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THE FAUNA OF THE HOXNIAN INTERGLACIAL DEPOSITS OF NECHELLS, BIRMINGHAM

By F. W. SHOTTON, F.R.S. and P. J. OSBORNE
Department of Geology, University of Birmingham

With an appendix on *Cytherissa lacustris* and other ostracods at Nechells

By P. C. SYLVESTER-BRADLEY

(*Received* 6 *March* 1964)

[Plate 30]

CONTENTS

The described fauna has been extracted from the sediments of the Nechells channel of Hoxnian Interglacial age, whose stratigraphy and flora have already been discussed. It comprises a small number of species of fish, ostracods, Cladocera, mites, molluscs and polyzoa and a considerable number of insects with beetles predominant. The distribution of these has been related to the floral zones of Kelly (1964).

The earliest sediments are those of a glacially dammed lake and the limited fauna associated with these are ostracods, *Daphnia*, *Cristatella* and, amongst the insects, the larvae of *Sialis*, trichoptera and chironomids. Shortly after, fish and molluscs appear and by Zone IN3, beetles first become significant. After IIN *a*, beetles form the predominant element of the fauna. Calcareous and phosphatic organisms disappear after IIN *a*, corresponding to a change in the nature of the bottom sediments, but this is largely explained by post-depositional solution. The time and climate distribution of *Daphnia* and *Cristatella mucedo*, both of which have winter resting stages, is discussed in relation to climate, as are beetles of the genus *Rhynchaenus* in relation to the occurrence of food plants, and the chironomids in relation to temperature and limnology.

The coleopterous fauna, the first of considerable size to be described from a period of the Pleistocene as old as the Hoxnian, is still essentially British and the identity with present-day species is striking. An exceptional case of this identity is provided by the aedeagus dissected from *Hydraena*

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riparia. Only three non-British species have been named and two of these, *Platypus oxyurus* and *Brachytemnus submuricatus*, from near the top of the sequence, have now a disjunct occurrence in southern Europe. *Micropeplus caelatus* has been identified and this now has a sporadic distribution in central Europe and is restricted in Britain to the extreme south-west of Ireland.

There are no beetles characteristic of cold climate but the earliest fauna as a whole clearly indicates glacial conditions. The climate ameliorates to reach its optimum, a little warmer but not much different from that of today, towards the end of the borehole sequence, and the deposits do not include a fauna characteristic of the second (cooling) half of an interglacial.

I. Historical background

In 1950, boreholes and excavations in the Nechells district of Birmingham revealed the presence of organic silts filling a deep hollow and lying beneath Older Drift gravels. A partial succession of these deposits was examined by Dr Suzanne L. Duigan (1956) who recognized the pollen zones of about two-thirds of the Great Interglacial succession of Hoxne (West 1956). In 1957 the Royal Society financed the sinking of a borehole sited, so it was hoped, to recover the fullest sequence of these interglacial deposits for the complete study of their lithology and floral and faunal content. Virtually complete core recovery was obtained and, in addition, there were temporary sections associated with sewer trenches and site exploration boreholes. Kelly (1964) has just described the Nechells deposits from a botanical point of view, correlating them closely with the zones established at Hoxne and in Ireland, and we shall accept his subdivisions as the framework for our faunal studies. By working out the stratigraphy of the whole area, he has also enabled us to allocate the specimens found at the other collecting points to their equivalent positions in the borehole sequence.

II. The source of the fauna, and its dating

The simplified history of the Nechells area is that, in a hollow within sands and gravels belonging to the First Welsh Glaciation (Mindel or Elster), a succession of laminated clays and silts, peaty silts and brushwood peats were deposited. Although basically the site of deposition is an ancient river valley, Kelly believes that the lower part of the hollow owes its origin to ice in the First Welsh gravels giving rise to a kettle hole, that the earlier half of the deposits are lacustrine, and only the later half are fluviatile. These sediments which initially are glacifluvial in origin, with all that this implies in climate, change to sediments of a temperate climate. They can be correlated unequivocally with the Great Interglacial (Hoxnian, Holstein, Mindel-Riss). Lying unconformably upon the channel deposits are gravels which are the earliest part of a succession belonging to the Second Welsh (Riss, Saale) Glaciation.

