
An Insect Fauna from Mid-Weichselian Deposits at Brandon, Warwickshire

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AN INSECT FAUNA FROM MID-WEICHSELIAN DEPOSITS AT BRANDON, WARWICKSHIRE

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[Plates 21 to 23]

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An insect fauna of 172 taxa, chiefly of coleoptera, is described from Mid-Weichselian deposits at Brandon, Warwickshire. This fauna includes two species that are now believed to be extinct and thirty-three that are no longer found living in Britain. All but one of these species live today in Arctic or sub-Arctic regions of north-east Europe and northern Siberia—the single exception being an insect of decidedly steppe environments. The fauna as a whole indicates an open treeless habitat closely analogous to the northern tundras of the present day to which several of the recorded species are exclusively confined. Details of the local environment of the times are inferred from the fossil insect fauna. An interpretation of the climatic regime based on the northern requirements of the species in this fauna, suggests that conditions were more severe than for any other entomologically investigated site. A moderate degree of continentality is inferred and an attempt is made to give a range of average monthly temperatures through the year. A comparison of this fauna with other known fossil insect assemblages suggests that these may be of value in correlation of Quaternary deposits.

GENERAL INTRODUCTION

At Brandon, near Coventry, Warwickshire, large gravel workings have, during the past few years, exposed extensive sections in Late Quaternary deposits. These sections have been described and their stratigraphy interpreted by Shotton (1968), who equated a large terrace feature with the No. 2 terrace of the river Avon (Shotton 1953; Tomlinson 1963). For a short period in 1964 when the excavators were working the terrace gravels, a bed of dark blue-grey organic silt was exposed, together with several isolated blocks of similar material that had probably once been part of a continuous bed now split up by post-depositional disturbance. These silts contained fragmentary plant remains, often concentrated into layers, a lithology very similar indeed to the insect-bearing deposits already investigated from Upton Warren (Coope, Shotton & Strachan 1961), Fladbury (Coope 1962) and from the Tame Valley (Coope & Sands 1966). There seemed every reason to believe that these deposits at Brandon should be similarly fossiliferous. Samples were collected from all the available blocks of silt and in each case about

20 lb of silt was obtained. From a more continuous bed that was quite obviously still in its position of deposition, it was possible to take large bulk samples. The detailed stratigraphy of this bed is described by Shotton (1968, figure 2). This bed was split horizontally by a seam of sand. The lower part was thicker with much coarser plant debris and yielded 330 lb. of material whilst the upper part faded out rapidly during excavation and yielded only 20 lb.

Though the silt showed no evidence of insect fossils in the field, all the samples yielded abundant insect fragments when processed in the laboratory. The technique for obtaining the fossils was simple. The silt was first disaggregated under water and washed over a fine sieve (300 μm). The still damp residue that remained on the sieve was then thoroughly mixed with paraffin (kerosene) in a large bowl. The surplus paraffin was then poured off and enough cold water was added to float the fossil insects well clear of the bulk of the plant debris which remained in the bottom of the bowl. The floating fraction was then decanted into a sieve and thoroughly washed, first, in detergent and then in alcohol to remove any trace of the paraffin. The insect remains were then sorted, using a binocular microscope, from the small amount of plant debris that had also floated, to ensure that very small specimens were not overlooked. Experience has shown that macroscopic sorting is quite inadequate and biases the collection heavily in favour of conspicuous species (Coope 1961). Insect fossils are best stored either by fastening them down to prepared cards by gum tragacanth or loose in tubes of alcohol. If they are stored under water they are likely to be attacked by mould which can rapidly enmesh the specimens inextricably in a felt of fungal hyphae. If they are left to dry without being fastened down to cards they usually warp and become so fragile that they disintegrate as soon as any attempt is made to restore them to their original condition.

THE FAUNA

Fossils from each block of silt have been kept separate from one another but since the assemblages were almost identical, they have been all grouped together in a single unit in the faunal list that follows. Most of the blocks yielded a monotonous assemblage dominated by small Omaliine staphylinids. Only in the large samples from the bed in its position of deposition was there any variety of species, where the mass of small sticks probably indicates that it represented flood debris swept together into its present position.

In the faunal list which follows, the nomenclature follows Kloet & Hincks (1945) as far as possible. For species, however, that are not on the 'British List' I have tried to adopt the most up to date of current usage. These species are indicated by * in the list if they are still living and by † if they are believed to be extinct. Numbers of the more important skeletal parts are given, where diagnosis of any part is unsure a question mark is used and where the part is fragmentary f. is used to indicate one individual and ff. to indicate more than one. Apart from the Hemiptera and Coleoptera no effort has been made to assess numbers of individuals.

INSECT FAUNA FROM MID-WEICHSELIAN DEPOSITS

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FAUNAL LIST

INSECTA

HEMIPTERA

Saldidae

<i>Salda littoralis</i> (L.)	20 individuals
<i>Salda morio</i> Zet.	8 individuals
* <i>Chiloxanthus stellatus</i> Curtis	1 individual
* <i>Calacanthia tribomi</i> (J. Sahlb.)	9 individuals
<i>Saldula</i> spp.	

Tingidae

* <i>Onchochila</i> sp.	2 individuals
-------------------------	---------------

Aphididae

1 individual

MEGALOPTERA

Sialidae

<i>Sialis</i> sp.	few larval mandibles
-------------------	----------------------

TRICHOPTERA

Gen. et sp. indet.	few larval fragments
--------------------	----------------------

COLEOPTERA

Carabidae

	heads	pronota	left elytra	right elytra
<i>Carabus arvensis</i> Hbst.	—	—	1	2
<i>C. violaceus</i> L.	?	3	3	1
<i>Pelophila borealis</i> Pk.	7	10	7	11
<i>Notiophilus aquaticus</i> (L.)	66	70	103	100
* <i>Diachila arctica</i> Gyll.	24	{ 5	2	6
* <i>D. polita</i> Fald.		{ 18	21	22
<i>Nebria gyllenhali</i> (Schoen.)	—	—	1	—
<i>Elaphrus cupreus</i> Duft.	—	—	—	1
<i>E. lapponicus</i> Gyll.	—	1	1	2
<i>E. riparius</i> (L.)	1	—	1	—
<i>Loricera pilicornis</i> (Fab.)	7	9	7	11
<i>Dyschirius globosus</i> (Hbst.)	1	—	1	1
* <i>D. septentrionum</i> Munst.	—	—	1	2
<i>Clivina fossor</i> L.	—	—	1	—
<i>Bembidion aeneum</i> . Germ.	18	32	31	34
<i>B. bipunctatum</i> (L.)	41	53	49	59
* <i>B. dauricum</i> Mkch.	?	?	5	—
* <i>B. difficile</i> Motsch.	?	32	{ 3	3
* <i>B. fellmani</i> Mnh.			{ 32	32
<i>B. femoratum</i> Sturm	—	—	2	1
* <i>B. hasti</i> Sahlb.	—	—	10	11 aedeagus
* <i>B. hyperboraeorum</i> Munst.	—	—	1	2
<i>B. lunatum</i> (Dufts.)	2	5	9	12
<i>B. obliquum</i> Sturm	—	—	3	1
<i>B. quadrimaculatum</i> (L.)	—	—	2	—
<i>B. schueppeli</i> Dej.	—	—	3	4
<i>B. virens</i> Gyll.	—	—	3	5
<i>Patrobus septentrionis</i> Dej.	10	11	7	10
<i>Amara alpina</i> (Fab.)	31	{ 39	37	33
* <i>A. torrida</i> (Ill.)		{ 6		
<i>A. quenseli</i> (Schoenh.)	27	27	29	44
<i>Feronia adstricta</i> (Eschs.)	—	2	1	—
* <i>F. blandulus</i> (Mill.)	28	31	47	49
* <i>F. kokeili</i> (Mill.)	—	1	1	—
<i>Calathus melanocephalus</i> (L.)	—	2	3	2
* <i>Agonum consimile</i> Gyll.	—	2	1	1
<i>A. ericeti</i> (Pz.)	—	—	2	—
<i>A. sahlbergi</i> (Chaud.)	—	1	1	1

Gyrinidae

<i>Gyrinus</i> sp.	1		—	—
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COLEOPTERA (cont.)

	heads	pronota	left elytra	right elytra
Dytiscidae				
* <i>Deronectes alpinus</i> Pk	—	—	—	— 2 metasterna
<i>Deronectes</i> sp.	—	—	f	—
<i>Hydroporus palustris</i> (L.)	—	—	2	1
* <i>H. arcticus</i> Thoms.	—	2	—	—
<i>Hydroporus</i> spp.	—	2	—	— metasterna
<i>Agabus arcticus</i> (Pk.)	—	1	—	—
<i>A. bipustulatus</i> (L.)	—	11	11	—
<i>A. congener</i> (Thunb.)	3	4	ff	ff
<i>Ilybius</i> sp.	—	1	1	4
* <i>Colymbetes dolabratus</i> Pk.	4	1	ff	ff 3 sets of abdominal segments
<i>Dytiscus</i> sp.	—	—	—	f
Hydrophilidae				
<i>Ochthebius dilatatus</i> Steph.	2	2\	14	16
<i>O. viridis</i> Pey.	2	1}		
<i>Helophorus aquaticus</i> (L.)	187	293	ff	ff
<i>H. brevipalpis</i> type	389	486	ff	ff
* <i>H. fennicus</i> (Pk.)	50	35	ff	ff
* <i>H. jacutus</i> Popp.	23	80	26+ff	29+ff
† <i>H. wandereri</i> D'Orch.	315	346	354	374
* <i>Hydrobius arcticus</i> Kuw.	6	4	3	9
<i>Cercyon</i> spp.	—	—	4	4
Silphidae				
<i>Necrophorus investigator</i> Zett.	—	—	—	— 1 leg
<i>Thanatophilus dispar</i> Hbst.	14	18	6	7
<i>Aclypea opaca</i> (L.)	4	6	—	1
<i>Catops</i> sp.	—	2	1	1
Leiodidae				
<i>Hydnobius punctatus</i> Sturm	—	—	4	1
<i>Leiodes</i> sp.	—	2	7	4
Clambidae				
<i>Clambus</i> sp.	—	—	1	1
Staphylinidae				
* <i>Pycnoglypa lurida</i> Gyll.	1	2	3	1
<i>Omalius excavatum</i> Steph.	2	2	—	—
<i>O. rivulare</i> Pk.	2	3	—	—
<i>Xylodromus concinnus</i> Marsh.	1	—	1	—
* <i>Olophrum boreale</i> Pk.	232	{ 10 }	382	386
<i>O. fuscum</i> (Grav.)	—	{ 299 }	—	—
<i>Arpedium brachypterum</i> (Grav.)	474	737	683	619
<i>Acidota crenata</i> (Fab.)	3	4	3	7
<i>Acidota quadrata</i> Zett.	—	1	—	—
<i>Lesteva longelytrata</i> Goeze	—	—	—	2
<i>Geodromicus plagiatus</i> Fab.	26	29	8	23
<i>Euedectus whitei</i> Shp.	—	2	2	—
* <i>Boreaphilus hennigianus</i> Sahlb.	67	56	43	54
* <i>B. nordenskiöldi</i> Makl.	79	79	33	45
<i>Trogophloeus corticinus</i> Grav.	6	2	?	?
<i>Oxytelus nitidulus</i> Grav.	6	2	?	?
<i>Platystethus cornutus</i> Grav.	6	2	?	?
<i>P. nitens</i> Sahlb.	4	1	?	?
<i>P. nodifrons</i> Sahlb.	3	3	?	?
<i>Bledius fuscipes</i> Rye	9	7	2	—
* <i>Bledius litoralis</i> Heer	1	1	—	—
<i>Stenus</i> spp.	184	204	47	44
<i>Euaesthetus ruficapillus</i> Boisd.	3	8	—	—
<i>Philonthus</i> spp.	23	16	?	?
<i>Gabrieus</i> sp.	—	1	?	?
<i>Staphylinus cupreus</i> Rossi	—	2	—	—

INSECT FAUNA FROM MID-WEICHSELIAN DEPOSITS

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COLEOPTERA (cont.)

Staphylinidae (cont.)

	heads	pronota	left elytra	right elytra
<i>S. pubescens</i> De G.	—	—	—	1
<i>Quedius boops</i> type	29	30	?	?
<i>Quedius</i> sp.	—	1	—	—
<i>Mycetoporus</i> sp.	—	—	2	—
<i>Bryoporus rugipennis</i> Pand.	—	—	1	1
<i>Tachinus elongatus</i> Gyll.	—	—	1	1
<i>Tachinus</i> sp. A	—	4	8	8 + term. segs. of hind body
<i>Tachinus fimetarius</i> Gr.	—	4	2	3 + term. segs. of hind body
<i>Aleochara bilineata</i> Gyll.	—	3	—	—
<i>Aleocharinae</i> gen. et sp. indet.	60	156	93	98 (mostly <i>Atheta</i>)
Cleridae				
* <i>Opetiopalpus</i> sp.	—	—	1	1
Elateridae				
* <i>Hypnoidus rivularis</i> Gyll.	—	—	4	6
Heteroceridae				
* <i>Heterocerus intermedius</i> Kus.	?	?	14	11
<i>Heterocerus</i> spp.	?	?	2	2
Byrrhidae				
* <i>Simplocaria metallica</i> Sturm	41	61	88	109
<i>S. semistriata</i> Fab.	31	73	110	121
<i>Cytilus sericeus</i> Forst.	2	5	9	7
<i>Byrrhus arietinus</i> Steff. and/or <i>fasciatus</i> Forst.	12	—	ff	ff
<i>B. pilula</i> L.	8	—	—	—
* <i>Syncalypta cyclolepidea</i> Munst.	1	—	—	—
Nitidulidae				
<i>Brachypterus</i> sp.	3	1	2	5
<i>Meligethes</i> sp.	1	1	—	—
Cryptophagidae				
<i>Cryptophagus</i> sp.	—	—	1	—
<i>Atomaria</i> sp.	—	—	1	1
Lathridiidae				
<i>Melanophthalma</i> sp.	1	—	—	—
Coccinellidae				
<i>Scymnus</i> spp.	1	1	14	14
* <i>Hippodamia septemmaculata</i> De G.	?	5	ff	ff
* <i>Anisosticta strigata</i> Thunb.	—	—	ff	—
<i>Coccinella undecempunctata</i> L.	1	2	ff	ff
Anobiidae				
<i>Caenocara bovistae</i> Hoffm.	—	1	2	—
Anthicidae				
* <i>Anthicus ater</i> Panz.	3	—	4	1
Scarabaeidae				
<i>Aphodius lapponum</i> Gyll.	25	8	12	8
† <i>Aphodius</i> sp. A	7	3	ff	ff
<i>Aphodius</i> spp.	337	81	ff	ff
<i>Aegialia sabuleti</i> Panz.	—	1	—	—
Chrysomelidae				
<i>Plateumaris sericea</i> L.	—	—	1	—
<i>Chrysolina marginata</i> L.	12	13	ff	ff
* <i>Chrysolina septentrionalis</i> group	15	20	ff	ff
* <i>Chrysomela collaris</i> L.	3	6	ff	ff
<i>Gastrophysa viridula</i> De G.	46	45	—	—
<i>Phaedon cochleariae</i> Fab.	14	22	ff	ff
<i>Phyllodecta vitellinae</i> L. or * <i>polaris</i> Schneid.	—	—	1	1
<i>Phyllotreta atra</i> Fab.	—	—	—	1
<i>P. flexuosa</i> type	—	—	1	1

COLEOPTERA (*cont.*)Chrysomelidae (*cont.*)

	heads	pronota	left elytra	right elytra
<i>Apthona</i> spp.	—	—	2	1
<i>Chaetocnema</i> sp.	—	—	2	1
<i>Galeruca tanacetii</i> L.	6	7	8	7

Curculionidae

<i>Apion</i> spp.	6	7	43	32
<i>Otiorrhynchus arcticus</i> (O. Fbr.)	5	5	ff	ff
<i>O. nodosus</i> (Muell.)	1	2	2	1
<i>O. rugifrons</i> (Gyll.)	193	107	187	184
<i>Sitona lepidus</i> Gyll.	1	—	1	1
<i>Sitona</i> spp.	59	29	49	45
<i>Notaris aethiops</i> (Fab.)	125	132	203	203
<i>N. bimaculatus</i> (Fab.)	—	2	1	1
<i>Grypus equiseti</i> (Fab.)	13	10	16	22
<i>Phytonomus diversipunctatus</i> (Sch.) (<i>elongatus</i> Payk.)	27	24	19	21
* <i>Phytonomus obovatus</i> Csiki	21	8	2	5
<i>Phytonomus</i> sp.	2	—	—	—
<i>Ceuthorrhynchus litura</i> (Fab.)	—	1	—	—
<i>Ceuthorrhynchus</i> spp.	1	1	1	1
<i>Litodactylus leucogaster</i> (Marsh.)	—	—	3	1
<i>Eubrychius velatus</i> (Beck)	—	1	?	1
<i>Phytobius canaliculatus</i> Fähr.	8	30	11	20
<i>P. quadrituberculatus</i> Fab.	6	9	7	8
<i>Rhynchaenus foliorum</i> (Muell.)	1	3	16	22

HYMENOPTERA

numerous fragments

DIPTERA

Tipulidae	abundant larval fragments
Chironomidae	abundant larval fragments
Bibionidae	numerous fragments of <i>Dilophus</i> sp.

