooler microclimates. The effect of a sharp deterioration of climate (chiefly a drop in temperature) would therefore be the rapid extermination of those species already at the northern limit of their tolerance. On the other hand, a rapid amelioration would cause the advance of more southern species without necessarily the immediate extinction of the earlier cold fauna, and for a short period there would be a mixed fauna with a number of species out of phase with the general climatic conditions.

The Upton Warren insect fauna with its mixture of northern and 'southern' elements may thus be indicative of an ameliorating climate. The presence of a large number of northern species suggests that in the recent past the climate had been severe, perhaps

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equivalent to north Sweden at the present day. The more southern species, however, suggest that the climate had then become milder with warmer, longer summers, and might be best matched with that of south Sweden of the present day.

(*m* 4) *Plants*

While the greater part of the flora is temperate, there is a distinct boreal and arctic-alpine element. Of these, *Draba incana*, *Thalictrum alpinum*, *Salix herbacea* and *Viscaria alpina* are the most notable. The rarity of tree pollen in the microflora would normally be interpreted as also indicating 'tundra' conditions in the area, but several of the plants present indicate a much more temperate climate. The *Dianthus* seeds are certainly not of a native British species and *D. carthusianorum* does not range at present further north than Denmark. The large *Linum* species are not recorded as native in Scandinavia and *L. anglicum* is at its northern limit at present in England. It is possible that the fossil seeds are correctly regarded as distinct (as described by Reid) since they are smaller than typical *L. anglicum*, and hence their climatic requirements might be different. *L. praecursor* has been recorded from the Lea Valley in a flora considered by E. M. Reid to be of subarctic type. Polunin (1959) records *L. perenne* agg. from the Arctic regions of Siberia, Yukon and Alaska so the fossil form might fit into that complex.

Potentilla sterilis, *Scabiosa columbaria* and *Potamogeton densus* do not range north of southern Scandinavia and can also be regarded as indicating temperate conditions. Three-quarters of the species occur throughout Scandinavia and there are no species with a more restricted Arctic range.

V. General conclusions

Forty-two thousand years ago the Early Würm ice sheet known in the Midlands as the Main Irish Sea Glacier, was already in retreat from its position of maximum extent at the Bridgnorth–Wolverhampton line. At this period the River Salwarpe, tributary to the Severn and with a volume well above that of the present day, was depositing extensive sheets of sand and gravel on its wide floodplain. At Upton Warren, about 150 ft. above contemporary sea level, shallow pools existed from time to time on this floodplain, long enough to be colonized by plants and animals and probably to be used as wallowing and drinking places by the larger mammals. In general these pools were neutral or slightly alkaline, as may be deduced from the assemblage of plants and animals, but one at least may be interpreted as mildly brackish so that it alone supported the ostracod *Cyprinotus salinus*. The two molluscs *Pisidium obtusale lapponicum* and *P. vincentianum* may owe their restriction to this pool to the same cause. Its salinity apparently led to the dwarfing and stunting of *Planorbis* and *Lymnaea* and to the exclusion of several species of mollusc and the plants *Myriophyllum* and *Potamogeton densus*. These effects were probably local and to be explained by an escape of salt from springs such as have always characterized the Droitwich area. Other brine springs on the land adjacent to the ponds could explain the presence of the beetle *Bembidion aeneum* and of such plants as *Glaux maritima*, *Triglochin maritima* and possibly also *Armeria maritima* and *Plantago maritima*.

The fauna and flora each provide evidence of dry sandy soil adjacent to the pools, but some of the plants required more alkaline soils which must have existed beyond the confines of the gravelly floodplain.

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There is no doubt that the climate of the time was more severe than at present in Worcestershire and the first impression given by the cryoturbation of the deposits, the remains of the larger mammals and above all by the occurrence of a group of beetles now restricted to northernmost Scandinavia or Russia is that of a rigorous Arctic climate. This inference received further support from the scarcity of tree pollen of *Betula* and *Pinus* and even of *Salix* remains, suggesting a tundra environment. We think that the scarcity of trees and shrubs is not due to a misleading accident of preservation for there are no insects present which feed upon birch or pine and the heliophilic habits of the carabid beetles support the concept of an open habitat. However, the flora is not that of Arctic tundra. It and the greater part of the fauna suggest a less severe climate more akin to that of southern Sweden at the present day. In this context the scarcity of trees is anomalous. Associated with this anomaly is the further one of the mixed coleopterous fauna, where many northern, even Arctic species co-existed with others of more southern aspect and their respective climatic requirements appear at the present day to be incompatible. We have already suggested that a climate ameliorating rapidly after the truly Arctic conditions of the Irish Sea Glacial Maximum would allow the more thermophilous insects from the south to advance before all the 'northern' species had been exterminated.

The problem presented by the flora is somewhat different, for here we have the presence of an advancing thermophilous ground flora virtually unaccompanied by trees and shrubs. For a solution to this problem a climatic explanation was at first sought. Normally, in an ameliorating climate, Arctic tundra conditions are followed by birch and then pine forest which in turn dwindles in competition with the mixed oak forest. No such competition can account for the scarcity of *Betula* and *Pinus* at Upton Warren, since there was a total absence of the trees of the mixed oak forest. It might be suggested that the speed of climatic change was so fast that the slow rate of maturing of the southern deciduous trees was the cause of their lagging behind the advance of the ground flora but this would not account for the rarity of *Betula* and *Pinus*. Any suggestion that Upton Warren was so cold, at least seasonally, as to be north of the tree line is incompatible with the ground flora and many of the insects. An alternative suggestion that the summers or winters were so dry or cold that steppe conditions developed, is not really supported by the flora or by the present-day distribution of most of the insects, despite a few species hinting at 'continental' distributions. Certainly also, whilst the pools represented by Bands 1 to 4 were in existence, they must have remained as sheets of water over a succession of years and this implies no serious fall of the water-table across the floodplain. We are therefore left with no single or simple climatic reason to explain the floral assemblage.