Figure 1 shows the lithological variation of the sequence in the three sources of fossil animal material—the Royal Society borehole, or No. 7* (SP 08728809) an auger hole, borehole 8 (SP 08678821) and a sewer tunnel section C1 (SP 08698818). Also shown are the limits of the examined samples and their relation to the pollen zones. It will be noted that the sequence of borehole 7 ends at Zone III N. *a*—higher zones are known only from borehole 8 (where it carried no animal fossils) and from the top of the sequence examined

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* It will prevent confusion if these three sections retain the identifying numbers given by Kelly.

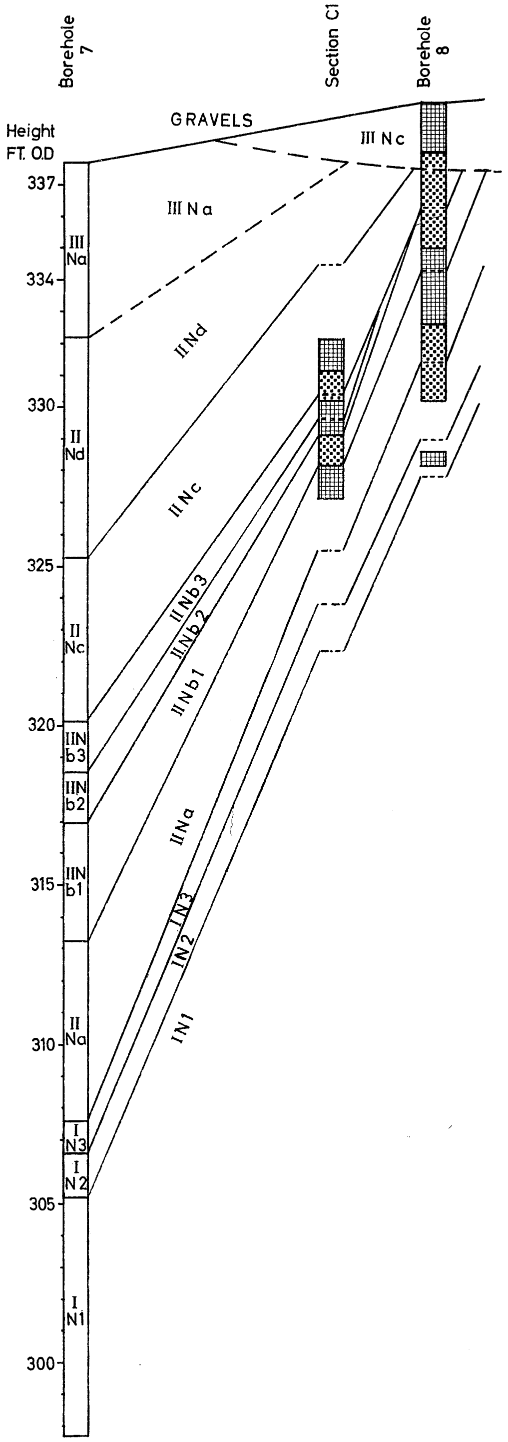

Figure 1. The correlation by palynology (after Kelly) of borehole 8 and section C1 with borehole 7. The units of ornament in C1 and borehole 8 indicate the extent of separate samples examined for fauna.

by Dr Duigan which was only collected in samples of a size suitable for pollen analysis. The scales of perch were found in a small sample from one of the original exploration boreholes at the site for the city's Nechells flats and its zonal position cannot be narrowly determined.