ARACHNIDA

Araneae	
Linyphidae	127 cephalothoraxes, mostly <i>Erigone</i> sp.
Acari	numerous mites

NOTES ON SELECTED SPECIES

***Carabus arvensis* Herbst.**

These fragmentary elytra probably represent about three individuals. At first sight they resemble *C. granulatus* L. having on each elytron three longitudinally arranged keels with a row of elongated tubercles between each. They differ from *granulatus*, however, in a number of constant ways. First, there is no ground granulation between the keels and tubercles on the disk of the elytra and in this way they differ from all specimens of *granulatus* that I have seen. In *arvensis* this ground granulation is absent from the disk but, as in the fossils, it is well developed round the edges of the elytra. In this respect the fossils also resemble *C. menetriesi* Fald. but they are consistently smaller than this species and the raised keels are more subdued. When wet the fossils were always bright green as are most specimens of *arvensis*. *C. menetriesi* on the other hand is usually black or coppery black and in this respect an undoubted specimen of *menetriesi* from the mid-Weichselian deposits at Four Ashes near Wolverhampton, was quite black when wet. The fossils differ from modern *arvensis* in their pronounced tendency to have transverse grooves across the keels. This grooving, however, was largely a *post mortem* effect as it became greatly intensified as the specimens dried out and if modern specimens of *arvensis* were adequately ill-treated, for

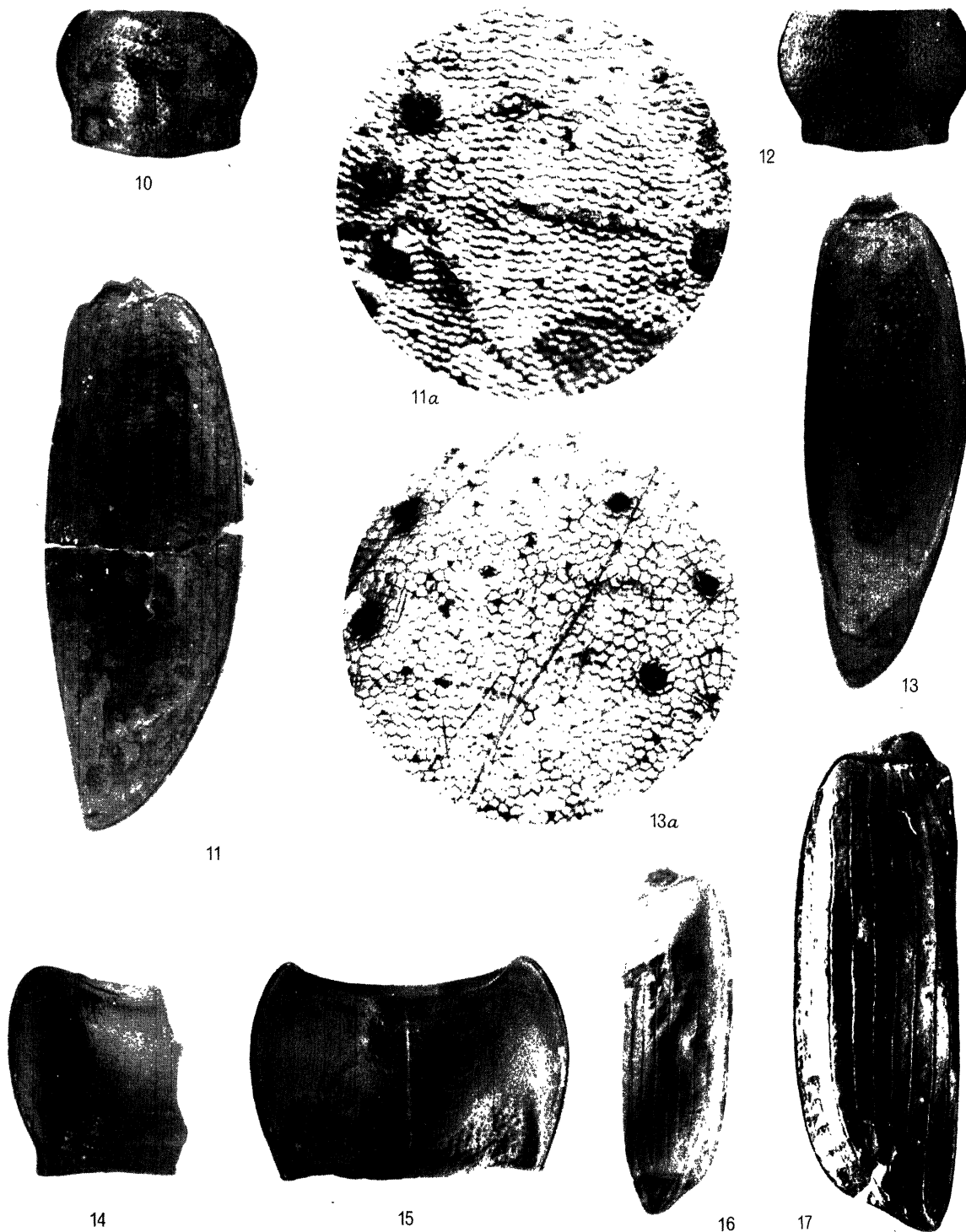


FIGURE 10. Pronotum of *Diachila arctica* Gyll. showing well-developed carinae on the posterior angles ($\times 20$).

FIGURE 11. Right elytron of *Diachila arctica* Gyll. ($\times 20$).

FIGURE 11a. Micro-ornament on disk of the elytron of *Diachila arctica* ($\times 250$).

FIGURE 12. Pronotum of *Diachila polita* Fald. Note the absence of carinae on the posterior angles ($\times 20$).

FIGURE 13. Right elytron of *Diachila polita* Fald. ($\times 20$).

FIGURE 13a. Micro-ornament on disk of the elytron of *Diachila polita* Fald—well developed micro-reticulation but more subdued than in *D. arctica* ($\times 250$).

FIGURE 14. Pronotum of *Amara torrida* Ill. ($\times 20$). Note the different form of the posterior angles.

FIGURE 15. Pronotum of *Amara alpina* Pk. ($\times 20$). Note the different form of the posterior angles.

FIGURE 16. Left elytron of *Agonum consimile* Gyll. ($\times 20$).

FIGURE 17. Left elytron of *Agonum ericeti* Pz. ($\times 20$).

example, if they were boiled in dilute potassium hydroxide, they also developed the same transverse lines and the intensity of these lines increased with the rigorousness of the treatment.

It is likely that the fragmentary *Carabus* elytra from the Tame valley also belong to this species but at the time of publication insufficient fossil material was available to permit a specific identification.

Though *arvensis* does not range into Arctic or Western Europe today, it is known from the Petschora district of north-east Russia and from the Siberian tundra (Lindroth 1945, p. 341).

***Diachila polita* Fald**

This typical tundra species is more numerous here than in any other known fossiliferous locality. Lindroth (1954) gives one of the diagnostic features of this species as the total absence of a carina on the posterior angles of the pronotum (figure 12, plate 21) which distinguishes the species from *D. arctica* Gyll. (figure 10, plate 21) in which it is well developed and from *D. fausti* Heyd. in which it is rarely developed. In this fossil series however there is evidence of an incipient ridge on the hind angles of six pronota. On certain elytra also there is a clear indication of a regular isodiametric microreticulation (figure 13*a*, plate 21) over the whole surface but this is never so well developed as in *arctica* (figure 11*a*, plate 21). The dilated middle of the elytra and the quite confused puncturation in the region of the shoulder leaves no doubt, however, that the specimens are true *polita*.

The species is known as a fossil from ten Weichselian localities in Britain (figure 1). It does not appear, however, to have survived in Britain into Late Glacial Times in contrast to its close relative *D. arctica* (figure 2).

***Bembidion aeneum* Germ.**

This specimen appears to be an obligate halophile, though the amount of salt required seems to be very small. Lindroth has shown (1949, p. 521) how the distribution of the species in southern Sweden corresponds to the area covered by deposits of the Yoldia sea, dated at around ten thousand years ago. He has also shown by experiment that the species shows a decided preference for salt. When the species was first discovered as a fossil at Upton Warren (Coope *et al.* 1961) we suggested that its presence alongside a number of maritime plants and a brackish water ostracod *Cyprinotus salinus* (Brady) might be due to the presence of surface brine springs in the area deriving their salt from the well known horizons in the Keuper Marl that directly underlie the fossiliferous deposit. Subsequently, however, *B. aeneum*, associated with maritime plants, has been found in several full glacial sites remote from any obvious source of salt and an alternative explanation seems called for. It is well known that in polar latitudes with high insolation, saline pools can develop because of the high rate of evaporation, even though the supply of salt is meagre. It is possible that the fresh glacial deposits, many of which contain marine shell debris, may have supplied the necessary salt without recourse to underground sources.

Bembidion hasti Sahlb. (figures 20, 20*a*, plate 22; figure 25, plate 23)

This is one of the few species in this assemblage of which we have the male genital armature preserved (figure 25). Both in outer form and in the detailed deposition of the internal structures this specimen is a precise match of the drawing supplied by Lindroth (1963, p. 295). The fossil is, however, a mirror image of the modern representative—a phenomenon known, but rarely, in certain individuals in present day populations. Unfortunately, since there is only one fossil specimen, its frequency in the fossil population cannot be ascertained.

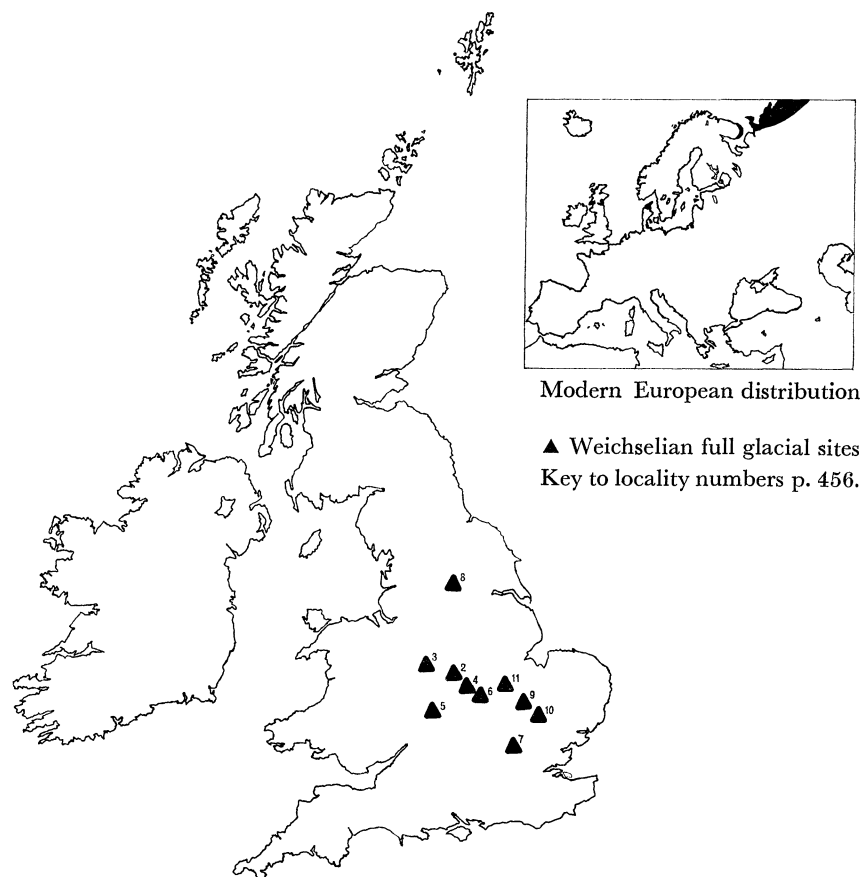


FIGURE 1. Fossil localities in Britain for *Diachila polita* Fald.

Bembidion fellmani Mnh. and difficile Motsch. (figures 22, 22*a* and 23, plate 22)

Species of the sub-genus *Plataphodes* are notoriously difficult to identify and there are probably several undescribed species in Arctic Siberia. I have compared the fossils with the two Scandinavian species *fellmani* and *difficile* which may be distinguished from one another on the micro-ornament of the elytra. In *difficile* the meshwork is stretched transversely so that the meshes may be several times as wide as they are long (figure 22*a*). In *fellmani* the ornament is much more equidimensional though the cells may be arranged in transverse rows (figure 23, plate 22). Both types of ornament were present in this fossil series, though the *fellmani* type was by far the most abundant. These two species may also be distinguished on the sinuation of the sides of the pronotum, but no attempt has been made to distinguish the fossil pronota because slight distortion can obliterate the difference.

It may be that other species are represented here as I have not seen specimens of *B. crenulatum* F. Sahlb. from north Russia which also belongs to this sub-genus.

Bembidion quadrimaculatum L.

These two elytra are smaller than any British specimens I have seen. The yellow marks at the base and apex are also smaller. I have, however, seen very small and dark specimens from the most northern part of the species range in Scandinavia, though the fossil specimens were even more extreme. There is a general tendency among species of Coleoptera that are parti-coloured for the dark areas to be larger in those specimens near to their northern limit of distribution. I will return to this subject later in particular in connexion with the coccinellids.

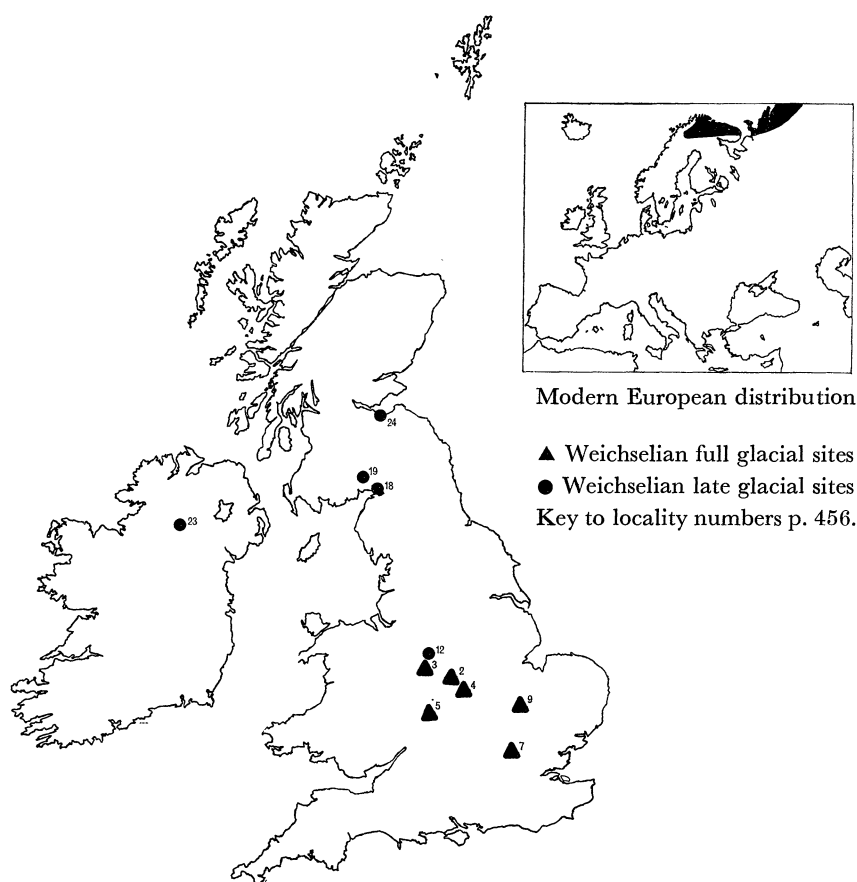


FIGURE 2. Fossil localities in Britain for *Diachila arctica* Gyll.

Feronia kokeili Mill

This is an opportunity to withdraw an earlier identification in a previous paper (Coope 1962). I recorded *Feronia* (*Cryobius*) sp. for a somewhat distorted but fairly complete specimen from a full glacial deposit at Fladbury, Worcs. This specimen is in fact *F. kokeili*, an identification corroborated by many beautifully preserved specimens from Four Ashes. At Brandon the species is represented by a single elytron and fragmentary pronotum. Today this species has a boreo-alpine distribution, occurring in northern Russia on the tundra of the Kanin Peninsula and in the Petschora region and in central Europe in the

Alps and Carpathian Mountains. In the northern part of its range it is a species of the well vegetated parts of the tundra and in the south it is a species of the Alpine zone, rarely found in grassy places at the upper limit of the forest zone. In Britain it is known as a fossil from five other full glacial sites, in three of which it was one of the most abundant of the Carabidae (figure 3).



FIGURE 3. Fossil localities in Britain for *Feronia kokeili* Mill.

***Feronia (Cryobius) blandulus* Mill.** (figures 18, 19, 19a to d, plate 22)

Species of the sub-genus *Cryobius* are notoriously difficult to separate. The sub-genus is best developed today in north-east America and eastern Siberia and there are probably many species in northern Siberia as yet undescribed. In Europe there are four species, *blandulus* Mill., *brevicornis* Kby. (*fastidiosus* Mn.), *middendorffi* J. Sahlb. (*deplanatus* Mtsch.) and *kaninensis* Popp. Only the first two species compare with the numerous fossil heads, pronota and elytra in size and in the shape of pronotum. In the specimens of *brevicornis* that I have seen the colour is more rufous than *blandulus* and the surface more reflective. The microsculpture of the elytra is made up of very transverse meshes whilst in *blandulus* the meshes are only slightly broader than they are long. There is some variation in the form of microsculpture of the fossil elytra (plate 22) so that occasionally individuals had meshes three or four times as wide as long. In no case, however, was the microsculpture as transverse as in *brevicornis*. In all other respects the fossils resemble *blandulus*. Bearing in mind that the northern Asian species have yet to be revised, all these specimens

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are, for the time being, grouped together as *blandulus*. The species is found throughout northern Siberia, from the Jenissie to the Lena rivers and in Arctic Russia on Vaigach Island and the Kanin Peninsula. It is also found in central Europe in the Tatra mountains (Holdhaus & Lindroth 1939, p. 139). According to Poppius it is found in Siberia, usually in large numbers, under stones and moss on the damp tundra and on river banks. The



FIGURE 4. Fossil localities in Britain for *Feronia blandulus* Mill.

species is rare in the Tatra mountains, being found predominantly in the Alpine zone but it has also been recorded from the highest parts of the forest zone. At Brandon it obviously thrived in considerable numbers and was the third most abundant species of the Carabidae. As a fossil the species occurred in the Barnwell Station beds at Cambridge from which three elytra were obtained (Coope 1968). These specimens all have the rather transverse ornament seen in some of the Brandon specimens. They are preserved in the Sedgwick Museum, Cambridge on a slide that has been labelled by P. Lesne '*Platyderopsis atrata* gen et sp nov.' A single pronotum has been recently recovered from mid-Weichselian deposits at the Oxbow open cast mining site near Leeds. The species is also known from full glacial deposits at Four Ashes near Wolverhampton and from Thrapston, Northamptonshire. (figure 4). In all these cases *blandulus* was associated with other species almost all of which are also recorded from Brandon.