There remains another possible explanation of the scarcity of trees and shrubs. The direct evidence of bones in the gravel and the indirect evidence provided by abundant dung and carcass beetles, shows that the large mammals were numerous—and in particular bison and mammoth. On the analogy of the North American prairies when they supported great herds of bison, we can picture a similar situation on the extensive and rather featureless lowland of the Severn basin. If this were so, the grazing of these large herbivores could explain the failure of colonization by the trees and shrubs. The low ground flora is compatible with such a suggestion, for it consists overwhelmingly of biennials or perennials

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with their resting buds at or just below ground level and so well adapted to survival in an area of heavy grazing.

Irrespective of whatever conviction may be carried by the various suggestions we have made, it is quite clear that when it is possible to catalogue a fauna and flora as extensively as has been done in this case, problems of climatic and ecological change become apparent which remain concealed with a more limited approach.

We gratefully acknowledge the great assistance in naming specimens from the following: Mr J. N. Carreck (microtine teeth), Dr E. Trewavas (fish), Miss A. G. Grandison (frogs), the late Mr A. G. Davis, Mr S. P. Dance, Mr A. W. Stelfox and Mr A. E. Ellis (molluscs), Dr J. P. Harding (ostracods), Dr W. E. China (hemiptera), Dr D. Bryce (chironomids), Professor Carl Lindroth, Mr J. Balfour Browne, Mr E. B. Britton and the Rev. C. E. Tottenham (beetles), Dr G. O. Evans (arachnids), Miss C. A. Lambert (seeds), Mr J. H. Dickson (moss).

Professor Lindroth allowed us to examine the collections at Lund and we are also indebted to the British Museum for repeated access to their collections, to the late Dr W. D. Hincks of the Manchester Museum and to Mr L. Bilton of the Birmingham Museum. We acknowledge also the great technical help of Mr P. J. Osborne, the assistance in photography of Mr L. W. Vaughan, and the help of Mrs A. M. Darley in preparing the paper for publication.

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Appendix. On the genus *Pisidium* at Upton Warren

By S. P. Dance

Zoology Department, British Museum (Natural History)

The species of the genus *Pisidium*, both fossil and recent, are well represented in Europe. A number of species have marked ecological preferences and may often provide helpful information on conditions past and present, especially when they constitute a significant percentage of a fresh-water molluscan assemblage otherwise poorly characterized, as at Upton Warren. The concurrence of *P. vincentianum* and *P. obtusale lapponicum* here is of sufficient interest to warrant this supplementary account of the *Pisidium* fauna. Many of the specimens are so well preserved that the periostracum, affording important diagnostic characters, is retained intact.

The following table gives some idea of the relative frequency of the species present in Bands 2 and 3. The numbers refer to separate valves.

	Band 2	Band 3
Pisidium casertanum (Poli)	2	5
P. subtruncatum Malm.	1	45
P. nitidum Jenyns	—	> 500
P. obtusale lapponicum Clessin	30	—
P. vincentianum Woodward	192	—

Notes on the species

P. casertanum. Although this is probably the commonest British fresh-water mollusc and ecologically the most tolerant, the paucity of specimens and their much-worn condition suggests an adventitious origin.

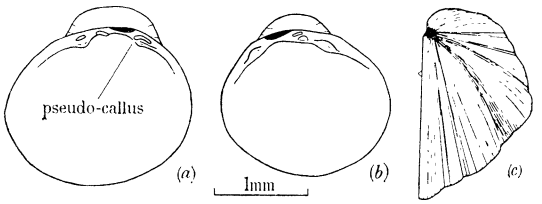

Figure 17. *Pisidium obtusale lapponicum* Clessin. (*a*) Right valve, *length* 2·1 mm, *height* 2·0 mm, (*b*) left valve, *length* 1·8 mm, *height* 1·7 mm, (*c*) profile view of right valve.

P. subtruncatum. Widely distributed in the British Isles in most sorts of habitat, though it seems to prefer running water.

P. nitidium. Widely distributed in the British Isles and very often found associated with *subtruncatum* in habitats where there is usually a constant flow of water. The specimens, found so abundantly in Band 3, are mostly of a very tumid, thin-hinged form, with very small cardinal teeth and marked growth ridges. The nepionic grooves, often so well seen in this species, are absent.

P. obtusale lapponicum. Only a few scattered references to this distinctive form of *P. obtusale* C. Pfr. are to be found in British literature and British specimens have never been figured. At first glance it appears to bear little relation to *obtusale*. Unlike 'typical' *obtusale*, *lapponicum* is very small, rarely exceeding 2 mm in length, and is very inflated, a complete specimen being often much broader than long or high (figure 17 (*a*) to (*c*)).