III. Techniques of collection and separation

In the drilling of the borehole, the first 20 ft. in gravel were percussed and lined with 11 in. casing. Below that depth, sampling was done by driving a special tool of 7 in. external and 6 in. internal diameter, fitted with a split cylindrical lining sleeve and central plate. The core was thus extracted as two half cylinders. After each length of core had been drawn, 8 in. diameter casing was hammered down to the bottom of the hole, scraping off the side of the boring in the process. This disturbed material was mainly picked up at the top of the next sample and, being easily distinguishable from the undisturbed stratified sediments, could be discarded; but that small part which lay beneath the cutting edge of the drilling tool could be driven down into the undrilled material and confused with it in the subsequent sample. In the skeletal fragments from any unit, therefore, a very small proportion might be contaminants from the previous core-length and there could even be a slender chance of contamination from a higher level. It would be difficult to recognize this except in the case of an isolated specimen in an anomalous position.

Extraction of specimens was done in the normal fashion. The sample was boiled, in sodium carbonate solution if this was necessary to destroy its coherence, and then washed through sieves, the finest being No. 52 (aperture diameter 0·295 mm). The retained material was kept wet, later examined under water with a binocular microscope and the remains of plants and animals picked out. It is now realized that the retaining sieve was too coarse to provide evidence of Cladocera fragments except for their comparatively large ephippia.

Beetle and other insect skeletal fragments were almost always dissociated and often rather fragmental as though they had suffered drastic transport, but preservation was otherwise excellent.

IV. List of identified animal remains

VERTEBRATA

Pisces

Scardinius erythrophthalmus (L.)	Rudd. Teeth. ? top of IN3. Whole of IIN.*a* (figure 9, plate 30)
Rutilus rutilus (L.)	Roach. Teeth. ? top of IN3. Upper IIN.*a*
Alburnus lucidus	Bleak. Tooth. Mid IIN.*a*
Esox lucius (L.)	Pike. Teeth. Base and near top of IIN.*a* (figure 10, plate 30)
Perca fluviatilis (L.)	Perch. Scales. Borehole No. 3 (Duigan), IIN.*a* or IIN.*b* (figure 8, plate 30)

ARTHROPODA

Ostracoda

Candona spp.	IN1, IN2, IN3, IIN.*a*
Cyclocypris sp.	IN2, IN3, IIN.*a*
Cytherissa lacustris (Sars.)	Top of IN1, IN2, IN3, IIN.*a*

CLADOCERA	
Daphnia sp.	Ephippia. IN1 and IN2
ARACHNIDA	
Acarini	Mites. IN3, IIN.*c*, IIN.*d*
INSECTA	
Hemiptera	
Chartoscirta cincta (Herr.-Schaef.) or *cocksi* (Curtis)	2 pronota from upper IIN.*c*, one from mid IIN.*d*
Megaloptera	
Sialis sp.	Mainly mandibles and head plates of larvae. IN1, IN3, IIN.*a*, IIN.*b*1, IIN.*b*2, IIN.*b*3, IIN.*c*
Trichoptera	Not specifically or generically determined. Thoraces of adults abundant from top of IN1 to middle IIN.*a* and an isolated occurrence at the top of IIN.*a*. Larval mandibles and sclerites from IIN.*b*2 to lower IIIN.*a*, one isolated occurrence at base of IIN.*a*
COLEOPTERA	
Carabidae	
Elaphrus cupreus Dufts.	IIN.*d*
Elaphrus cupreus or *uliginosus* F.	IIN.*a*, IIN.*b*3
Clivina sp. probably *collaris* (Hbst.)	IIN.*d*
Dyschirius globosus (Hbst.)	IN 3, IIIN.*a*
Dyschirius sp.	IN 3 or IIN.*a*
Bembidion schuppeli Dej.	IIN.*d*
Bembidion assimile Gyll.	IIN.*b*3
Bembidion spp.	IN1, IN3, IIN.*b*2, IIN.*d*
Trechus secalis (Payk.)	IIIN.*a*
Trechus rivularis (Gyll.)	IN 3 or IIN.*a*
Trechus sp.	IIIN.*a*
Amara sp.	IIN.*b*1
Feronia vernalis (Pz.)	IIN.*d*
Feronia nigrita (F.)	IN 3 or IIN.*a*
Feronia strenua (Pz.)	IIN.*a*
Feronia spp.	?IN 3, IIN.*a*, IIN.*b*3
Dytiscidae	
Hydroporus sp.	IN1
Agabus bipustulatus (L.)	IIN.*a*