***Agonum consimile* Gyll.**

The only species with which *consimile* is likely to be confused is the tundra species *A. exaratum* Mnh. The pronota are, however, distinctive. I have compared the Brandon specimens with both these species and the evenly curved lateral margin and rounded hind angle match *consimile*. This is not a usual tundra species being more typical of the *Betula* zone of the Scandinavian mountains where it lives in very wet clearings with a close moss cover. As a fossil it is known from three other full glacial sites and from several localities of Late Glacial age as late as Zone III.

***Amara alpina* (Fab.) and *torrida* (Ill.)**

These two closely related species are here separated on the shape of the lateral margin of the pronotum. In *alpina* the margin is evenly curved from the anterior to the posterior angle where it turns outwards sharply to form a small projection. In *torrida* the margin is decidedly sinuate in its basal third and though the posterior angle projects it does so as a natural continuation of the sinuate margin (figures 14, 15, plate 21). There is, however, some variation in the pronotal form of *alpina* which makes the distinction of the occasional fossil pronotum rather uncertain. I can find no consistent difference between the heads and elytra of these two species.

***Calathus melanocephalus* (L.)**

In Britain most specimens of this species have a reddish brown prothorax but both the fossil thoraxes are dark pitchy-black. I do not believe that this colour is due to preservation factors since in other deposits of similar lithology the colour is normal in fossils of this species. This tendency for species at the northern limit of their range to be darker than their more southern relatives has been noted previously (*vide Bembidion quadrimaculatum*).

***Agonum sahlbergii* Chaud.**

This species might be most easily confused with *A. muelleri* Hbst. The margin of the pronotum is, however, more explanate in *muelleri* especially in the region of the setigerous

DESCRIPTION OF PLATE 22

FIGURE 18. Pronotum of *Feronia blandulus* Mill. ($\times 20$).

FIGURE 19. Left and right elytron of *Feronia blandulus* Mill. ($\times 20$).

FIGURE 19*a*. Micro-ornament of disk of elytron of modern specimen of *Feronia blandulus* from the Tatra Mts. ($\times 250$).

FIGURE 19*b*. Micro-ornament of disk of elytron of fossil *F. blandulus* from Brandon ($\times 250$).

FIGURE 19*c*. Micro-ornament of disk of elytron of fossil *F. blandulus* from Brandon ($\times 250$).

FIGURE 19*d*. Micro-ornament of disk of elytron of fossil *F. blandulus* from Brandon ($\times 250$).

FIGURE 20. Right elytron of *Bembidion hasti* Sahlb. ($\times 20$).

FIGURE 20*a*. Micro-ornament of *Bembidion hasti* Sahlb. ($\times 250$).

FIGURE 21. Micro-ornament of *Bembidion virens* Gyll. ($\times 250$).

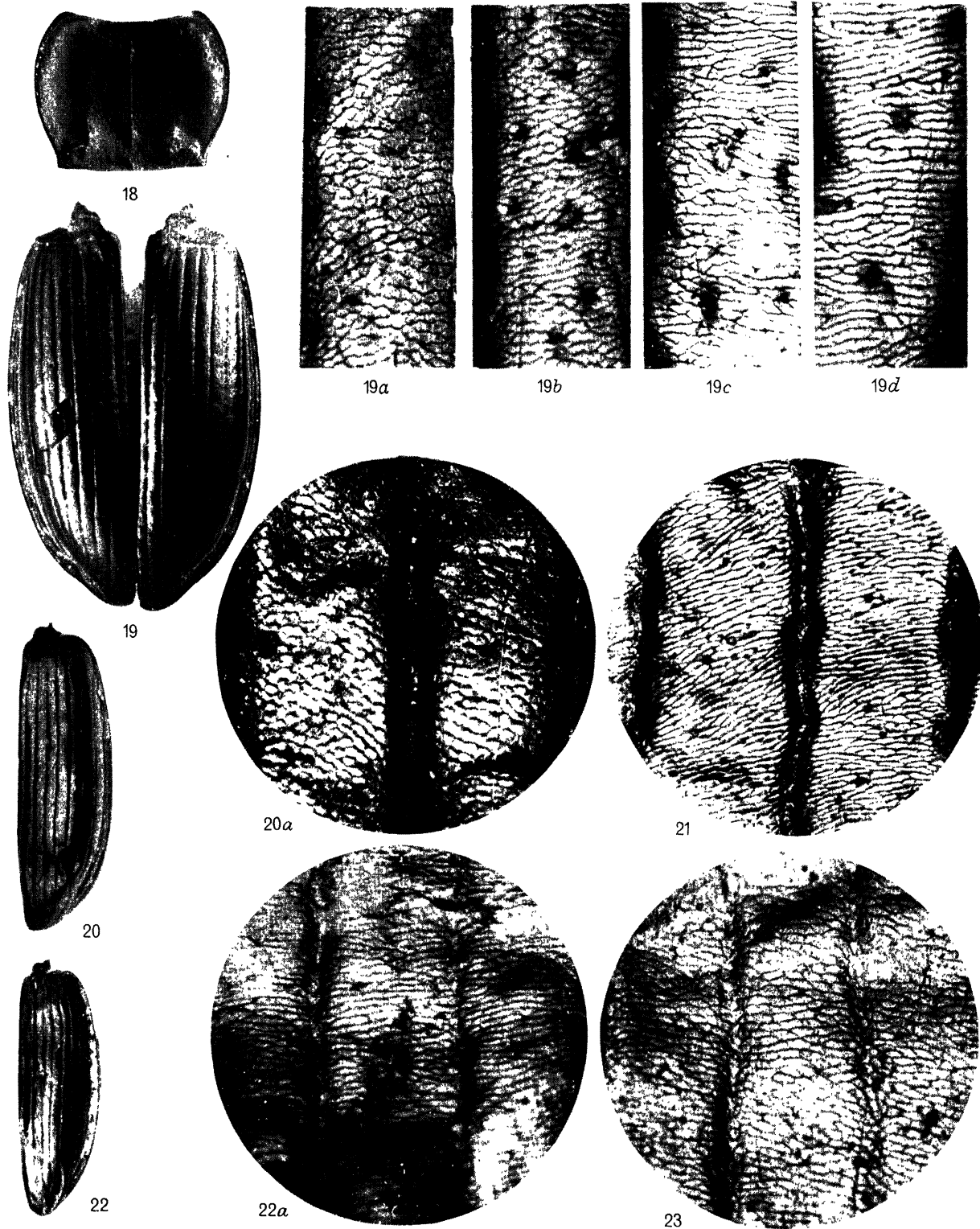
FIGURE 22. Right elytron of *Bembidion fellmani* Mnh. ($\times 20$).

FIGURE 22*a*. Micro-ornament of disk of elytron of *Bembidion difficile* ($\times 250$).

FIGURE 23. Micro-ornament of disk of elytron of *Bembidion fellmani* Motsch. ($\times 250$).

Coope

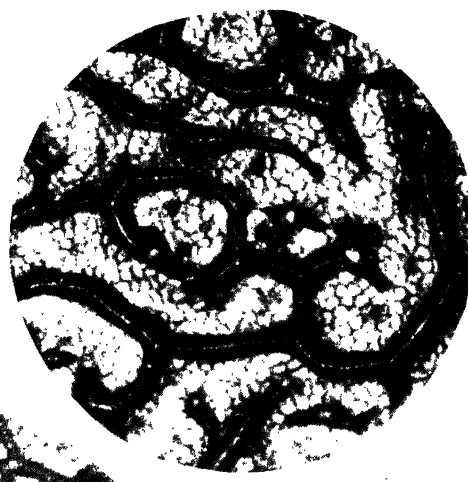
Phil. Trans. B, volume 254, plate 22



(Facing p. 436)



24a



24b



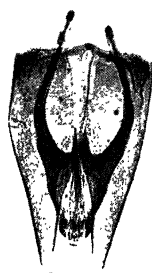
24c



25



26



27



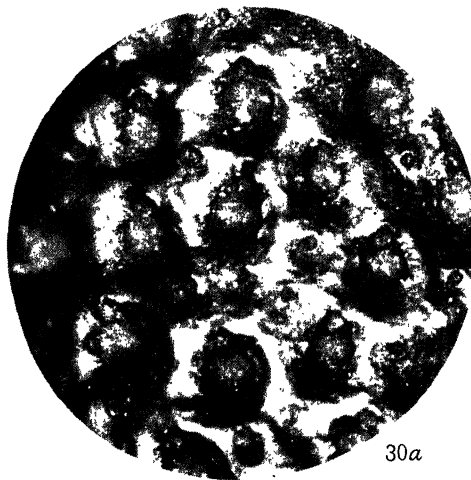
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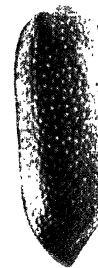
29a



29b



30a



30

pore at the rounded posterior angle of the pronotum. A note on the distribution of this interesting species has been given previously (Coope *et al.* 1961).

***Colymbetes dolabratus* Pk.** (figures 24*a, b, c*, plate 23)

The only species of *Colymbetes* in Europe with which *dolabratus* might be confused is *striatus*. *Dolabratus* is however much narrower and smaller than *striatus*. One of the most useful characters in the determination of fossil specimens is the sculpture of the central part of the prothorax. Though similar in general style the grooving is decidedly meandering in *dolabratus* but is streaked out in *striatus* (figures 24*a* to *c*, plate 23).

***Helophorus wandereri* D'Orch** (figure 27, plate 23)

This is probably an extinct species, though if it is alive anywhere today it might be expected in northern Russia or Siberia. I have searched in vain in collections from northern Scandinavia in the hope of finding the odd specimen doing duty for *H. nubilis* Fab. to which it is superficially similar. The species was described by D'Orchymont on the basis of two fossil elytra and the description has been amplified by us to include the head and thorax (Coope & Sands 1964). In this fauna the abundance of this species was extraordinary—see faunal list—and the figures probably under-represent considerably the actual numbers present since many uncountable fragments were noticed. As a fossil this species is widespread in deposits of the Weichselian glaciation, often in considerable numbers, and it has also been recorded from a deposit attributed to an early phase of the Saale glaciation (Osborne & Shotton 1968, p. 419). It has also been recovered from Late Glacial (Zone III) deposits in the English Midlands. It is strange therefore that a species so successful during the Last Glaciation, should in the short Post-Glacial period, have become completely extinct.*

DESCRIPTION OF PLATE 23

FIGURE 24*a*. Micro-ornament of pronotum of modern *Colymbetes striatus* L. ($\times 250$).

FIGURE 24*b*. Micro-ornament of pronotum of modern *Colymbetes dolabratus* Pk. ($\times 250$).

FIGURE 24*c*. Micro-ornament of pronotum of fossil *Colymbetes dolabratus* Pk. from Brandon ($\times 250$).

FIGURE 25. Aedeagus of *Bembidion hasti* Sahlb ($\times 50$).

FIGURE 26. Aedeagus of *Arpedium brachypterum* Grav. ($\times 50$).

FIGURE 27. Aedeagus of *Helophorus wandereri* D'Orch. ($\times 100$).

FIGURE 28. Aedeagus of *Simplocaria metallica* Sturm ($\times 50$).

FIGURE 29*a*. Head of *Boreaphilus nordenskiöldi* Makl. ($\times 20$).

FIGURE 29*b*. Thorax of *Boreaphilus nordenskiöldi* Makl. ($\times 20$).

FIGURE 30. Left elytron of *Opetiopalpus* sp. ($\times 20$).

FIGURE 30*a*. Micro-ornament of disk of elytron of *Opetiopalpus* sp. ($\times 250$).

* It is not extinct after all. Since the above was written Mr Angus has found that *H. wandereri* agrees precisely with *H. obscurellus* Popp. a species that is distributed today from N. Russia (Kanin) eastwards across Siberia to the Lena River.

***Helophorus aquaticus* (L.) and *fennicus* Pk.**

These two species are closely related and often difficult to distinguish as fossils. There are two main differences that are of value to the palaeontologist. First, the alternate interstices near the base of the elytra are raised in *fennicus* and often carry short hairs that remain attached even in badly smashed material. On the elytra of *aquaticus* these interstices are almost flat and do not carry hairs. The second difference lies in the ornament of the internal intervals of the pronotum and on the centre of the head mid-way between and slightly posterior to the eyes. In *fennicus* this area is covered by discrete mammilate tubercles that are usually clearly separate from one another. In *aquaticus* these tubercles are much closer together and flattened so that at times they coalesce to form an irregular, shiny, pitted surface.

In this fossil assemblage specimens typical of both species are present but the elytra are dominantly of *fennicus* type whilst most of the pronota are more like *aquaticus*. Two factors may be responsible for this discrepancy. First, very few elytra of *Helophorus* are preserved in recognizably large pieces and the somewhat stouter, corrugated elytra of *fennicus* are more easily preserved than the rather frailer *aquaticus* elytra. The second factor is that there is some variation in the spacing of the tubercles on the head and pronotum of both species. Thus, though most specimens fall easily into one category or the other, there are always a few intermediates which remain indeterminate. In most of these cases I have adopted the conservative attitude and grouped them with *aquaticus*. If *H. aequalis* Th. is a good species and not merely a variant of *aquaticus*, it is likely that it also is represented in this assemblage.

***Helophorus jacutus* Popp.**

This species represented by numerous fragments was identified by R. B. Angus of the Dept. of Zoology, Oxford. The species resembles a very large *H. nanus* but differs in the angulation of the sub-median grooves on the pronotum. Today its range is exclusively east Siberian (Irkutsk, Jakutsk and Usolie) but it has been found previously (though unrecognized) in Weichselian deposits at Fladbury (Coope 1962) and it has also occurred in the Brandon Channel fauna (Osborne & Shotton 1968).

***Arpedium brachypterum* (Grav.)**

This was by far the most abundant species in this fauna. Among the large number of pronota were some which had a more rounded outline than typical *brachypterum*. It has not been possible yet to relate these to any other species and so for the time being they are grouped with *brachypterum*.

***Boreaphilus nordenskioldi* Makl.**

This Siberian and north-eastern European species was very abundant in this fauna. It is now known from six other full glacial sites in England, in particular at Four Ashes near Wolverhampton where it is one of the commonest of the Staphylinidae. This species, though very common in full glacial deposits, appears to have become extinct in Britain prior to the Late Glacial phase unlike its relative *B. hennigianus* which survived in large numbers into Zone III times (figure 5). The species is discussed in Coope & Sands (1966).

***Tachinus* Sp A.** of Upton Warren

First described from Upton Warren (Coope *et al.* 1961, p. 396) this species has now been found in six other sites including a Late Glacial deposit (^{14}C dated about 12000 years B.P.) in the Isle of Man. This recent occurrence of this distinctive beetle tends to support the view that it is merely a form of *rufipes*, a view which has recently been reinforced by W. O. Steel (personal communication) who states that he has taken a living specimen of *rufipes* which has the same characteristic bifid apex to the median projection on the last tergite of the hind body in the female. It is perhaps significant that I have seen no fossil specimens of typical *rufipes* in deposits of the Last Glaciation and there is no evidence of any gradual change from forms with 'bifid' tergites to forms with the single spike of typical *rufipes*. If our fossils are indeed varieties of *rufipes* the possibility emerges that they represent the originally indigenous population of *rufipes* displaced by typical *rufipes* in post-glacial times. With this view in mind it is intriguing that Steel's specimen was taken in the north-west of Scotland on the island of Rhum.

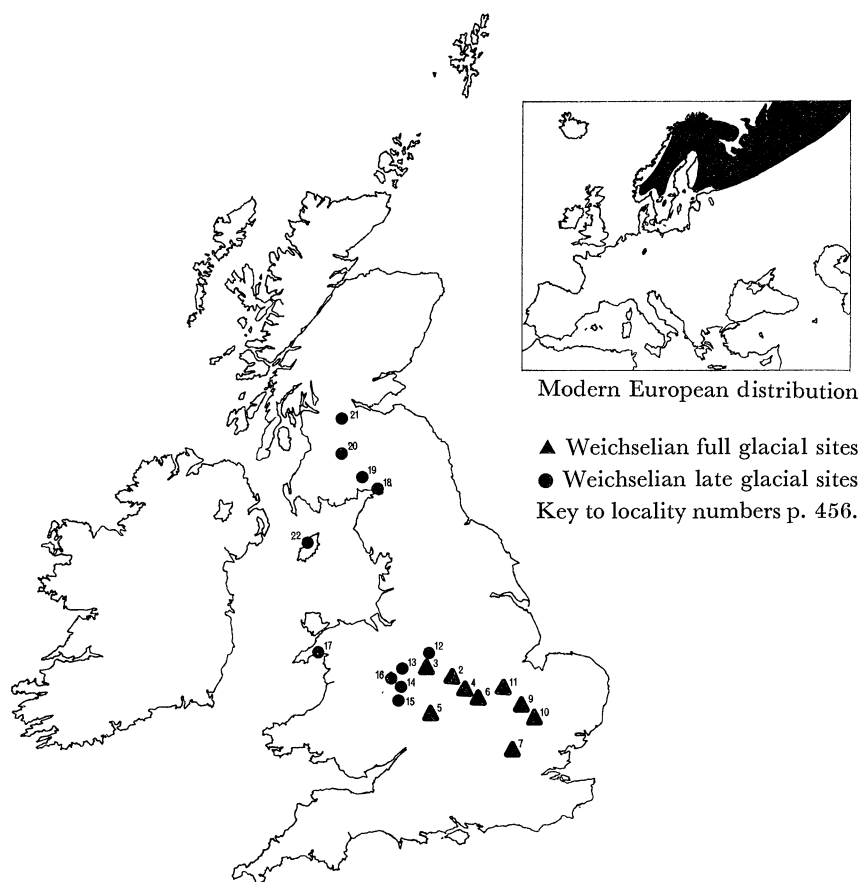


FIGURE 5. Fossil localities in Britain for *Boreaphilus henningianus* Sahlb.