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However, the dentition, especially of the right valve, is essentially that of 'typical' *obtusale*. In each, the posterior lateral P_3 tends to curve across the anterior end of P_1 producing a more or less distinct lump—the 'pseudo-callus'—a feature found in no other known European *Pisidium*. The ligament pit occupies only half the breadth of the hinge plate. The cardinal tooth C_3 in the right valve is thin and nearly three-quarters the length of the ligament pit, while both cardinals C_2 and C_4 in the left valve are very short. Most of the Upton Warren examples have very marked growth ridges, another characteristic of this form. Although there is some justification for regarding *lapponicum* as an Arctic subspecies, forms transitional to *obtusale* are known to occur, sometimes in the same biotope (Odhner 1951). Favre & Jayet (1938) give excellent figures of *lapponicum* and discuss the use of the name.

The first British specimens were found by Stelfox in the early Post-Glacial marls of the White Bog, Killough, Co. Down (Stelfox in Erdtmann 1928, p. 168). More recently it has been recorded from the Ponders End Stage at Nazeing, north London (Allison, Godwin & Warren 1952); an early Holocene tufa at Letchworth, Herts (Kerney 1955); the Lower Gravel at Swanscombe, Kent, possibly the earliest fossil occurrence (Dance 1956); and early Post-Glacial deposits near Laceby, Lincolnshire, and Aylesford, Kent (Burchell & Davis 1957). Apart from these published records I have seen specimens from Late-Glacial deposits at Ham Hill, Snodland, Kent; Bognor, Sussex; Market Drayton, Shropshire; and Roddans Port, Co. Down. It is known from a number of deposits in northern Europe (Altena 1957; Altena & Kuiper 1945; Favre & Jayet 1938; 1950; Steusloff 1937). Recent specimens are known from Klin, Russia (Favre 1943, p. 38); northern Sweden (Clessin 1873; Odhner 1951); and from Arctic North America (Herrington 1954). Specimens dredged by R. J. Welch in Lough Neagh have been referred to this form (Ellis 1951; Kerney 1955), although these are much less inflated than recent specimens I have seen from Lapland. In northern Sweden *lapponicum* is found in *Carex* swamps and *Sphagnum* ponds (Odhner 1951).

P. vincentianum. This interesting *Pisidium* is distinguished from all other European species, fossil and recent, by the remarkably depressed ligament pit (figure 18 (*a*) and (*b*)), a feature that can be seen to advantage by tilting the valve and looking across the ventral edge towards the hinge. The cardinal C_3 in the right valve is extremely bent, resembling a staple in form, with the thickened, blunt, posterior end projecting over the inner margin of the hinge plate. The well-marked growth ridges (figure 18 (*c*)) usually present in this species, are evident on most of the Upton Warren examples though some are nearly smooth. The periostracum is straw coloured, of a dull sheen, regularly and finely striate. Several minute specimens, probably fry, measure 1·1 mm length, 1·0 mm height. They are rather more swollen than the fry of other *Pisidium* species though they resemble that of *P. pulchellum* Jenyns in their tetragonal outline. This is the most abundant *Pisidium* in Band 2.

There are only three published records for this species in the British Isles. It was first taken sparingly in sands beneath the marl of the White Bog, Killough, Co. Down (Stelfox 1929), and it is reported also from the 'Pleistocene' of Sittingbourne, Kent (Oldham 1935) and the early Post-Glacial of Aylesford, Kent (Burchell & Davis 1957). I have also seen specimens from a Late-Glacial deposit (Sparks, personal communication) at Market Drayton, Shropshire. As a Pleistocene and Holocene fossil, the species is known from a

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number of localities in north-western Europe (Altena 1957). The recent distribution of *vincentianum* comprises a number of localities in the Mediterranean area and one or two in western Asia (Altena 1957).

Altena discusses the anomalous distribution of fossil and recent *vincentianum*. Whereas almost all the recent localities are in the warm Mediterranean area, the fossils are all from the cold Pleistocene of north-western Europe. Altena suggests that the recent form must be at least subspecifically different from the fossil form. He does not consider that the fossil shells differ significantly from the recent ones, though Kuiper, who has seen most of the specimens recorded from the Mediterranean area, tells me that there are slight conchological differences. A table of maximum measurements of specimens from most of the fossil and recent localities corroborates Altena's statement that fossil specimens are usually larger than recent specimens: 3·45 mm length, 3·35 mm height, for the largest fossil measured (Lersö, Copenhagen, Denmark), and 2·5 mm length, 2·35 mm height, for the largest recent specimen (Preveza, Greece).

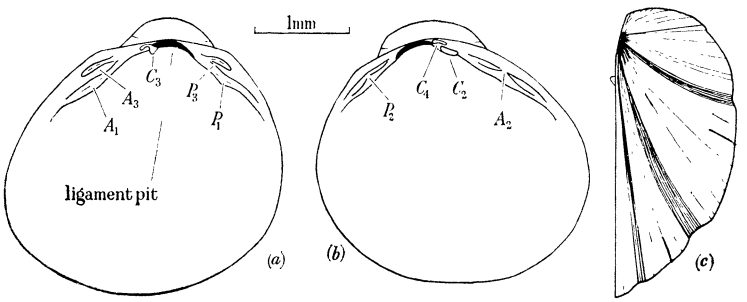

FIGURE 18. *Pisidium vincentianum*, B. B. Woodward. (*a*) Right valve, *length* 2·65 mm, *height* 2·65 mm, (*b*) left valve, *length* 2·66 mm, *height* 2·65 mm, (*c*) profile view of right valve.