Gyrinidae	
Gyrinus sp.	IIN.*b*2
Hydrophilidae	
Ochthebius bicolon Germ.	IN1, IIN.*b*, IIN.*d*
Ochthebius minimus (F.)	IN3, IIN.*b*1, IIN.*b*3, IIN.*c*, IIN.*d*
Ochthebius sp.	IN1
Hydraena riparia Kug. and *riparia*?	IIN.*a* to IIN.*d*
Hydraena sp.	IN.3 (?), IIN.*a*, IIN.*b*3, IIN.*c*
Helophorus sp.	IIN.*b*, IIN.*b*3, IIN.*c*
Sphaeridium sp.	IIN.*a*
Cercyon spp.	IN3, IIN.*a*, IIN.*b*, IIN.*b*2, IIN.*b*3, IIN.*c*, IIN.*d*, IIIN.*a*
Hydrobius fuscipes (L.)	IIN.*b*1, IIN.*b*3
Silphidae	
Ptomophagus sp.	IIN.*b*1
Leiodidae	
Agathidium sp.	IIN.*a*
Clambidae	
Clambus pubescens Redt.	IIN.*b*2
Orthoperidae	
Corylophus cassidioides (Marsh.)	IIN.*c*, IIN.*d*
Ptiliidae	
Ptenidium sp.	IIN.*b*3, IIN.*c*, IIN.*d*
Acrotrichis sp.	IIN.*b*3, IIN.*c*, IIN.*d*
Staphylinidae	
Micropeplus staphylinoides (Marsh.)	IIN.*b*2, IIN.*c*
Micropeplus fulvus Erichs.	IIN.*d*
Micropeplus caelatus Erichs.	IN3 or IIN.*a*
Micropeplus sp.	IIN.*b*3
Omalium sp.	IIN.*d*
Acidota crenata (F.)	IIN.*a*
Lesteva sp. probably *heeri* Fauvel	IIN.*d*
Carpelimus (*Trogophloeus*) *rivularis* Motsch.	IIN.*d*
Carpelimus elongatulus Erichs.	IIN.*d*
Carpelimus spp.	IIN.*b*3, IIN.*c*, IIN.*d*, IIIN.*a*
Oxytelus rugosus (F.)	IIN.*b*2, IIN.*b*3, IIN.*c*, IIN.*d*
Oxytelus fulvipes Erichs.	IIN.*c*
Bledius sp.	IN3
Stenus juno F.	IIN.*a*, IIN.*b*2, IIN.*c*, IIN.*d*

Stenus bimaculatus Gyll.	IIN.*d*
Stenus brunnipes Steph.	IIN.*b*2, IIN.*b*3
Stenus cicindeloides (Schall.)	IIN.*d*
Stenus spp.	IN3 or IIN.*a*, IIN.*a*, IIN.*b*1, IIN.*b*2, IIN.*c*, IIN.*d*
Euaesthetus ruficapillus Boisduval	IIN.*a* or IIN.*b*
Lathrobium spp.	IIN.*a*, IIN.*b*, IIN.*c*, IIN.*d*
Ochthephilum fracticorne (Payk.)	IIN.*d*
Bolitobius sp.	IIN.*c*
Tachinus sp.	IIN.*b*3
PSELAPHIDAE	
Brachygluta sp.	IIN.*b*
Reichenbachia impressa (Pz.)	IIN.*b*
Bryaxis sp.	IIN.*c*
HISTERIDAE	
Hister sp.	IIN.*b*1, IIN.*c*
ELATERIDAE	
Adelocera murina (L.)	IIN.*a*, IIN.*b*1, IIN.*b*2, IIN.*b*3
Melanotus rufipes (Hbst.)	IIN.*d*
Prosternon tesselatum (L.)	IIN.*a* (?), IIN.*b*1
Dalopius marginatus (L.)	IIN.*a*
TRIXAGIDAE	
Trixagus dermestoides (L.)	IIN.*d*, IIIN.*a*
DASCILLIDAE	
Dascillus cervinus (L.)	IN3(?), IIN.*a*, IIN.*b*1, IIN.*b*2, IIN.*b*3, IIN.*c*
DRYOPIDAE	
Dryops sp.	IIN.*b*
Elmis maugei Bedel	IIN.*b*3, IIN.*c*
Esolus parallelopipedus (Müller)	IIN.*b*2, IIN.*b*3, IIN.*c*
Limnius troglodytes Gyll.	IN3, IIN.*a*, IIN.*b*1, IIN.*b*2, IIN.*b*3, IIN.*c*, IIN.*d*
Riolus cupreus (Müller)	INI, IN3, or IIN.*a*
Riolus nitens (Müller)	IIN.*c*
RHIZOPHAGIDAE	
Rhizophagus sp.	IIN.*b*
PHALACRIDAE	
Phalacrus caricis Stürm	IIN.*b*1
COLYDIIDAE	
Cerylon fagi Brisout.	IIN.*a* or IIN.*b*1
Cerylon sp.	IIN.*a*, IIN.*d*