***Opetiopalpus* sp.** (figures 30, 30a, plate 23)

At first sight the occurrence of this steppe genus seems unlikely in an association of so many tundra species. Today it is widely distributed in eastern Europe and in Asia but its life history is poorly known. Though these two elytra match this genus precisely in shape, colour and ornament they are slightly larger than *O. scutellaris* Panz., the only species

found in western Europe. I am reluctant therefore to identify them more exactly. Similar elytra have been recovered from deposits of full glacial age from Earith and Four Ashes which suggests that the species was widespread and not uncommon at this period.

***Simplocaria metallica* Sturm**

Though a rare species today *S. metallica* must have been a common species during the Last Glaciation. Not only is it abundant in this fauna but it has been found in five other full glacial sites in Britain and survived into the Late Glacial (Zone III) in the English midlands. The present-day distribution of this species is extremely disjunct and is clearly a meagre remnant of a once thriving population.

***Syncalypta cyclolepidia* Munst.**

The identification of this single head of this rare species has been confirmed by Lindroth. He writes as follows: 'This head is separated from that of *paleata* by the finer puncturation and the somewhat irregularly microsculptured interstices between the punctures; from that of *setigera* by the presence of only circular scales; from both by the series of extremely coarse punctures inside the anterior margin. Especially this last-named character convinces me that the fossil belongs to *cyclolepidia*.' The species is known from high latitudes in Scandinavia and in the mountains, and also from Irkutsk (Strand 1944, p. 427). In Britain it has recently been discovered as a fossil from full glacial deposits at Earith and Thrapston and from Late Glacial deposits of the Isle of Man and at Orleton, Shropshire (figure 6).

***Coccinella 11-punctata* L. and *Hippodamia 7-maculata* De G.**

Both these species are represented by dark varieties. In the case of *11-punctata* the discrete spots of the *forma typica* have coalesced into more or less transverse bands. In the case of *7-maculata* the spots are large and the pronotum almost completely black except for a thin testaceous margin. Coccinelids from the most northerly parts of their range frequently show this increase of the dark patches at the expense of the coloured areas, an adaptation, no doubt, to improve the absorption of radiation at their surface in districts where the amount of heat available is small. In our full glacial faunas the occurrence of these two species together with *Anisosticta strigata*, another dark species, probably is indicative of a thermal environment that was near to the acceptable limit for the species.

***Aphodius* Sp. A of Upton Warren**

The distinctive features of this species are that it is a medium-sized *Aphodius* (about the size of a large *A. fmetarius*) with a median tubercle on the head that is distinctly bifid. The pronotum has a groove running along the entire length of the anterior margin. The elytra are red. This distinctive species was first discovered in the full glacial deposits at Upton Warren and a request for information about any similar living species has so far gone unsatisfied. It has now been found in six other full glacial localities but so far it has not occurred in Late Glacial deposits. It seems likely that this species is either completely extinct or may await discovery in some part of northern Siberia; but, being absent

apparently from Late Glacial deposits it may be a zone fossil of the Upton Warren Interstadial and earlier.

Chrysolina septentrionalis group

The recognition of this most interesting species I owe to Professor Carl Lindroth. I sent him a long series of fossil pronota of *Chrysolina* from Brandon because they did not match any European species known to me. *C. septentrionalis* Men. belongs to a Siberian–Alaskan group that is in part difficult to separate and not finally revised. I have compared the fossils only with *septentrionalis* from Novaya Zemlya and Vaigach Island and though several of them agree perfectly there appears to be a tendency in some of the fossils to be more finely punctured along the sides of the pronotum. This difference can hardly be due to preservational factors since these usually result in a deepening of the punctures. However, the difference is not constant and even the modern series varies in this respect. Until this group has been more fully studied it is perhaps wisest to leave the more exact identification of these fossils to a subsequent date.

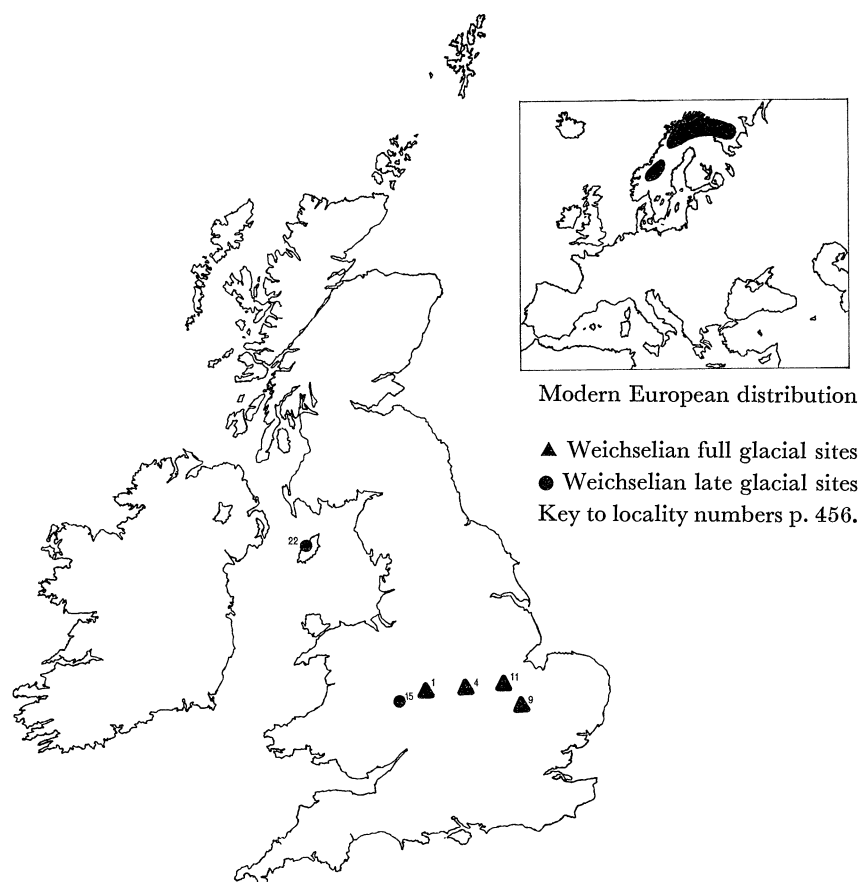


FIGURE 6. Fossil localities in Britain for *Syncalypta cyclolepidia* Munst.

Phytonomus obovatus Csiki

The numerous heads, thoraces and elytra of *Phytonomus* were difficult to determine. Clearly there were at least two species represented but only in those cases where the scales were still preserved could satisfactory identifications be made. The larger species was without doubt *diversipunctatus* Sch. (*elongatus* Pk.) and was represented by many fragments

with the scales intact. The smaller species had the scales more rarely preserved and at first sight came closest to *pedestris* Pk. The scales when highly magnified were, however, constantly different, in particular those near the scutellum. In this respect the fossils were an exact match with *obovatus*, a northern Scandinavian and Siberian species. Though only three elytra had enough scales for specific determination, I have grouped all the denuded elytra of similar size and ornament with this species.

Calacanthia tribomi J. Sahlb.

This is the first fossil record of this distinctive saldid. It has a circumpolar distribution in high latitudes. The species was probably considerably more common than appears in the faunal list as many uncountable fragments were noticed during sorting.

ECOLOGICAL IMPLICATIONS OF THE FAUNA

Species of Coleoptera are often very precisely adapted to narrowly defined ecological situations. Taken as a whole, however, the beetles occupy a wide spectrum of environments. In the account that follows, the present-day occurrences of the species found as fossils at Brandon will be discussed in an effort to build up a picture of the local environment at the time when the deposits were being laid down. I have endeavoured to keep apart the climatic implications of the fauna which are dealt with under a separate heading.

TABLE 1. SPECIES OF CARABIDAE FOUND AS FOSSILS AT BRANDON, GROUPED ACCORDING TO THEIR DEMAND FOR SOIL MOISTURE

Hygrophilous species

<i>Pelophila borealis</i>	<i>B. difficile</i>
<i>Diachila arctica</i>	<i>B. hasti</i>
<i>Nebria gyllenhali</i>	<i>B. hyperboreaorum</i>
<i>Elaphrus lapponicus</i>	<i>B. lunatum</i>
<i>E. riparius</i>	<i>B. obliquum</i>
<i>E. cupreus</i>	<i>B. schüpelli</i>
<i>Loricera pilicornis</i>	<i>B. virens</i>
<i>Dyschirius septentrionum</i>	<i>Patrobus septentrionis</i>
<i>D. globosus</i>	<i>Feronia (Cryobius) blandulus</i>
<i>Bembidion aeneum</i>	<i>Agonum sahlbergi</i>
<i>B. bipunctatum</i>	<i>A. ericeti</i>
<i>Bembidion femoratum</i>	<i>A. consimile</i>
<i>B. fellmani</i>	

Mesophilous species

<i>Carabus violaceus</i>	<i>Feronia adstricta</i>
<i>Diachila polita</i>	<i>F. kokeili</i>
<i>Notiophilus aquaticus</i>	<i>Amara alpina</i>
<i>Clivina fossor</i>	<i>A. torrida</i>
<i>Bembidion quadrimaculatum</i>	<i>Calathus melanocephalus</i>

Xerophilous species

<i>Carabus arvensis</i>	<i>Amara quenseli</i>
<i>Bembidion dauricum</i>	

Carabidae

The Carabidae are ground beetles that, to a large extent, indicate the condition of the soil and the degree of vegetation cover. They are general scavengers eating both plant and animal matter and are rarely dependent on any particular source of food.

Most of the species (66%) in this fauna are hygrophilous and only three are xerophilous. The remainder (26%) are more or less indifferent to the moisture content of the soil.

Several of the hygrophilous species are characteristic of gravelly margins to running water where they live on dead insects washed up among the stones. In this group *Bembidion fellmani*, *B. hasti* and *B. virens* were the most abundant whilst *B. hyperboreaorum* was less common. All of them live on completely sterile habitats. *B. difficile* is ecologically similar to *fellmani* but with a greater liking for light vegetation often shaded by *Salix* bushes. It was much less common than *fellmani* in this assemblage. *Nebria gyllenhali* is also associated with stony margins of running water but it is not exclusively confined to such habitats and in Iceland is quite eurytopic. Many of the other hygrophilous species are found in boggy places with more or less rich vegetation of *Carex*, *Scirpus*, etc., usually with an organic soil. (*Pelophila borealis*, *Elaphrus cupreus*, *Loricera pilicornis*, *Bembidion aeneum*, *B. obliquum*, *B. schüppelli*, *B. lunatum* and *Agonum consimile*). *Elaphrus lapponicus* appears to require a rather particular habitat, namely, wet moss carpets round springs and cold trickles of water. It is one of the few carabid species that is stenoionous with a preference for water with pH between 6.8 and 7.2. As far as it is known the habitat of *Diachila arctica* is similar to that of *Elaphrus lapponicus* and both are most often found as imagos in the springtime. *Agonum ericeti* is, on the other hand, a species of wet heathland often in moss (*Sphagnum*) where the water is decidedly acid (pH 4.6). Among the other hygrophilous species *Elaphrus riparius*, *Bembidion quadrimaculatum* and *B. bipunctatum* require open stretches of sand or clay in the vicinity of water but with a very little vegetation. These conditions are also suitable for the largely fossorial species *Clivina fossor*, *Dyschirius septentrionum* and *D. globosus*. The last-named species is rather eurytopic and capable of tolerating a coarser substrate than other species of the genus.

Open grassy habitats, not necessarily wet, are required by *Feronia adstricta*, *Amara torrida* and *Calathus melanocephalus*.

The xerophilous species are only represented in this fauna in large numbers by *Amara quenseli* which lives on dry sand on open unshaded areas with little or no vegetation cover. *Bembidion dauricum* is one of the few xerophilous species of this genus and lives on fine sand or on peaty soils with little vegetation. *Carabus arvensis* lives on dry, open sand and gravel, often on rather acid *Calluna* heaths.

A number of species in this fauna are pronounced heliophiles, running about in the bright sunlight. (*Carabus arvensis*, *Diachila polita*, *Elaphrus riparius*, *Bembidion bipunctatum* and *Agonum ericeti*.) Only one species (*C. violaceus*) is usually associated with woodland and therefore shaded habitats, though it is not confined to such places today. It is possible that this species found adequate shade under dwarf willow bushes.

One of the curious features of this and several other full glacial sites is the abundance of the halophilous species *Bembidion aeneum*. It is probable also that *Agonum sahlbergi* is a halophile, though not much is known of its ecology.

Gyrinidae

The almost complete absence of *Gyrinus* from this fauna might indicate the lack of open water. There are, however, few gyrids recorded from any full glacial site. This is not a

matter of preservation as I have seen well preserved fossils from many Late Glacial localities and from Pilgrimstad in Sweden.

Dytiscidae

The relatively small number of species of this family, few also in number of individuals, were all from the horizon of small sticks from which the large bulk samples were taken. They were probably brought together in the flood refuse. All the species are characteristic of small bodies of standing water. *Colymbetes dolabratus* is the only species now absent from the British Isles. It is a circumpolar species known from N. Fennoscandia, N. Russia, Siberia, N. America, Greenland and Iceland. *Agabus congener* and *A. arcticus* are both species of high altitude pools except for the north of Scotland where they are found lower down. There can be no doubt therefore that this assemblage indicates cold water ponds.

Hydrophilidae

One of the outstanding features of this fauna is the extraordinary abundance of *Helophorus*, a genus which is an excellent flier and can rapidly colonize even very small and temporary pools usually with abundant rotting vegetation and to which it swarms often in enormous numbers. Taken in conjunction with the paucity of dytiscid water beetles they suggest that the local puddles were temporary.

Silphidae

Thanatophilus dispar is common in almost all full glacial fossil assemblages but it is rather rare in Britain today. Though often found on the coast it is by no means exclusively maritime being found under dead fish on the margins of lakes and rivers. *Aclypea opaca* is a frequent, though less numerous companion, of *T. dispar* in full glacial deposits. It is also a carcass beetle.

Staphylinidae

One of the most outstanding features of this fauna is the large number of omaliines. Most of these form a characteristic assemblage of species found under moss and leaf debris in damp places beneath *Salix* bushes in the Alpine or sub-Alpine regions (*Arpedium brachypterum*, *Olophrum fuscum*, *O. boreale* and *Boreaphilus*). It is significant that these species made up the bulk of the faunas from all samples of silt and they suggest a monotonous expanse of *Salix* scrub over much of the area. Both *Geodromicus nigrita* and *Bledius* spp. are typical of sandy banks and they were found only in the bulk samples taken from the horizon rich in small sticks and which may represent flood debris washed together.

Elateridae

Hypnoidus rivularis, the only species of this family in this fauna, is found under stones and plant debris in sandy or grassy places.

Heteroceridae

Species of this family burrow in more or less clean damp sand and are ecologically related to *Dyschirius* spp. and *Bledius* spp. Three species are represented in this fauna, of which only *H. intermedius* can be recognized with certainty.

Byrrhidae

Species of *Simplocaria* were common in all the samples investigated. Sometimes *S. metallica* outnumbered *S. semistriata* and at other times vice versa. This variation in the relative abundance of the two species may be due to their slightly different requirements since, though both live on short moss carpets in sandy places, *semistriata* prefers drier moss at least as an imago, whilst *metallica* prefers damper conditions close to water. *Syncalypta cyclolepidea*, *Cytillus sericeus* and species of *Byrrhus* also live on moss, often in sandy places.

Coccinellidae

Elytral fragments were not at all uncommon in this fauna but were only rarely big enough to permit specific identification. The family is probably therefore rather under-represented in the faunal list. *Hippodamia septemmaculata* and *Anisosticta strigata* are most usually associated with rather grassy marshes and *Coccinella 11-punctata* with more sandy habitats. Both larvae and adults of these species prey upon aphids.

Anobiidae

The single species representing this family, *Caenocara bovista* is found in large fungi, in particular *Lycoperdina bovista* and *Bovista plumbea*.

Anthicidae

Anthicus ater is found in damp places often in *Sphagnum*.

Scarabaeidae

Remains of *Aphodius* were very abundant in most sites but could only rarely be specifically identified. The genus is characteristically found in the dung of large herbivorous mammals and it seems strange that no bones were recovered from the gravel workings. There does not appear to be any physical reason why they should be absent as they are known from other excavations in this terrace. *Aegialia sabuleti* is not a dung feeder but is found under stones in damp sandy places.

Chrysomelidae

This family is made up exclusively of plant feeders many of which are restricted to certain hosts. They thus provide independent evidence of the flora of the times. The table that follows lists the host plants upon which the beetles in this fauna are found living today.