Altena had no measurements of specimens from the easternmost locality, Chatir Kul (a lake situated above 10 000 ft. in the western Tien Shan Mountains, Turkestan), the first record of living *vincentianum* (Woodward 1914). One might expect specimens from this mountain lake to be large like the fossils. The A. S. Kennard collection in the British Museum (Natural History) contains six of Woodward's original Chatir Kul specimens, the largest of which measures 3·0 mm length, 2·7 mm height. This compares well with the dimensions of the large 'fossil' form. However, a close inspection of the Chatir Kul material throws doubt on the correctness of their original identification as *vincentianum* by Woodward (the author of the species). This identification has not previously been questioned although there are two additional species described from Tibet that are worth considering as possibly conspecific with the Chatir Kul examples; *P. stewarti* Preston (1909) and *P. prashadi* Odhner (1937). *P. stewarti* was collected at an altitude of 14 500 ft. in the Gyantse Valley, and *prashadi* at 12 300 ft. in Kham Province. From the descriptions and figures of the shells of these two species I am unable to find any characters that warrant their specific separation. Moreover, they, like the Chatir Kul specimens, are 'large' forms; *stewarti* measures 3·0 mm length, 2·25 mm height, and *prashadi* 3·5 mm length, 3·0 mm height. I suggest that, for the present, the Chatir Kul specimens be referred to *stewarti*.

Until more fossil and recent material is available, it may be best to regard the fossil form as subspecifically different from the form still living in the Mediterranean area.

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However, any attempt to establish the relationships between them and *stewarti* should be considered in the light of Odhner's (1940) suggestion that the members of the '*vincentianum* group' are of a tropic origin.

I am indebted to the late Mr A. G. Davis for the opportunity to report on this material and for helpful advice. Mr A. W. Stelfox has examined a number of specimens and supplied valuable notes on them for which I am very grateful. Much information on *P. vincentianum* was gained in conversation with M. J. G. J. Kuiper. Mr B. W. Sparks kindly lent material from Market Drayton. I am indebted to Mr I. C. J. Galbraith for critically reading the manuscript.

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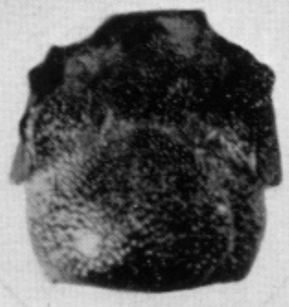

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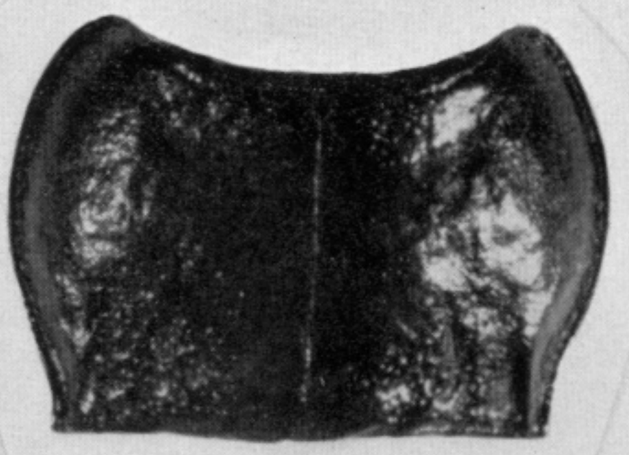

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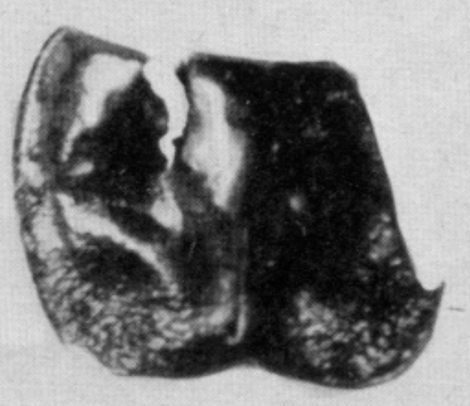

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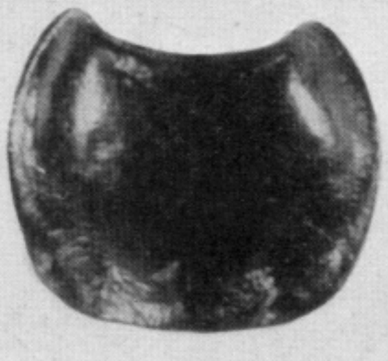

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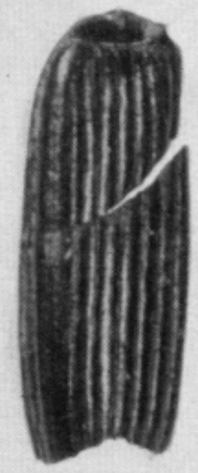

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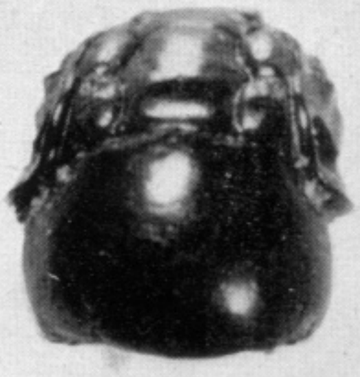

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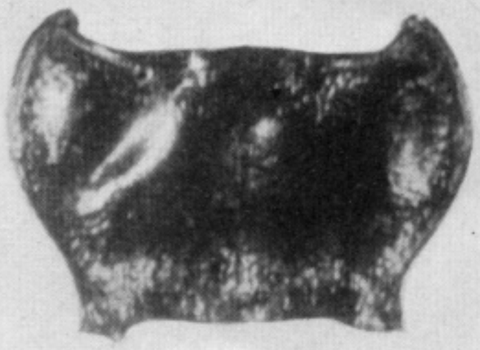