Anobiidae	
Grynobius excavatus (Kug.)	IN3 or IIN.*a*, IIN.*a*, IIN.*d*, IIIN.*a*
Xestobium rufovillosum (Deg.)	IIN.*d*
Anthicidae	
Anthicus sp. cf. *antherinus*	IN1
Scarabaeidae	
Aphodius merdarius or *pusillus*	IIN.*b*2
Aphodius spp.	IN2, IN3, IIN.*a*, IIN.*b*, IIN.*b*2, IIN.*b*3, IIN.*c*
?*Ataenia brevicollis* (Wollaston)	IIN.*c* (base)
Chrysomelidae	
Donacia cinerea Hbst.	IIN.*a*
Donacia spp.	
Plateumaris sp.	
Curculionidae	
Apion simile Kirby	IIN.*b*
Apion subulatum Kirby	IN3, IIN.*b*2
Apion ?*filirostre* Kirby	IIN.*b*2
Apion apricans Hbst.	IIN.*b*, IIN.*c*
Apion ? *difforme* Ahrens	IIN.*b*1
Apion spp.	IN3 (?), IIN.*a*, IIN.*b*, IIN.*d*
Otiorrhynchus ovatus (L.)	IIN.*b*
Barynotus sp.	IIN.*c*
Sitona suturalis Steph.	IIN.*a*
Sitona sp.	IIN.*b*
Brachytemnus submuricatus Schönh.	IIN.*a*, IIN.*d*, IIIN.*a*
Rhyncolus lignarius (Marsh.)	IIN.*d*, IIIN.*a*
Bagous sp.	IIN.*b*1
Tanysphyrus lemnae (Payk.)	IIN.*a*, IIN.*b*1, IIN.*b*3, IIN.*c*, IIIN.*a*
Notaris scirpi (F.)	IIN.*c* (top), IIN.*d*
Notaris acridulus (L.)	IIN.*b*2, IIN.*b*
Anthonomus sp.	IIN.*a*, IIN.*b*1, IIN.*b*
Curculio sp.	IIN.*b*2, IIN.*c*
Ceuthorrhynchus spp.	IN2, IIN.*a*, IIN.*b*1, IIIN.*a*
Rhynchaenus quercus (L.)	IN1 (? contaminant), IIN.*a*, IIN.*b*1, IIN.*b*2, IIN.*b*3, IIN.*c*
Rhynchaenus avellanae (Donovan)	IN1 (? contaminant), IIN.*a* or IIN.*b*1, IIN.*b*1, IIN.*b*2, IIN.*b*3, IIN.*c*
Rhynchaenus sp. ? *pilosus* (F.)	IIN.*a*
Rhamphus pulicarius (Hbst.)	IIN.*b*3