<i>Plateumaris sericea</i>	Many aquatic plants, especially <i>Carex</i>
<i>Chrysolina marginata</i>	Polyphagous (found especially in sandy places)
<i>C. septentrionalis</i>	Unknown
<i>C. collaris</i>	<i>Salix</i>
<i>Gastrophysa viridula</i>	<i>Rumex</i>
<i>Phaedon cochliariae</i>	Umbelliferae
<i>Phyllodecta vitellinae/polaris</i>	<i>Salix</i>
<i>Phyllotreta atra</i>	Cruciferae
<i>P. flexuosa</i>	Cruciferae
<i>Galeruca tanacetii</i>	Many listed plants including <i>Achillea millefolium</i> , <i>Cerastium arvense</i> , <i>Cardamine pratensis</i> , <i>Chrysanthemum vulgare</i> and <i>Tanacetum vulgare</i>

Curculionidae

This family comprises the weevils, exclusive plant feeders that are often confined to particular hosts. In conjunction with the Chrysomelidae listed above, they also provide independent evidence of the composition of the local flora. Tabulated below are the host plants upon which the weevils in this fauna may be found living today.

<i>Otiorrhynchus arcticus</i>	Polyphagous (on rather dry grassland with very light vegetation)
<i>O. nodosus</i>	Polyphagous (on rather richer vegetation than <i>O. arcticus</i>)
<i>O. rugifrons</i>	Amongst other species <i>Thymus serpyllum</i> appears to be the most important food plant. The larvae also mine the leaves of <i>Saxifraga</i> sp.
<i>Sitona lepidus</i>	Larvae attack roots of <i>Lotus uliginosus</i> and <i>Trifolium pratense</i>
<i>Notaris aethiops</i>	Chiefly <i>Sparganium ramosum</i> but also <i>Carex</i>
<i>N. bimaculatus</i>	The larvae feed on <i>Typha latifolia</i> . The adults are also known on the grass <i>Phalaris arundinacea</i>
<i>Grypus equiseti</i>	<i>Equisetum</i> spp.
<i>Phytonomus diversipunctatus</i>	<i>Stellaria crassifolia</i> and <i>uliginosa</i> , <i>Cerastium</i> and <i>Plantago</i>
<i>Phytonomus obovatus</i>	Often under <i>Astragalus alpinus</i>
<i>Ceuthorrhynchus litura</i>	On <i>Carduus arvensis</i> (also <i>C. crispus</i> and <i>Cirsium arvense</i>)
<i>Litodactylus leucogaster</i>	<i>Myriophyllum</i> and <i>Potamogeton</i>
<i>Eubrychius velatus</i>	<i>Myriophyllum</i>
<i>Phytobius canaliculatus</i>	<i>Potamogeton natans</i> and <i>Polygonum hydropiper</i>
<i>P. quadrituberculatus</i>	<i>Glaux maritima</i> , <i>Polygonum lapathifolium</i> and <i>persicaria</i>
<i>Rhynchaenus foliorum</i>	<i>Salix</i>

Synopsis of ecology

The sedimentary structure of the organic layers leaves little doubt that they were water lain and the laminations, crudely sorted into coarse and fine fractions strongly suggest that the deposit represents the accumulation resulting from successive floods. This interpretation is further strengthened by the fact that the bulk of the plant debris was broken twigs and leaves of terrestrial species, chiefly of *Salix*. Likewise, much of the insect fauna was essentially riparian rather than strictly aquatic. The fauna, taken as a whole, represents the inhabitants of a wide spectrum of environments swept together into their present position, rather than a fauna of a local pond or stream.

Two rather distinct aquatic environments are indicated by this fauna. First, there was much marshy ground with abundant shallow, eutrophic pools of more or less temporary nature testified by the extraordinary abundance of species of *Helophorus*. Some of these pools must, however, have been permanent enough to support such aquatic plants as *Myriophyllum* and *Potamogeton*, the host plant for several of the weevils, but these are not abundant, suggesting that such pools were rare. The general scarcity of Dytiscidae also suggests that there was little open water available and this may also account for the almost total lack of Gyrinidae. Round the margins of the pools the soil was, at least in part,

very organic and thickly covered with a rich vegetation of *Carex* and grasses and probably *Sparganium ramosum* and *Typha latifolia*. This habitat is strongly indicated by a suite of carabid ground beetles and also by the abundance of the weevil *Notaris aethiops*. Some of this marshy ground undoubtedly supported *Equisetum* upon which *Grypus* feeds exclusively. Not all the wet ground was clothed in rich vegetation however. Several of the Carabidae demand sparse vegetation with much open sand or clay (*Elaphrus riparius*, *Bembidion quadrimaculatum* and *B. bipunctatum*) and this habitat is also required by such fossorial species as the carabids *Clivina fossor*, *Dyschirius septentrionum* and *D. globosus* and also by the staphylinid *Bledius* and by *Heterocerus*. From the abundance of several of these species these rather open sand or mud banks must have been rather extensive.

The second aquatic habitat, suggested by some of the Carabidae, is running water with gravelly margins. The large numbers of individuals of *Bembidion fellmani* and *B. hasti* show that this habitat was locally important. It is also likely that *Elaphrus lapponicus* also fits in here, since it is characteristic of mossy areas round springs or cold trickles of neutral water.

There is some suggestion from the beetle fauna that the environment was somewhat saline. Today many species in this assemblage are restricted to coastal areas. In most cases, however, this restriction is due to the limitation of open sandy habitats to such places and not to a demand for a saline habitat. Nonetheless, two species in this fauna, *Bembidion aeneum* and *Ochthebius viridis*, appear to be obligate halophiles, though the amount of salt available need only have been extraordinarily small.

Much of the poorly drained ground must have been covered with dwarf willow scrub since in every sample investigated from all sites in this pit, there was an extraordinary abundance of the small staphylinid beetles that live in the leaf litter under *Salix* bushes and the exclusive willow-feeding weevil *Rhynchaenus foliorum* was equally ubiquitous. The suggestion that the *Salix* bushes were of the dwarf variety comes from the fact that *R. foliorum* is a minute weevil and there is a complete lack in this fauna of any of the larger weevils that drill willow sticks or live under bark. The abundance of byrrhid beetles, particularly species of *Simplocaria*, in all the samples investigated is indicative of a well developed moss carpet over much of the area. The only evidence from the beetles of *Sphagnum* or *Hypnum* is provided by *Agonum ericeti*.

Away from the water the better drained sandy ground supported a poor, rather acid, heathland indicated by *Carabus arvensis*. The vegetation was probably very sparse however as many species are pronounced heliophiles. This very barren environment is the typical habitat of *Amara alpina* which was one of the most abundant carabid beetles in this fauna. This is also the most usual habitat for the weevil *Otiorrhynchus arcticus*.

This austere picture of the ancient environment of Brandon receives added support from one important piece of negative evidence. Although the fauna was extensively sampled, there were no species found to indicate the presence of any trees; no evidence from the insect fauna even of *Betula* which might have been expected and nothing to suggest that the *Salix* present was anything other than very small bushes. This open bare landscape with the only abundant vegetation confined to poorly drained hollows, must have closely resembled the tundras of northern Europe today.

CLIMATIC IMPLICATIONS OF THE FAUNA

One of the most outstanding features of this fauna is the relatively large number of species that are no longer to be found living in Britain. Out of just over 150 species recognized, 38, two Hemiptera and the rest Coleoptera, belong to this group. They represent species which have for the most part, restricted ranges today in the far north of Europe and at high altitudes further south.

SPECIES NOT NOW FOUND LIVING IN BRITAIN

Hemiptera

Chiloxanthus stellatus
Calacanthia tribomi

Coleoptera

Diachila arctica
D. polita
Dyschirius septentrionum
Bembidion dauricum
B. difficile
B. fellmani
B. hasti
B. hyperboreaorum
Amara torrida
Feronia blandulus
F. kokeili
Agonum consimile
Deronectes alpinus
Colymbetes dolabratus
Hydroporus arcticus
Helophorus fennicus
Helophorus jacutus

Coleoptera (*cont.*)

H. wandereri
Hydrobius arcticus
Pycnoglypta lurida
Acidota quadrata
Olophrum boreale
Boreaphilus henningianus
B. nordenskiöldi
Bledius litoralis
Tachinus fimetarius
Opetiopalpus sp.
Hypnoidus rivularis
Heterocerus intermedius
Simplocaria metallica
Syncalypta cyclolepidia
Hippodamia septemmaculata
Anisosticta strigata
Anthicus ater
Chrysolina septentrionalis group
Chrysomela collaris
Phytonomus obovatus

To this assemblage of 'Non-British' species may be added the very considerable list of species which, though still living here, are only to be found today in the northern mountains but which fossil evidence shows once had a much more general distribution in these islands.

TABLE OF SPECIES RESTRICTED, IN BRITAIN, TO THE NORTH

<i>Pelophila borealis</i>	<i>A. congener</i>
<i>Nebria gyllenhali</i>	<i>Arpedium brachypterum</i>
<i>Elaphrus lapponicus</i>	<i>Eudectus whitei</i>
<i>Bembidion virens</i>	<i>Bryoporus rugipennis</i>
<i>Patrobus septentrionis</i>	<i>Aphodius lapponum</i>
<i>Amara alpina</i>	<i>Chrysolina marginata</i>
<i>A. quenseli</i>	<i>Otiorrhynchus arcticus</i>
<i>Feronia adstricta</i>	<i>Notaris aethiops</i>
<i>Agonum sahlbergi</i>	<i>Phytonomus diversipunctatus</i>
<i>Agabus arcticus</i>	

The factors which limit the range of beetle species are often complex (Coope 1967). Nevertheless, it is inescapable that one of the most important of these is climate and in particular the thermal environment. There can be little doubt therefore that the Brandon fauna indicates a very cold climatic regime similar to that of the tundras of northern Europe.

Any precise comparison, however, between the glacial climate of Warwickshire and the climate of Arctic Europe today is made almost impossible by the great disparity in latitude between the two areas and the consequent difference in day length. It is possible to avoid this problem of latitude by tabulating the occurrences today of the modern representatives of our fossil species, at different altitudes in mountainous areas where a range of thermal environments is available. The vertical distribution of a species will then reflect its thermal preference. The actual altitude at which a species finds optimum thermal conditions will, of course, increase equatorially so that the occurrences of species must be related to the floral zones which provide a constant index of the thermal environment regardless of latitude.

Unfortunately the zonal distributions of species of Coleoptera are adequately known for only one family, namely, the Carabidae, whose distribution in the floral zones of the Scandinavian mountains has been tabulated by Lindroth (1949, pp. 440–448). It is extremely fortunate therefore that this family is well represented in fossil assemblages and also that they are ground beetles living for the most part on the soil surface and thus in a habitat that reflects the macroclimate. This is a decided advantage over certain other families of beetle which may live in habitats buffered against fluctuations in the macroclimate; say in heaps of decaying vegetable refuse where the temperature and humidity bear little relationship to the macroclimate. The Carabidae have another advantage over many other families of Coleoptera since they are general scavengers and little restricted to any particular source of food. More fastidious species may be limited in their range by the availability of an acceptable food supply.

Figure 7 shows the Carabidae from this fauna in the order of their abundance and against each species its known range in the floral zones of the Scandinavian mountains is shown. The numbers of individuals for each species represents the minimum number that must have been present in the fauna and is taken as the maximum number of any particular skeletal element. The occurrences in the zones are scored according to the system described previously (Coope & Sands 1966) namely 2 for a regular occurrence and 1 for rare or accidental records.

At first sight this table suggests that the Brandon Carabidae, taken as a whole, would be best at home near the top of the conifer zone. However, many species, often numerically well represented in the fauna, do not normally extend as low as this (*Amara alpina*, *Feronia blandulus*, *F. kokeili*, *Diachila polita*, *Bembidion fellmani*, *B. dauricum*, *B. hasti*, *B. hyperboreaorum* and *Agonum consimile*). There is also a corresponding absence in this fauna of the large number of carabid species that would be expected if the fauna was really representative of a climate similar to that at the top of the conifer zone. I have argued elsewhere, however, that it is the relatively thermophilous species that are most sensitive to adverse thermal conditions (Coope *et al.* 1961; Coope 1967) and thus the best temperature indicators. It is important therefore to examine more closely the ranges of the five species that do not live today above the timber limit of the Scandinavian mountains.

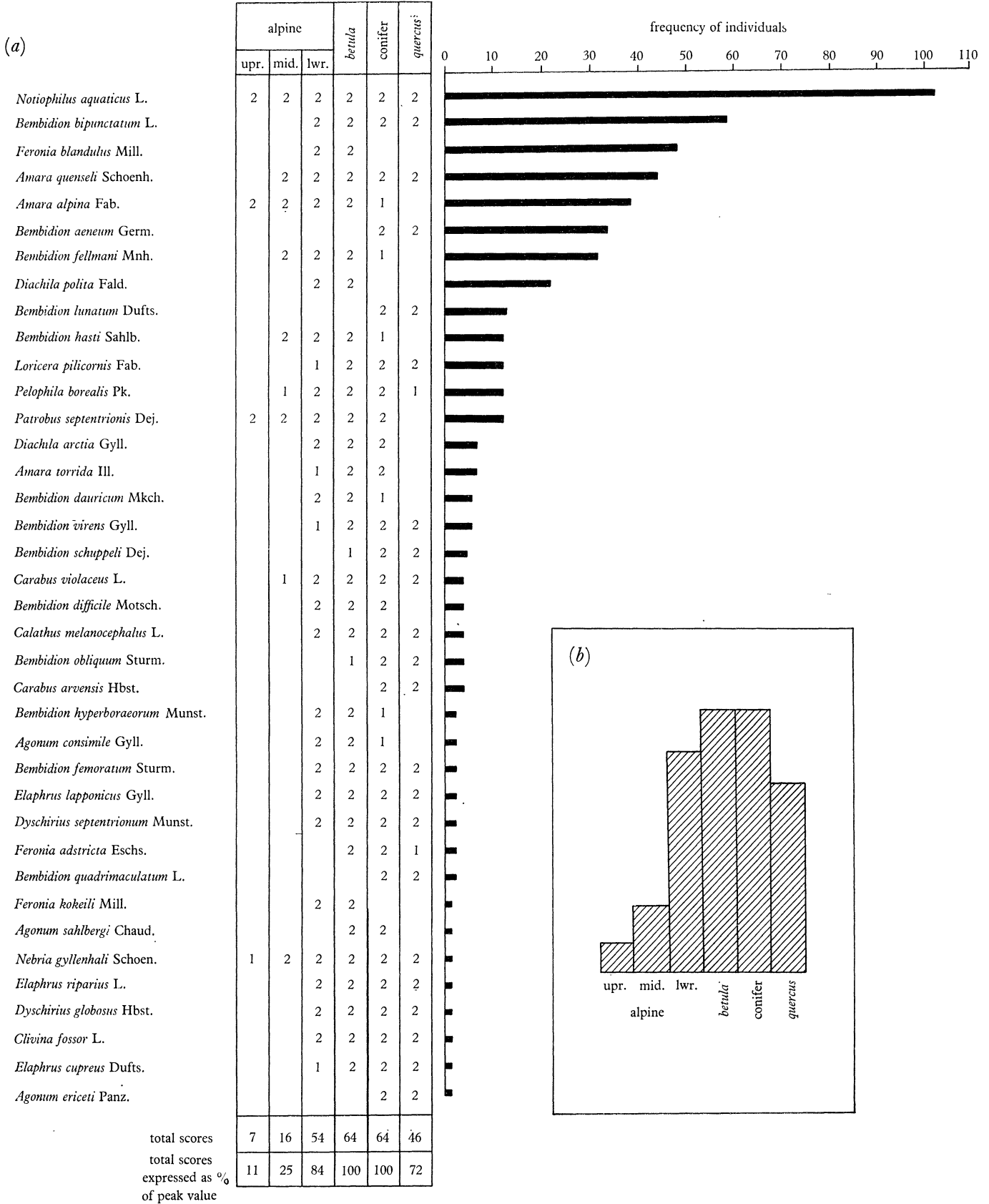


FIGURE 7. (a) Modern distribution of fossil Carabidae from Brandon, Warwickshire, in the Floral zones of the Scandinavian mountains (data from Lindroth, 1949). The scores in each column are 2 for a regular occurrence and 1 for an accidental occurrence. (b) Graphic representation of the scores for the Brandon fauna expressed as percentage of their peak value.

Carabus arvensis is known in Europe from as far north as the Pechora River of northern Russia and also from the north Siberian tundra (Lindroth 1945, p. 341).

Bembidion aeneum occurs north of the Arctic circle only in western Norway, no further north than the Lofoten Islands. It also occurs in north Finland. It is, however, a frequent member of the glacial fauna of Britain. Its absence from high altitudes in Scandinavia may be due, at least in part, to its halophilous nature.

Bembidion lunatum is known from the Kolwa River on the tundras of North Eastern Russia.

Bembidion quadrimaculatum is known as far north in Scandinavia as latitude 69° and also from the Pechora region of northern Russia. The fossil specimens from Brandon are smaller and darker than any specimens that I have seen from northern Scandinavia perhaps suggesting that they lived in an even more severe climate.

Agonum ericeti is known from as far north as latitude 69° in Scandinavia and from Mezen north of Archangel. It is known also from several other full glacial sites in Britain.

There can be little doubt therefore that none of these species can be considered as reliable thermophiles in spite of their apparent reluctance to range above the tree line in Scandinavia. The carabid fauna from Brandon is clearly most similar to the fauna living today in the *Betula* or Lower Alpine Zones.