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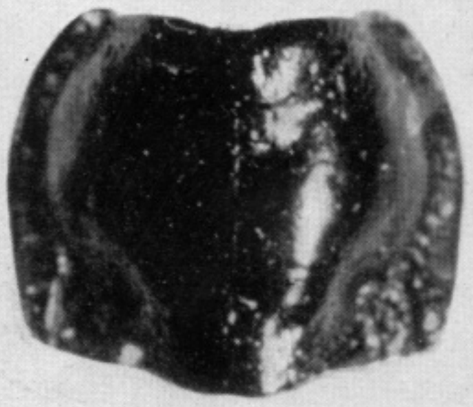

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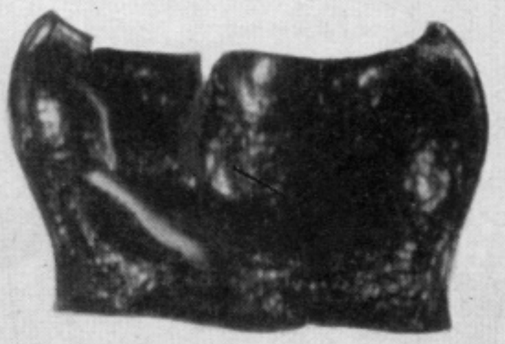

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Figures 19 to 40

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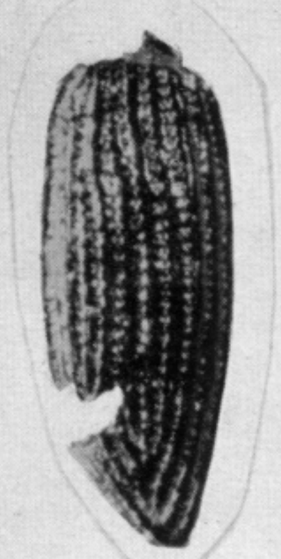

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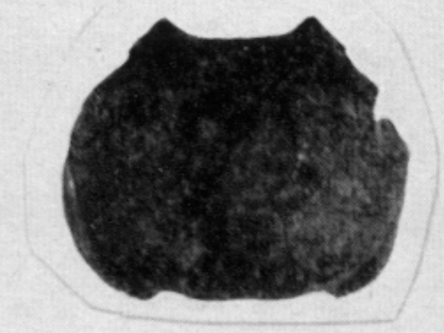

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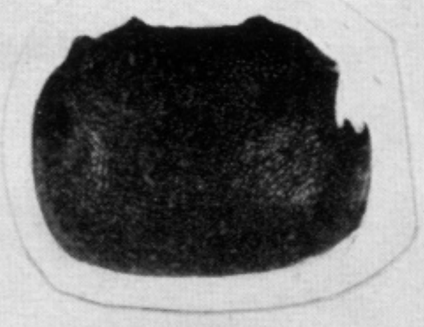

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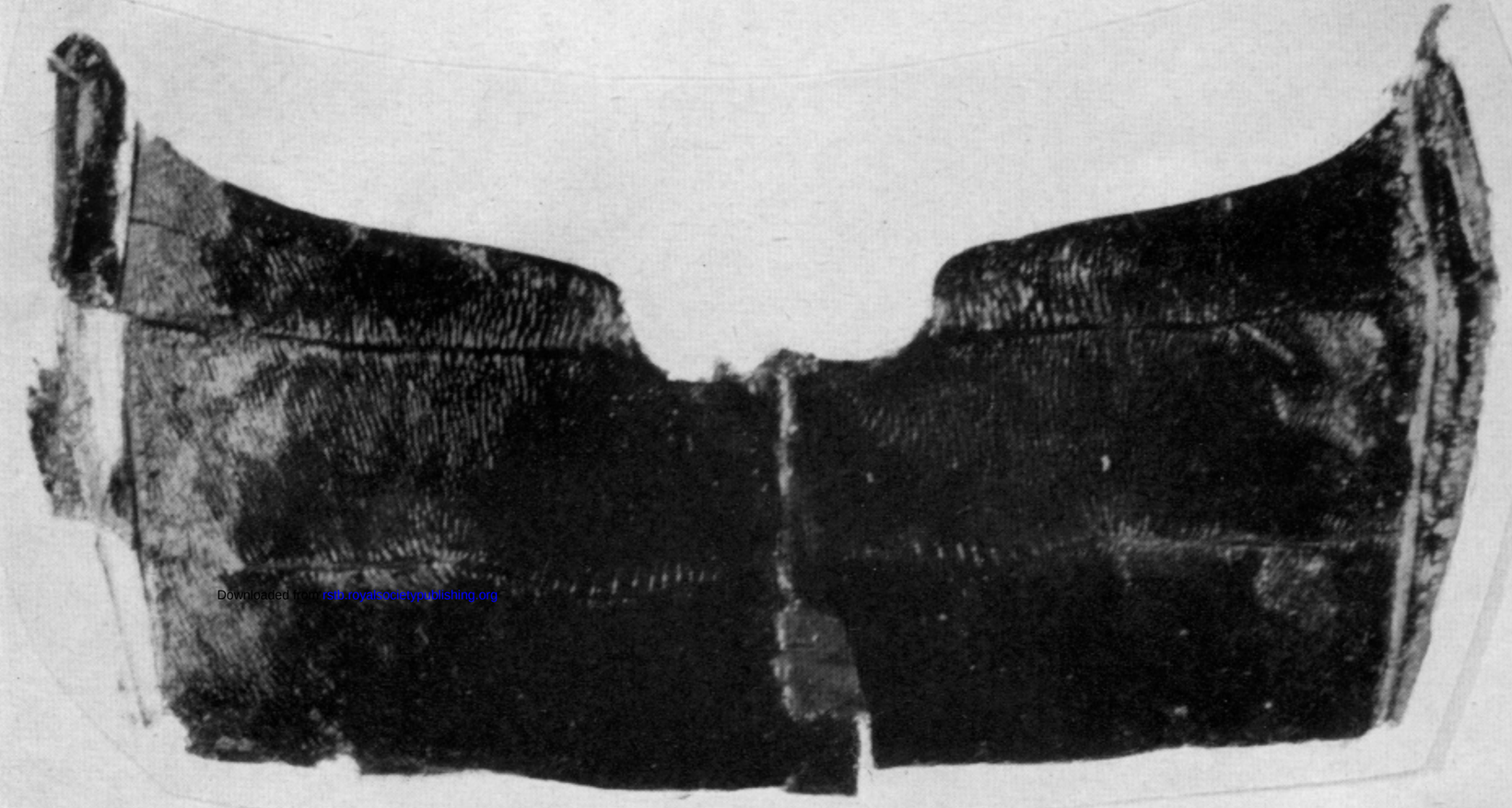