If the Brandon zonal diagram is compared with the similar diagram from the Tame Valley fauna (Coope & Sands 1966, p. 408) several significant differences may be noted. The Tame Valley fauna resembled most closely the fauna at the boundary between the conifer zone and the *Betula* zone. The Brandon assemblage is largely made up of the same species but includes also several species unrecorded from the Tame Valley, such as the two low temperature stenotherms *Amara alpina* and *Feronia blandulus* (*F. kokeili* is represented in the Tame Valley fauna by a single pronotum not recognized at the time of publication). The Tame Valley fauna on the other hand contains several more southern species such as *Bembidion gilvipes*, *Trechus rivularis*, *Feronia coerulea*, *Amara tibialis* and *Cymindis macularis* which though widespread in Scandinavia are largely confined to the southern regions. If, however, the faunas are compared quantitatively then another outstanding difference becomes at once apparent. Such decided Arctic stenotherms as *Diachila polita* and *Bembidion fellmani* are relatively numerous in the Brandon fauna but represented by single fragments in the Tame Valley assemblage. Diagrammatically (figure 8) this difference can be illustrated by comparing the relative numbers of individuals in each fauna of two pairs of species in which the species in each pair are closely related but have somewhat different thermal requirements. In the first of these species pairs, *Diachila polita* is the extreme low temperature stenotherm living today almost exclusively on the tundra, whilst its relative *D. arctica* can live in the upper parts of the conifer zone. Whereas in the Tame Valley fauna *D. arctica* was quite common and *D. polita* was very rare, in the Brandon fauna the representation is reversed. In the second species pair *Amara alpina* is the low temperature stenotherm, one of the most widespread and characteristic beetles of the high alpine zones and the tundra, whilst its close relative *A. torrida* is most usually found in open areas at the top of the conifer zone. Their relative abundance in the two sites is similar to that of the first species pair except that *A. alpina* was completely absent from the Tame Valley fauna.

There can be little doubt then that the Brandon assemblage of Carabidae indicates a climate that was considerably more rigorous than that of the Tame Valley. It is difficult to find an optimum zonal position for this fauna especially as one of the commonest species, *Feronia blandulus*, does not occur in Scandinavia today and as *Diachila polita*, also so well represented here, only qualifies by virtue of a few occurrences on the extreme east of the Kola Peninsula. Perhaps in view of the presence of the few species that do not range high in the Scandinavian mountains the best course is to equate our fauna with that at the boundary between the *Betula* zone and the Lower alpine zone. It must be borne in mind, however, that this is almost certainly a conservative estimate.

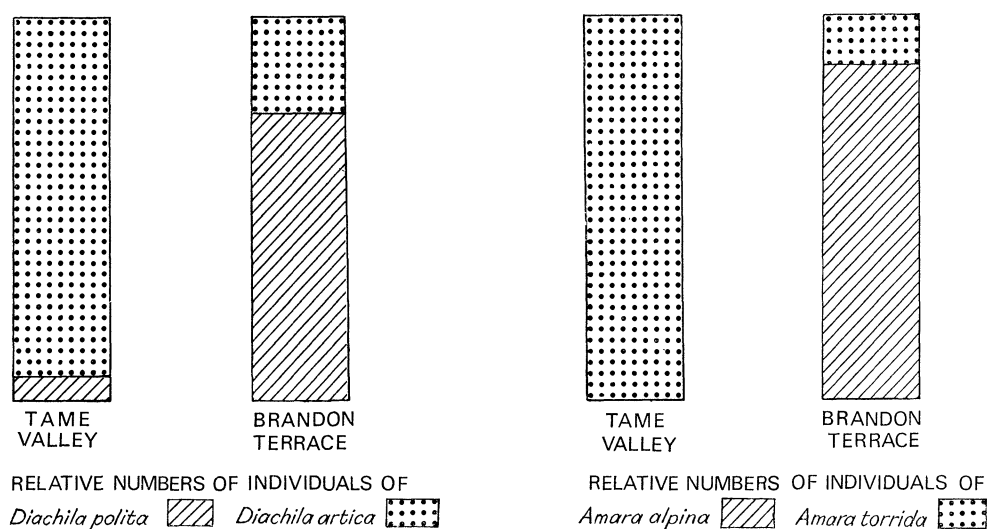


FIGURE 8. Comparison of relative abundance of two pairs of species of carabid beetle showing the higher proportion of the more extreme arctic stenotherm of each pair in the Brandon fauna.

The thermal environment of the Lower Alpine zones of the Scandinavian mountains may be summarized as follows (data largely from Lundquist 1953). The hottest month of the year is July with an average temperature of 10 °C (in Warwickshire the average July temperature is about 17 °C). There was thus a depression of 7 °C in the July average temperature at the time when the fossil fauna lived at Brandon, compared with the present day. The 'vegetative period', defined as the period during which the daily minimum temperature rises above 0 °C is about 90 days and starts in the second half of May.

It is not possible to make direct inferences about the winter temperatures from fossil insect assemblages because at these latitudes insects hibernate and are thus to a large extent immune from the rigours of winter. Many species, however, find relatively warm damp winters intolerable, either because they find it difficult to hibernate successfully or because the hibernating animal is attacked by fungi or predators. In the Brandon fauna there are a number of species with well marked continental distributions today. *Helophorus jacutus* is confined to east Siberia and the ranges of *Feronia blandulus*, *F. kokeili*, *Diachila polita*, *Chrysolina septentrionalis* and *Boreaphilus nordenskiöldi** barely reach westwards as far as eastern Europe. Many others are found over much of Scandinavia but avoid the west coast of Norway with its decidedly oceanic climate. Though the actual factors limiting

* Also *Helophorus obscurellus*, see page 437.

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the distribution of these species is unknown, it seems likely that they find something unacceptable in the oceanic climate. The few exclusively western species in this fauna, *Otiorrhynchus arcticus* and *O. nodosus* are special cases because their photophobic nature limits their distribution in the arctic to areas with adequate cloud cover to permit them to complete their life cycle. Further south they avoid high insolation by being nocturnal. At the latitude of Brandon this solution was clearly possible.

If a moderate degree of continentality of climate is permitted for the Brandon fauna a seasonal fluctuation in the average monthly temperatures of about 30 °C might be expected. Such a range of temperatures is to be found today in the region of Leningrad or Archangel where, incidentally, almost all of the species found fossil at Brandon can be found living today. If this range of average monthly temperatures is then related to the 10 °C average July temperature inferred from the zonal distribution of the Carabidae, some idea of the annual variation in thermal environment may be obtained.

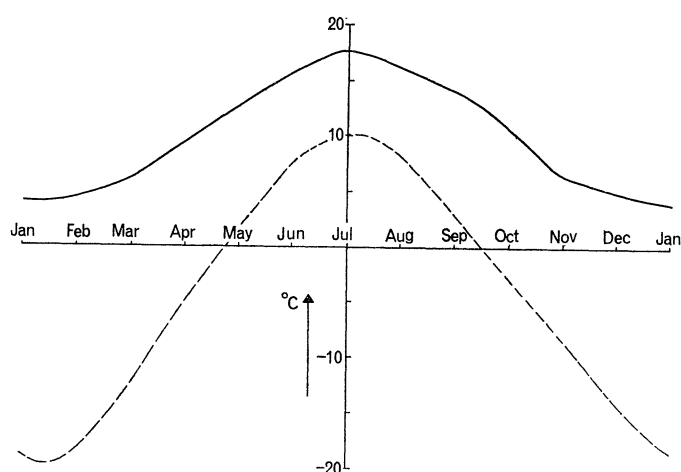


FIGURE 9. The present-day monthly average temperatures of the Brandon area of Warwickshire (—) compared with those estimated for the ancient climate (----) as indicated by the fossil insect fauna.

This picture of the thermal environment at Brandon receives added support from the present structure of the organic beds and their enclosing gravels. The organic bed was often tilted at a high angle and in places involuted, strongly suggestive of frost heaving. The extensive development of frost wedges at various levels in the gravels also implies a fierce Arctic-like environment with average annual temperatures at least as low as -5 °C (Péwé; personal communication).

COMPARISON OF THE BRANDON FAUNA WITH OTHER FOSSIL INSECT FAUNAS

At the present moment there are nine other insect faunas from deposits which, I believe, date from the same general period as the Brandon fauna. Descriptions of three have already been published—Upton Warren (Coope *et al.* 1961); Fladbury (Coope 1962) and the Tame Valley (Coope & Sands 1966). These three sites have stratigraphical relations and ^{14}C dates which leave no doubt that they are of approximately the same age as the Brandon fauna. A fourth site at Four Ashes near Wolverhampton has provided several ^{14}C dates of the same general age from organic silts that are yielding

enormous numbers of fossil insects. The six other sites, though not yet investigated completely, have very similar insect faunas—Great Billing, Northamptonshire; St Albans, Hertfordshire; Oxbow open cast site near Leeds, Yorkshire; Earith, Huntingdonshire; Thrapston, Northamptonshire and the classic site at Barnwell Station, Cambridge.

Without entering into a detailed comparison of the faunas from all these sites some general conclusions are appropriate here. All the faunas indicate a remarkably similar local environment, namely a barren treeless landscape with lush vegetation confined to poorly drained hollows or the margins of water courses. Among these faunas the Upton Warren assemblage is outstanding because of the presence of a relatively high proportion of temperate species and the comparative rarity of the low temperature stenotherms that are so characteristic of the faunas from all the other sites. Nonetheless, in spite of the great qualitative similarity of these faunas to one another, the quantitative representation, particularly of the low temperature indicators, varies greatly from site to site (see comparison of the Brandon and Tame Valley faunas p. 451) which suggests that the thermal environment of the period varied greatly from the cool temperate conditions indicated by the Upton Warren fauna to the Arctic—sub-Arctic conditions indicated for instance by the fauna from Fladbury. In this context the Brandon fauna, both qualitatively and quantitatively, indicates the most severely Arctic conditions for any of the insect bearing sites so far investigated.

The close faunal similarity of all these sites, which all probably date from the full glacial phase of the Weichselian glaciation, suggests that the Coleoptera as well as proving delicate indicators of local environment and climate, may also be of value in attempts to correlate Quaternary deposits over relatively short distance. The insect faunas, briefly discussed above, come from terrace gravels along the courses of several unconnected valley systems in the English Midlands and may prove a means of correlating these terraces in the different drainage areas.

Later Weichselian faunas from the Late Glacial in Britain contain several of the group of low-temperature stenotherms that characterize the earlier faunas, but there is a notable absence in them of the more extreme members of this group and the presence, often in considerable numbers, of such species as *Chlaenius costulatus*, *Adoxus obscurus* and *Barynotus squamosus* which are unknown in the full glacial faunas. To date, there is little chance of confusing these Late Glacial insect faunas with those of the full glacial.

An insect fauna is known from the early Weichselian interstadial deposits at Chelford, Cheshire (Coope 1959), where the local environment was mature pine and spruce forest with its associated and characteristic insect fauna. This was so different from the situation at Brandon as to make comparisons of the faunas almost meaningless.

The only earlier insect fauna which bears any close resemblance to the Brandon Terrace assemblage is that from the neighbouring channel at Brandon described by Osborne & Shotton (1968, the preceding paper). This channel on stratigraphical grounds has been placed in the early part of the Saale glaciation (Shotton 1968, this volume). The fauna, which indicates a broadly similar environment, contains many species in common with the one described in this paper, including the extinct species *Helophorus wandereri** and the exclusively east Siberian species *H. jacutus*. The commonest carabid in

* See footnote p. 437.

the Brandon Channel fauna was *Bembidion aeneum* a species that was also one of the most abundant carabids in this fauna. The Brandon Channel fauna however lacks all the low temperature stenotherm element that is so characteristic of the Brandon Terrace fauna and includes a number of relatively southern species unknown from any faunas of the Weichselian glaciation.

In the absence of other insect faunas from cold phases of earlier glaciations it is difficult to evaluate the differences between the Brandon Terrace fauna and that from Brandon Channel. Nevertheless, what differences there are encourage us to believe that further investigations into these earlier faunas may provide a means of distinguishing on entomological grounds, the deposits of the various glacial periods.

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REFERENCES

- Coope, G. R. 1959 A Late Pleistocene insect fauna from Chelford, Cheshire. *Proc. Roy. Soc. B* **151**, 70–86.
- Coope, G. R. 1961 On the study of Glacial and Interglacial insect faunas. *Proc. Linn. Soc. Lond.* **172**, 62–65.
- Coope, G. R. 1962 A Pleistocene coleopterous fauna with arctic affinities from Fladbury, Worcestershire. *Quart. J. Geol. Soc. Lond.* **118**, 103–123.
- Coope, G. R. 1967 The value of Quaternary insect faunas in the interpretation of ancient ecology and climate. *Proc. VII Congr. I.N.Q.U.A.* (Boulder, 1965), **7**, 359–380.
- Coope, G. R. 1968 Coleoptera from the “Arctic Bed” at Barnwell Station, Cambridge. *Geol. Mag.* **105**, 482–486.
- Coope, G. R. & Sands, C. H. S. 1963 The discovery in British late pleistocene deposits, of the extinct species *Helophorus wandereri* d’Orch. (Col. Hydrophilidae) *Upusc. Ent.* **28**, 94–97.
- Coope, G. R. & Sands, C. H. S. 1966 Insect faunas of the last glaciation from the Tame Valley, Warwickshire. *Proc. Roy. Soc. B* **165**, 389–412.
- Coope, G. R., Shotton, F. W. & Strachan, I. 1961 A late Pleistocene flora and fauna from Upton Warren, Worcestershire. *Phil. Trans. B* **244**, 379–421.
- Hansen, V., Klefbeck, E., Sjöberg, O., Stenius, G. & Strand, A. Revised by Lindroth, C. H. 1960 *Catalogus-Coleopterorum Fennoscandiae et Daniae*. Entomologiska Sällskapet I. Lund.
- Holdhaus, K. & Lindroth, C. H. 1939 Die europäischen Koleopteren mit borealpiner Verbreitung. *Annln. naturh. Mus. Wien* **50**, 123–293.
- Kloet, G. S. & Hincks, W. D. 1945 *A check list of British insects*. Stockport: Kloet and Hincks.
- Lindroth, C. H. 1945 Die Fennoscandischen Carabidae, Eine tiergeographische Studie, vols. I and II, *Goteborgs Vetensk. Samh.* (6) Ser. B 4.
- Lindroth, C. H. 1949 Die Fennoscandischen Carabidae, Eine tiergeographische Studie, vol. III, *Goteborgs Vetensk. Samh.* (6) Ser. B 4.
- Lindroth, C. H. 1954 A revision of *Diachila* Motsch. and *Blethisa* Bon. *Acta. Univ. Lund.* Ser. 2, **50**, no. 2, 1–28.

- Lindroth, C. H. 1963 The Ground beetles of Canada and Alaska Part 3, *Opusc. Ent.* supplement 24, 201–408.
- Lundquist, M. (Editor) 1953 *Atlas Over Sverige*. Utgiven av Svenska Sällskapet for Anthropologi och Geographi.
- Osborne, P. J. & Shotton, F. W. 1968 The fauna of the channel deposits of early Saalian age at Brandon, Warwickshire. *Phil. Trans. B* **254**, 417–424.
- Shotton, F. W. 1953 The Pleistocene deposits of the area between Coventry, Rugby and Leamington. *Phil. Trans. B* **237**, 209–260.
- Shotton, F. W. 1968 The Pleistocene succession around Brandon, Warwickshire. *Phil. Trans. B* **254**, 387–400.
- Strand, A. 1946 Nord-Norges Coleoptera. *Tromsø Mus. Arsh. Naturkist. Aud.* No. 34, **67**, n1, 1–629.
- Tomlinson, M. E. 1963 The Pleistocene chronology of the Midlands. *Proc. Geol. Ass. Lond.* **74**, 187–202.

EXPLANATION OF FIGURES

Insets on maps. Present-day European distribution.

Key to locality symbols for figures 1 to 6: ▲ Weichselian full glacial sites; ● Weichselian Late Glacial sites.

Key to locality numbers for figures 1 to 6

- | | |
|---|---|
| (1) Upton Warren, Worcestershire (SO/935673) | (12) Penkridge, Staffordshire (SJ/924113) |
| (2) Tame Valley, Warwickshire (SP/212924) | (13) Dorrington, Shropshire (SJ/574079) |
| (3) Four Ashes, Staffordshire (SJ/916082) | (14) Heyfords Farm, Shropshire (SJ/365104) |
| (4) Brandon, Warwickshire (SP/391753) | (15) Orleton, Shropshire (SO/497677) |
| (5) Fladbury, Worcestershire (SO/975468) | (16) Church Stretton, Shropshire (SO/459939) |
| (6) Great Billing, Northamptonshire (SP/617826) | (17) Avon Wen, Caernarvonshire (SH/449373) |
| (7) St Albans, Hertfordshire (TL/185050) | (18) Redkirk Point, Dumfriesshire (NY/300653) |
| (8) Oxbow opencast site near Leeds, Yorkshire (SE/362300) | (19) Big Holm, Dumfriesshire (NY/315813) |
| (9) Earith, Huntingdonshire (TL/385748) | (20) Sanquhar, Dumfriesshire (NS/782105) |
| (10) Barnwell Station, Cambridge (TL/472596) | (21) Airdrie, Lanarkshire (NS/784667) |
| (11) Thrapston, Northamptonshire (SP/988805) | (22) Kirkmichael, Isle of Man (SC/314915) |
| | (23) Drumurcher, Co. Monaghan |
| | (24) Corstorphine, Edinburgh (NT/210720) |

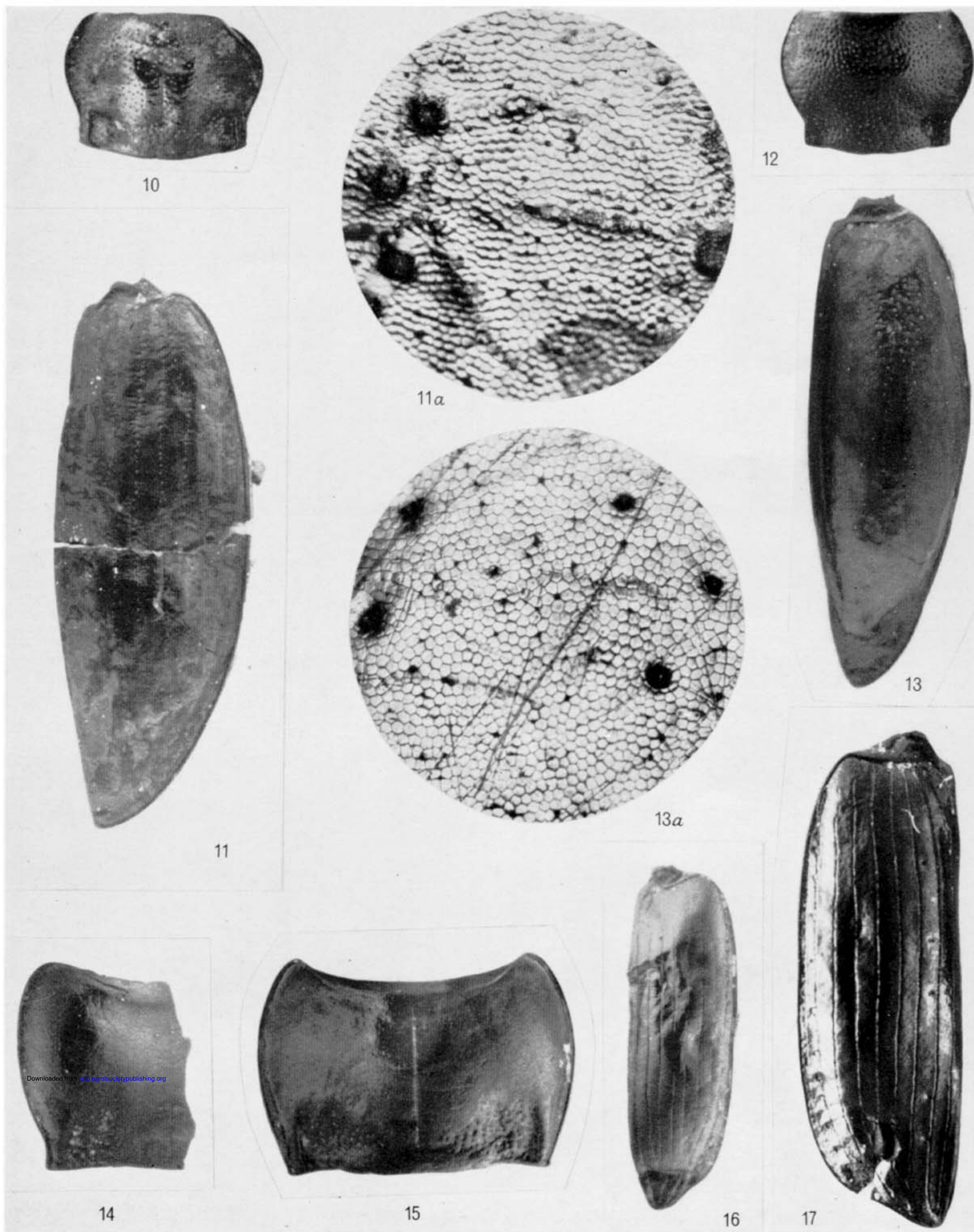


FIGURE 10. Pronotum of *Diachila arctica* Gyll. showing well-developed carinae on the posterior angles ($\times 20$).

FIGURE 11. Right elytron of *Diachila arctica* Gyll. ($\times 20$).

FIGURE 11a. Micro-ornament on disk of the elytron of *Diachila arctica* ($\times 250$).

FIGURE 12. Pronotum of *Diachila polita* Fald. Note the absence of carinae on the posterior angles ($\times 20$).

FIGURE 13. Right elytron of *Diachila polita* Fald. ($\times 20$).

FIGURE 13a. Micro-ornament on disk of the elytron of *Diachila polita* Fald—well developed micro-reticulation but more subdued than in *D. arctica* ($\times 250$).

FIGURE 14. Pronotum of *Amara torrida* Ill. ($\times 20$). Note the different form of the posterior angles.

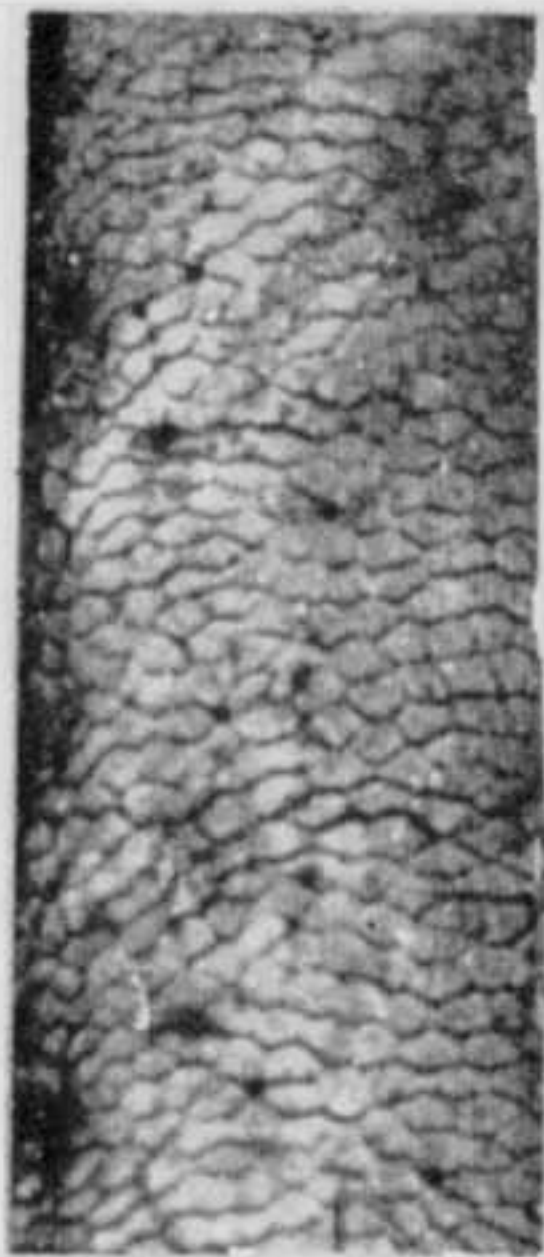
FIGURE 15. Pronotum of *Amara alpina* Pk. ($\times 20$). Note the different form of the posterior angles.

FIGURE 16. Left elytron of *Agonum consimile* Gyll. ($\times 20$).

FIGURE 17. Left elytron of *Agonum ericeti* Pz. ($\times 20$).



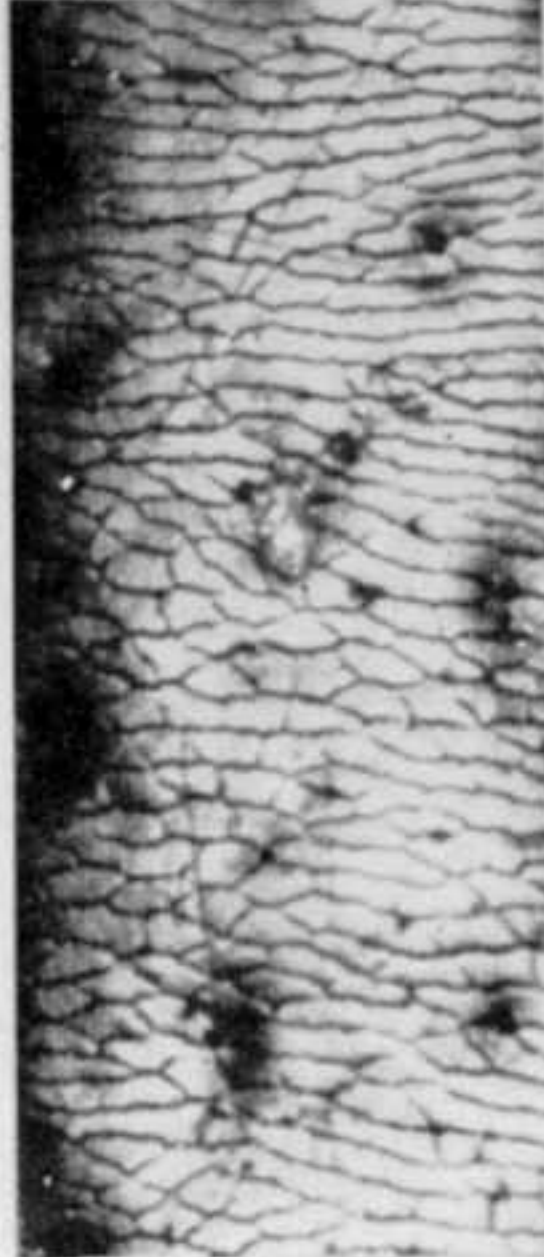
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19a



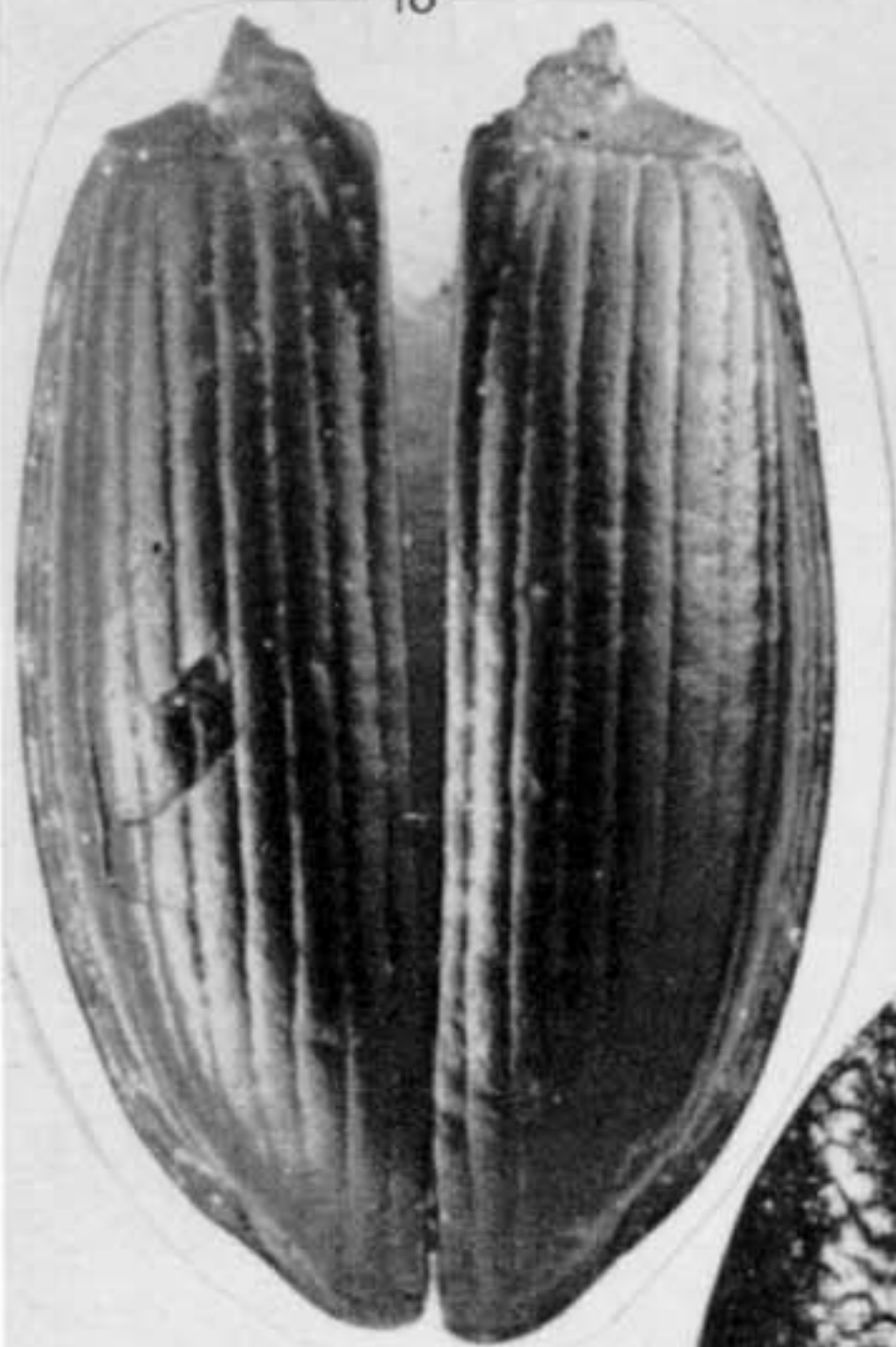
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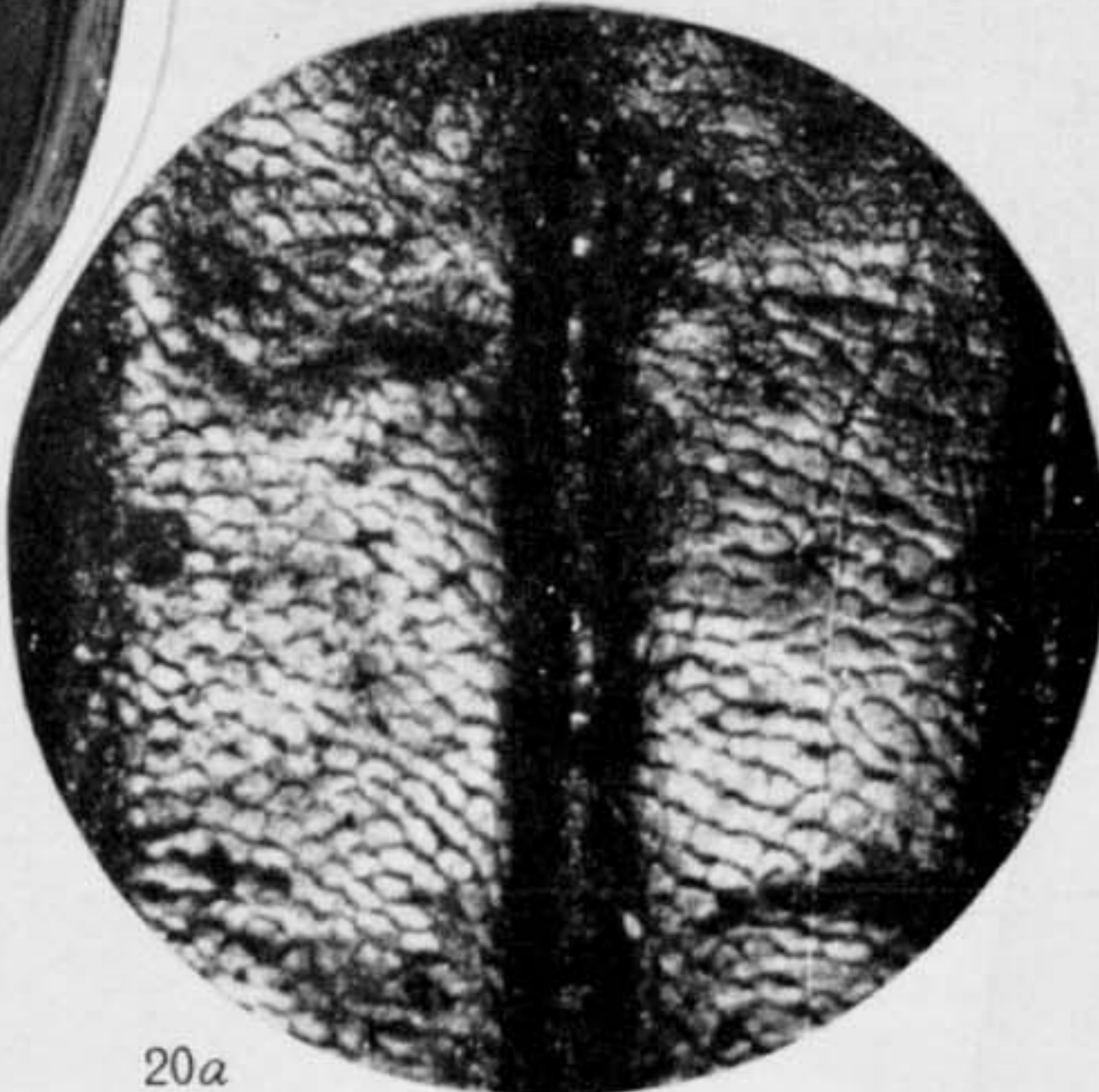
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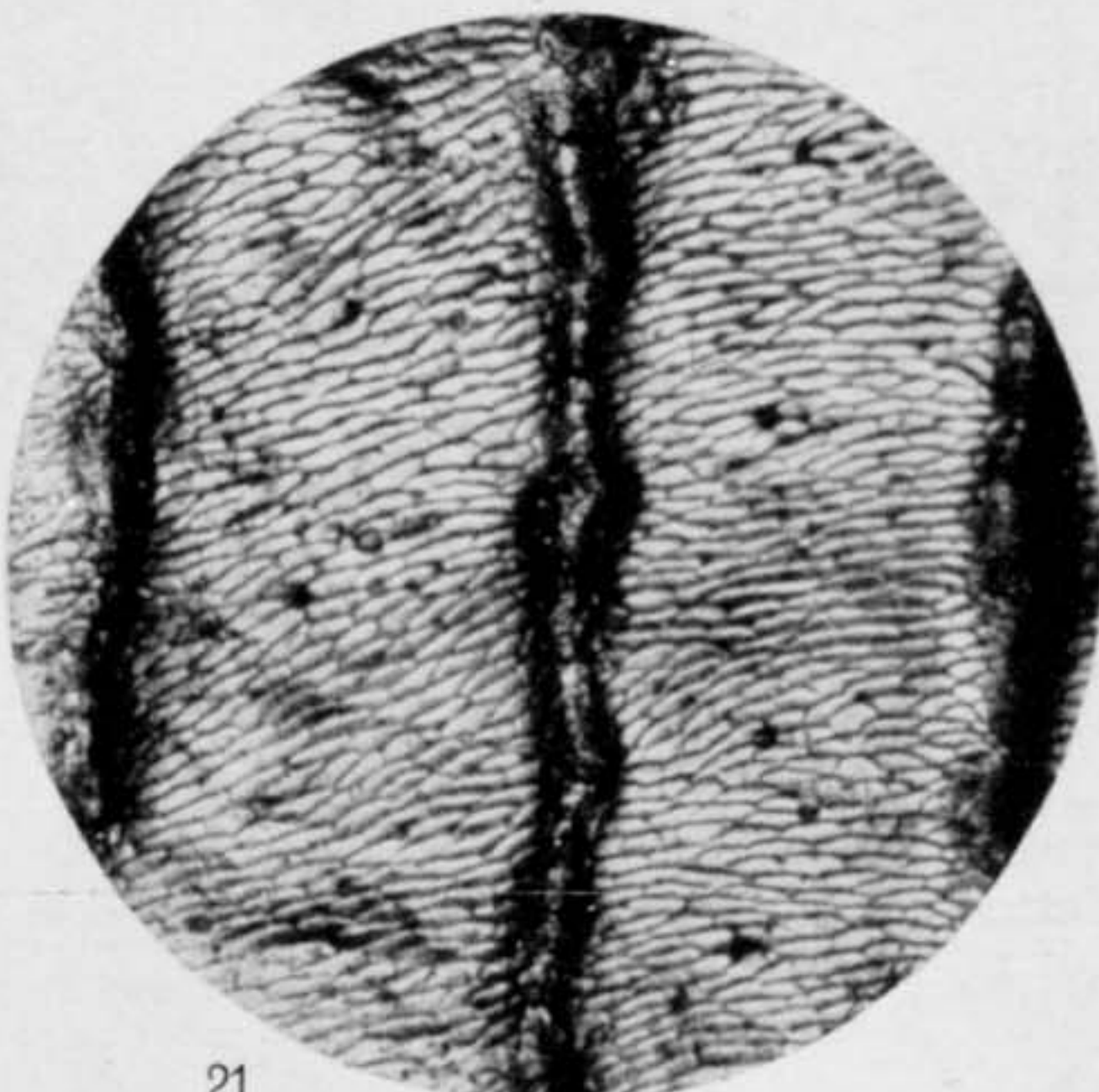
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20a