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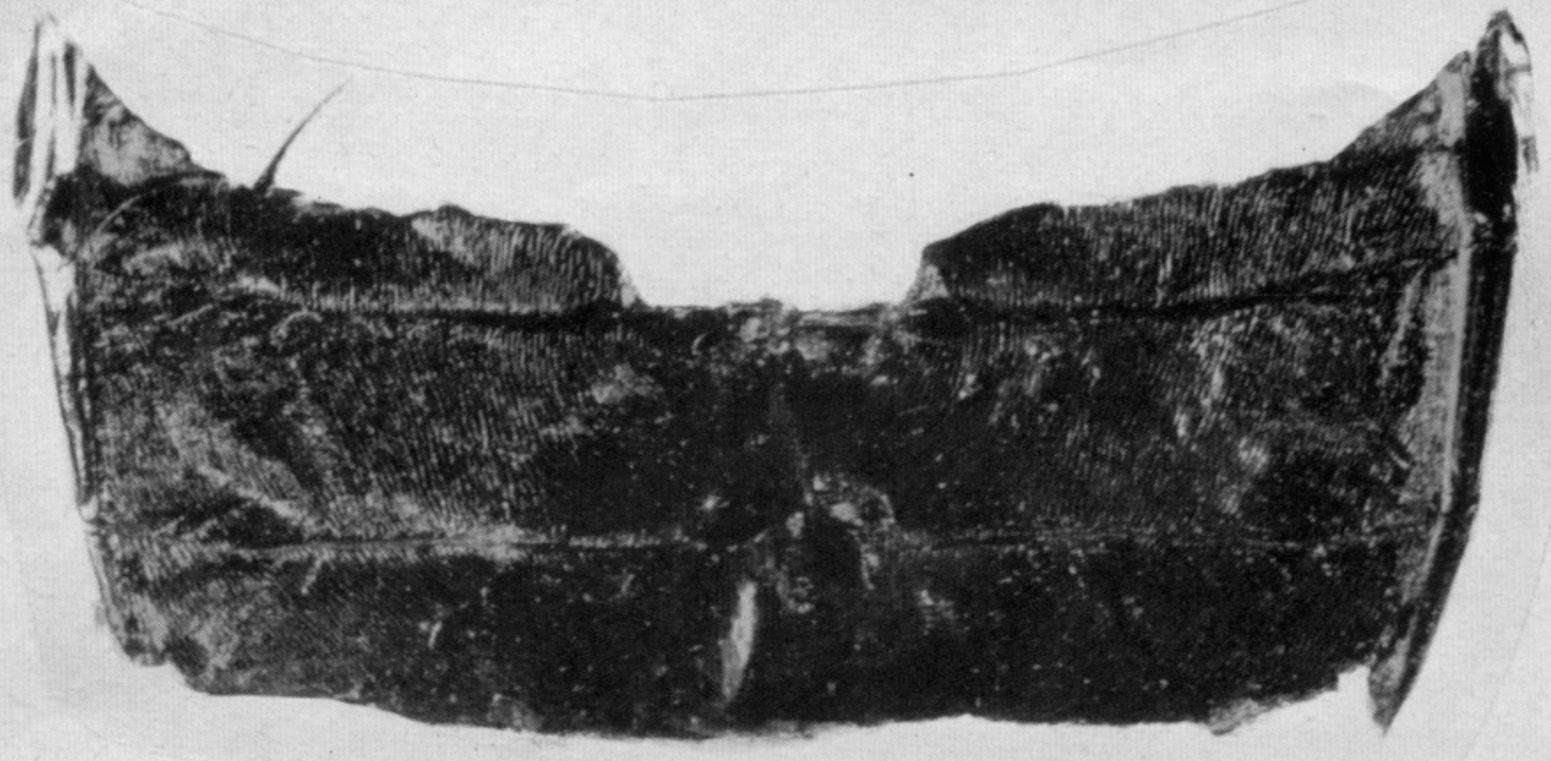

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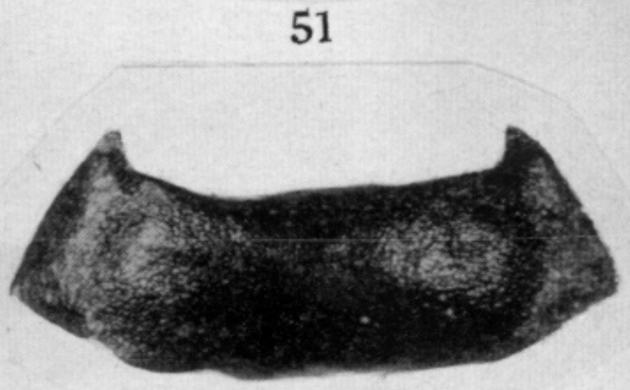

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FIGURES 41 TO 53

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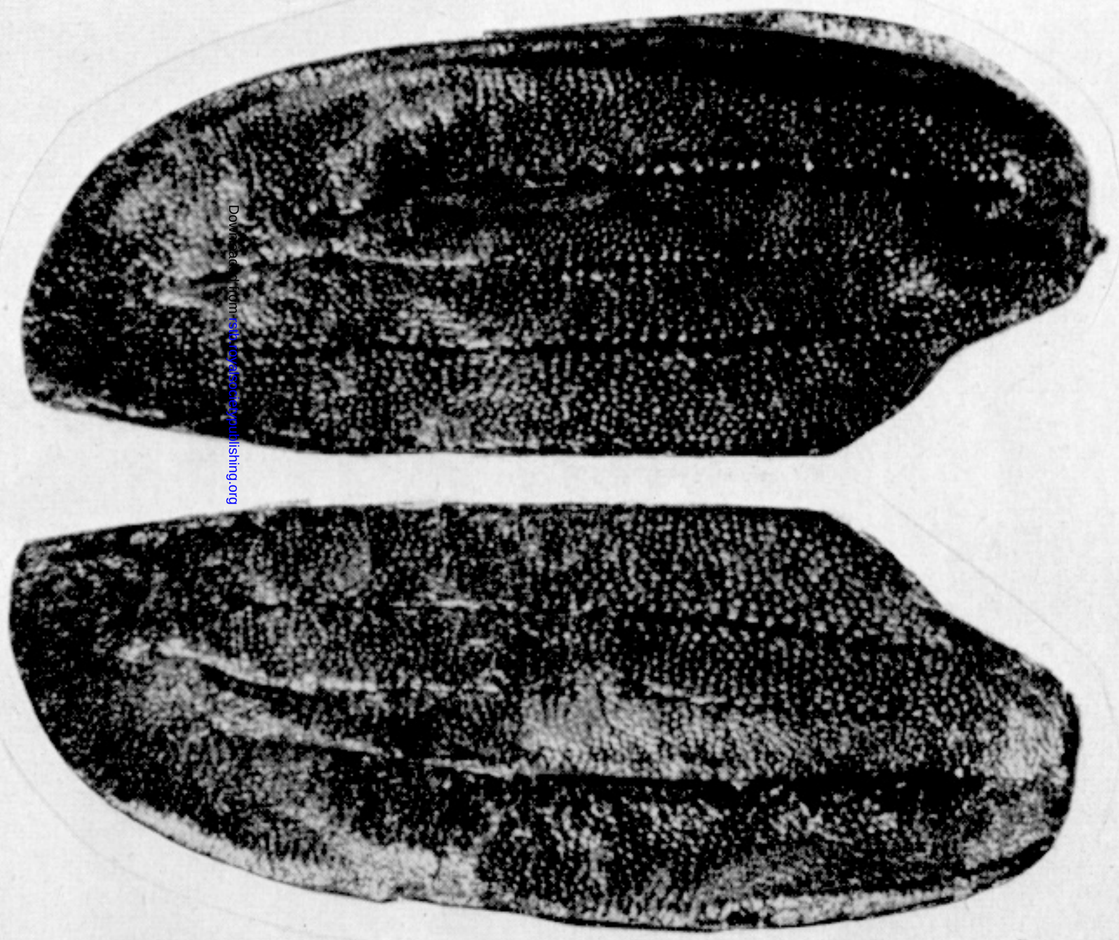

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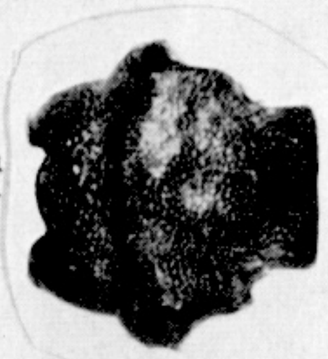

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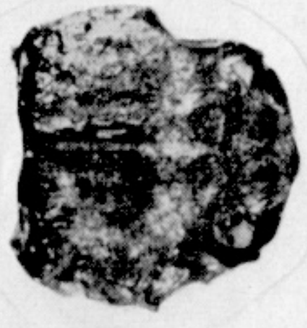