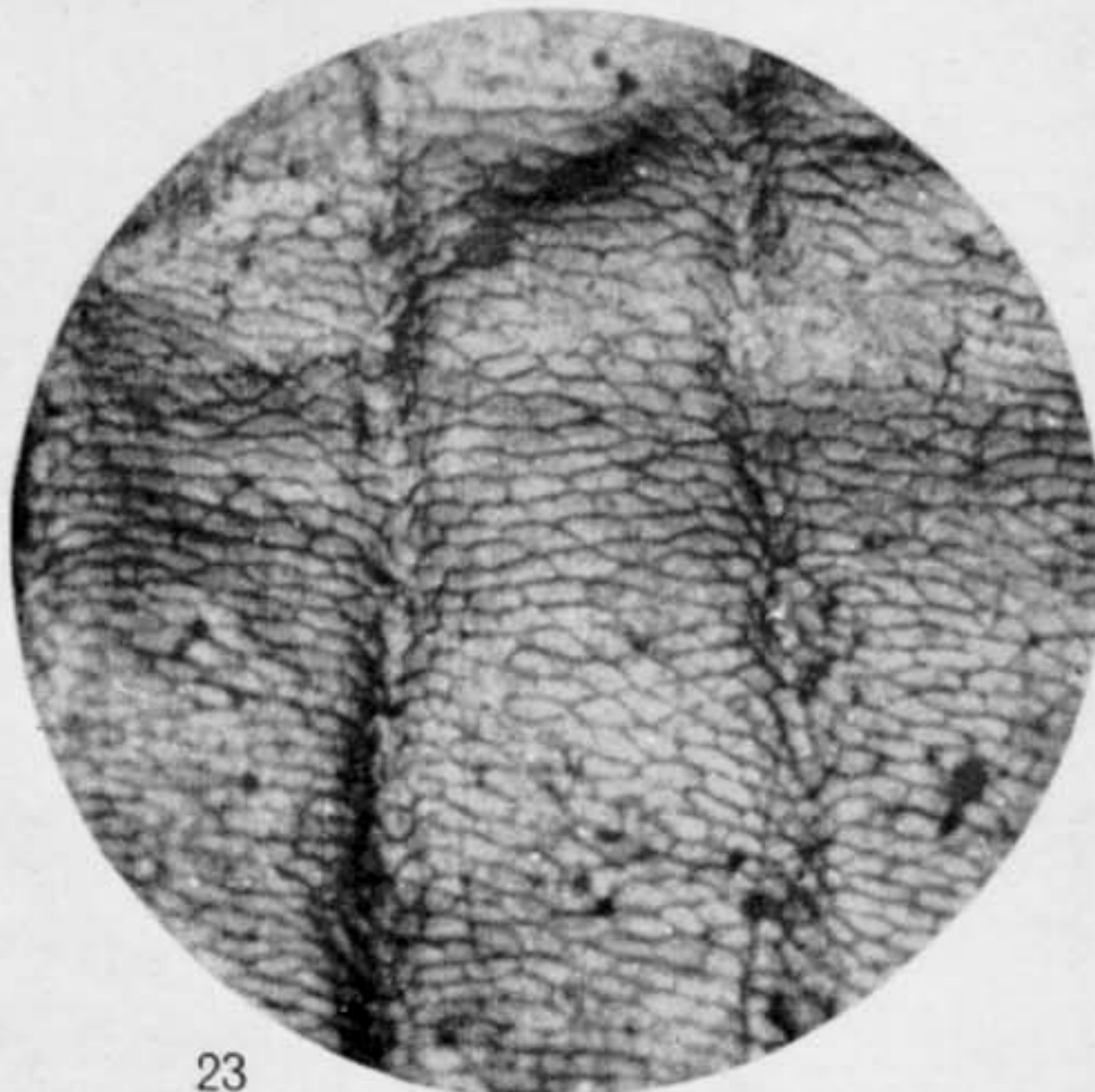
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20



22a



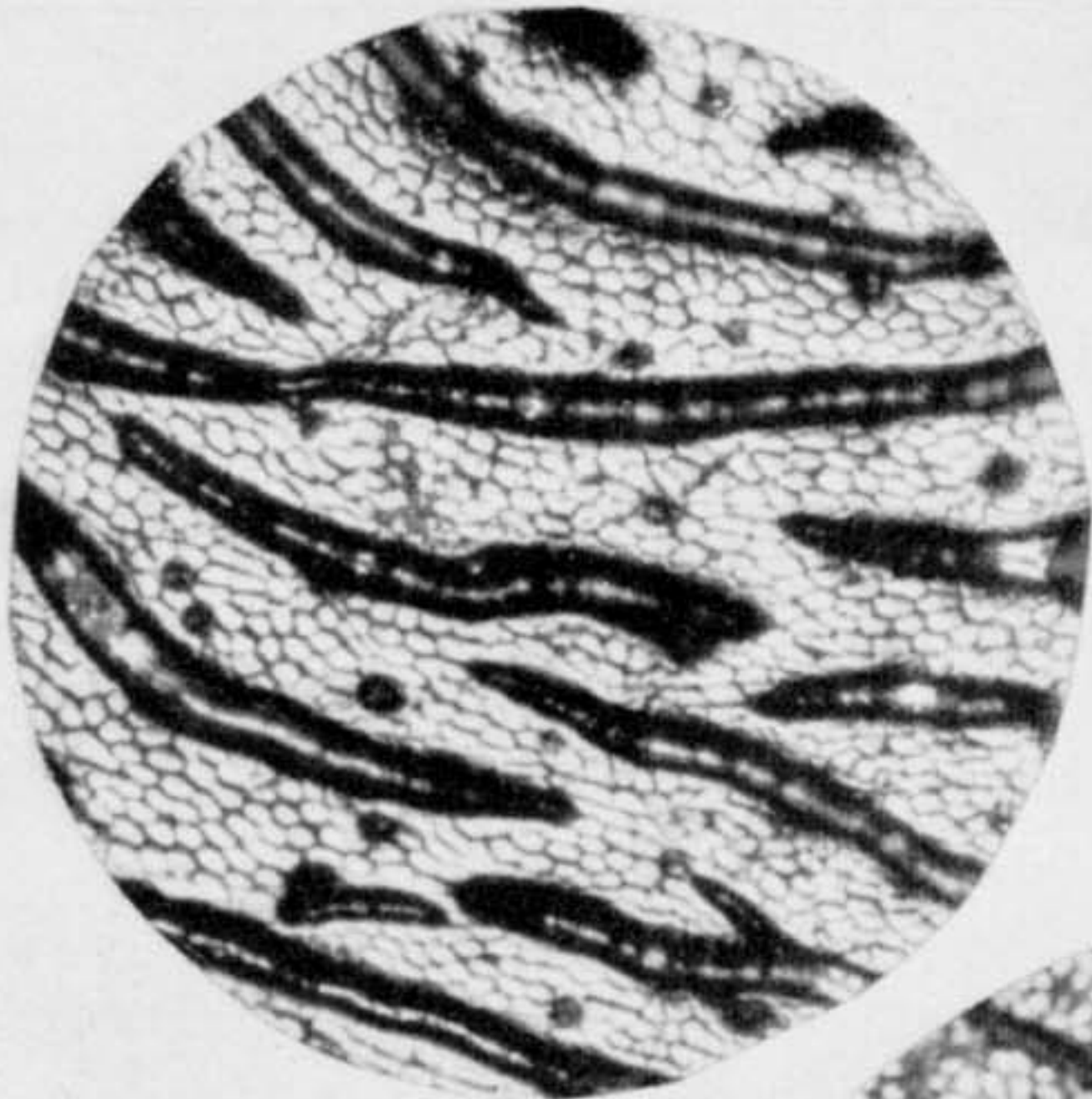
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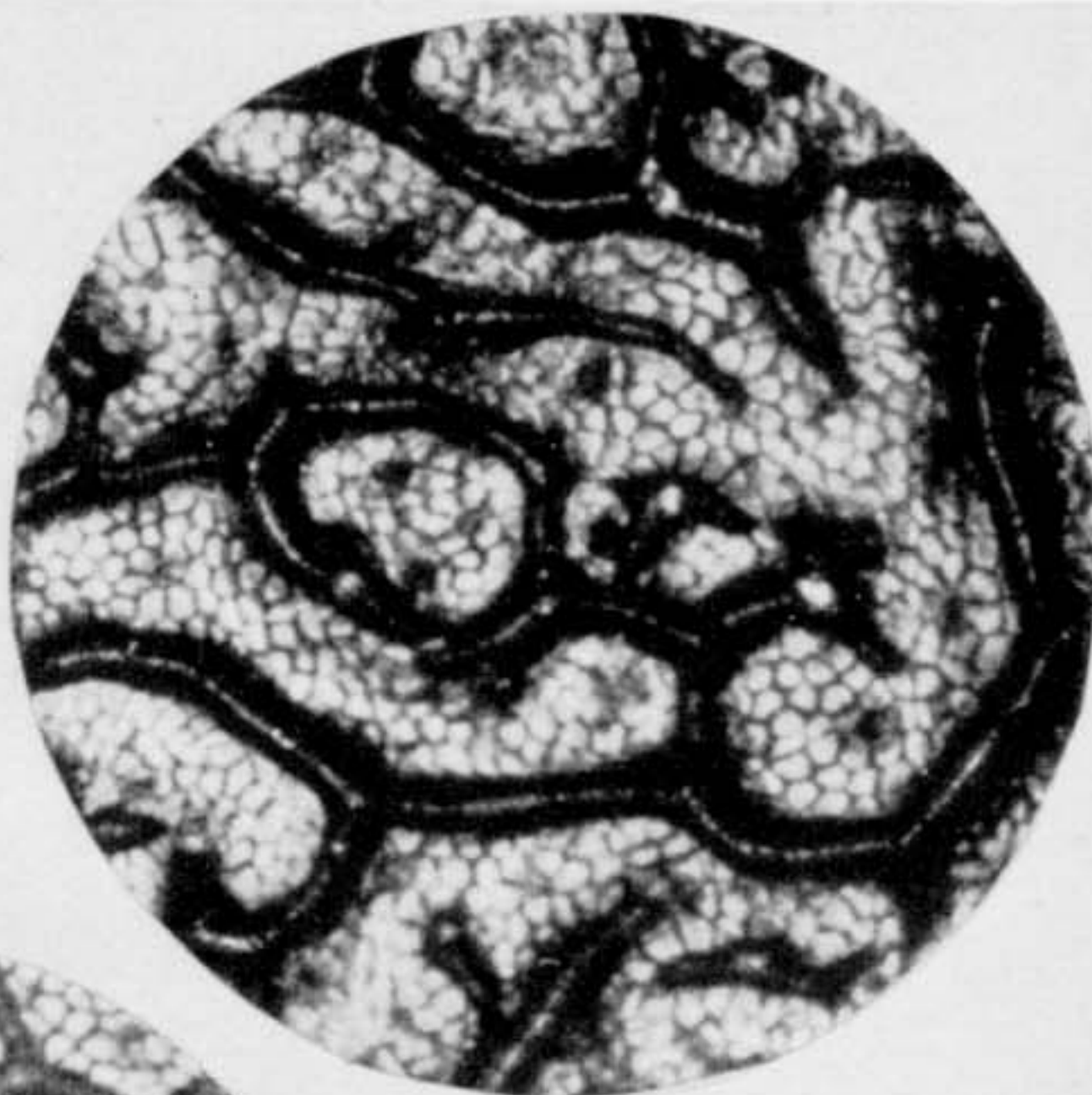
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24a



24b



24c



29a



29b



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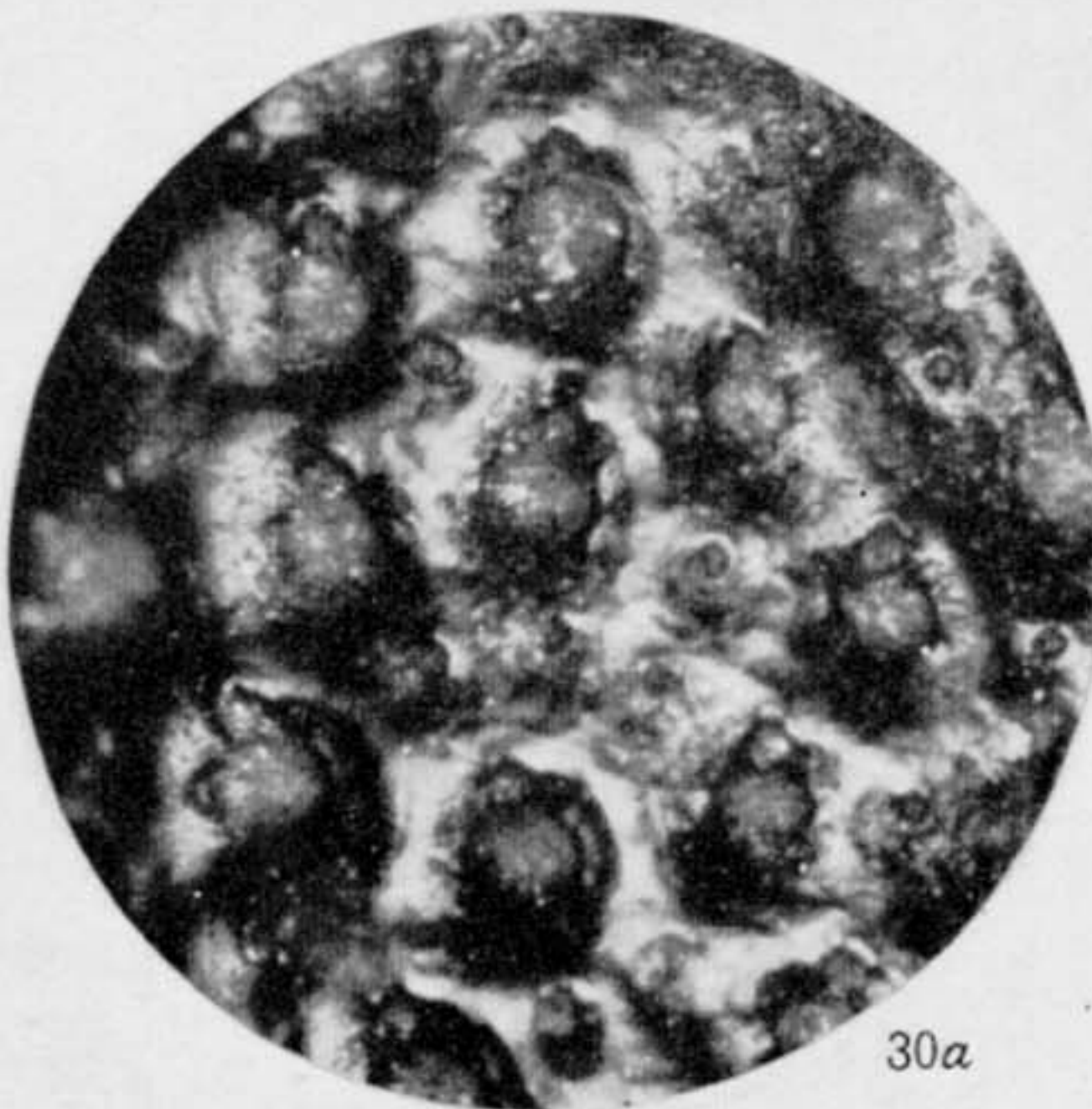
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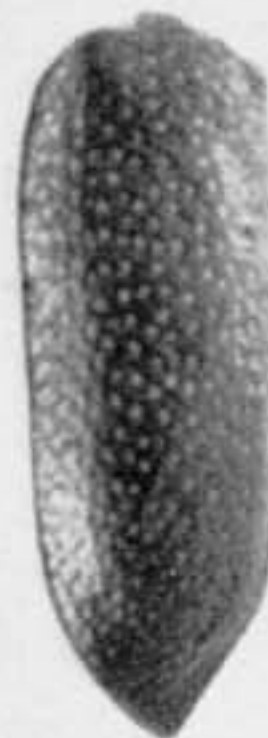
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28



30a



30