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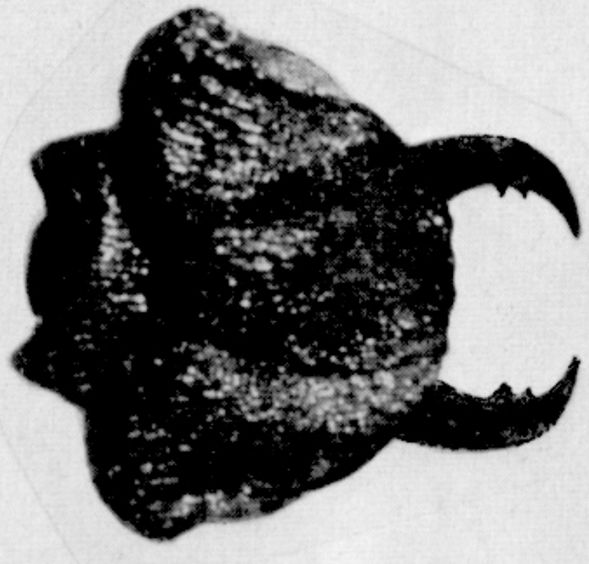

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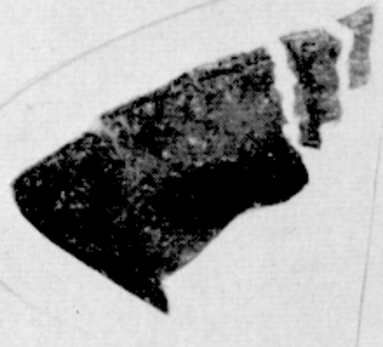

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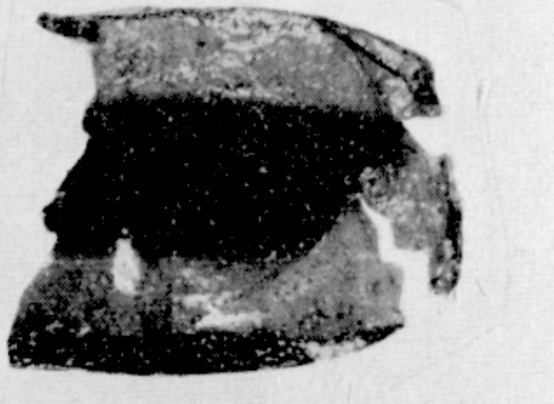

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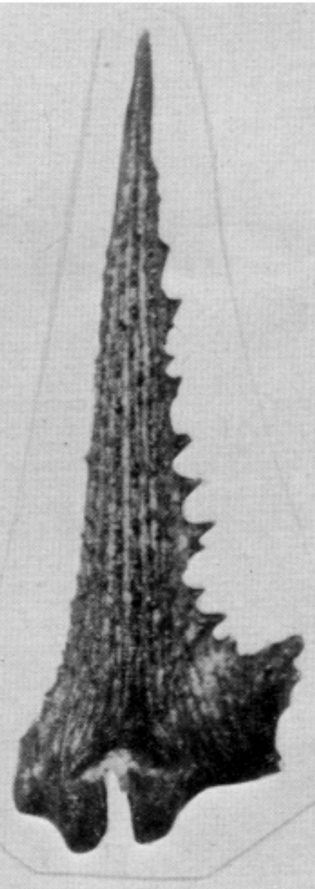

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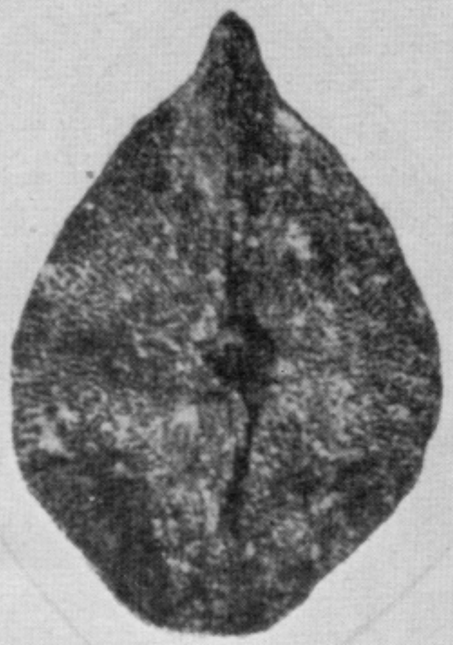

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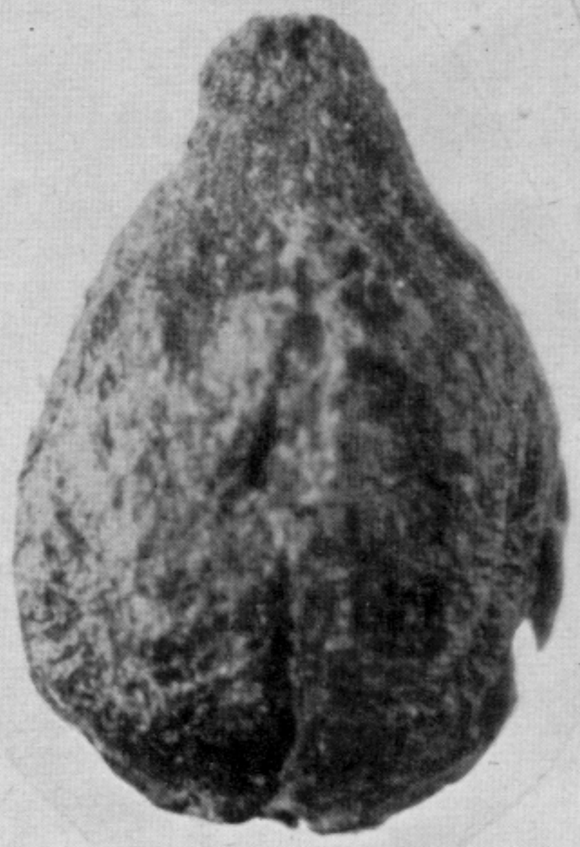

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FIGURES 70 TO 85