SCOLYTIDAE	
Hylesinus crenatus (F.)	IIN.*b*
PLATYPODIDAE	
Platypus cylindrus (F.)	IIIN.*a*
Platypus oxyurus Duf.	IIN.*d*
DIPTERA	
CHIRONOMIDAE. All as larval head capsules.	
Pentaneura	IN1
Anotypina	IN1
Procladius	IN1 (?), IN3
Chironomus	IN1, IN3, IIN.*a*, IIN.*b*1, IIN.*b*2, IIN.*b*3, IIN.*c*
Cryptochironomus	IIN.*a*, IIN.*b*1
Glyptotendipes	IIN.*b*1, IIN.*b*2, IIN.*c*
Microtendipes	IN1, IN2
Dicrotendipes	IIN.*b*2
Tanytarsus	IN1, IIN.*a* (?)
HYMENOPTERA	
FORMICIDAE	4 mandibles, IIN.*a*, IIN.*b*2, IIN.*c*
MISCELLANEOUS, mainly HYMENOPTERA PARASITICA	14 heads, part of a thorax, IIN.*a*, IIN.*c*
MOLLUSCA	
Bithynia tentaculata (L.).	145 opercula from IN3 to top of IIN.*a*
Valvata cristata Müller	1 pyrite mould from base of IIN.*a*
Lymnaea ? *peregra* (Müller)	1 pyrite mould from near base of IIN.*a*
Pisidium spp.	13 pyrite moulds from IN2, IN3 and base of IIN.*a*
POLYZOA	
Cristatella mucedo Cuvier	Statoblasts. Scarce in the upper part of IN1, thereafter in IN2 and continuously upwards to mid IIN.*c*, where they cease at the brushwood peat

V. NOTES ON IDENTIFICATIONS

Chartoscirta cincta or *cocksi*. Amongst the Saldidae, *Chartoscirta* has an unmistakable type of pronotum, and of the three modern British species, *elegantula* is easily distinguished from *cincta* or *cocksi* by its proportions. Our specimens correspond exactly with either of the last two which cannot be distinguished in the absence of any other skeletal parts.

Elaphrus spp. Only three skeletal fragments of this distinctive genus have been found at widely separated intervals. The highest, half a pronotum, is distinctive of the species *cupreus* but the other two specimens are small fragments of elytra with a most characteristic ornament which, however, fails to separate *cupreus* from *uliginosus*. Thus, whilst *Elaphrus cupreus* is certainly present, there is no certainty that *uliginosus* also occurs.

Dyschirius sp. A single elytron which is only generically determinable is listed separately from *D. globosus* because it is clearly not that species.

Agabus bipustulatus. Dytiscids are surprisingly rare in strata which might have been expected to be rich in them. The only agabine to be recognized is represented by a small piece of elytron which fortunately carries the unique reticulation of *bipustulatus*.

Ochthebius bicolon (figure 24, plate 30). Two pronota of this species were found. They can be distinguished from all other British species except *auriculatus* and *impressicollis* by the presence of 'colons' and large 'ears'. From *auriculatus* they can be separated by the presence of a closed depression outside the 'colons' and the relatively small size of the 'ears', and from *impressicollis* by the puncturation and their smaller size.

Hydraena. The large numbers of fragments of *Hydraena* have been split into three groups. The first contains all those judged to be *H. riparia* on the pronotum and, in one case, the aedeagus and all other parts that could be this species found in the same samples. This group comprises 8 heads, 23 pronota, 28 elytra, 10 metasterna and 1 abdomen containing an aedeagus. Several elytra were in associated pairs, one pair being also attached to part of a pronotum, and one head and pronotum were joined together.

Description of plate 30

Figure 8. Scale of *Perca fluviatilis*: perch. (× 10.)
Figure 9. Tooth of *Scardinius erythrophthalmus*: rudd. (× 10.)
Figure 10. Tooth of *Esox lucius*: pike. (× 10.)
Figure 11. Statoblast of *Cristatella mucedo*. (× 50.)
Figure 12. *Cytherissa lacustris*. (× 50.)
Figure 13. *Daphnia* ephippium. (× 50.)
Figure 14. *Micropeplus caelatus*, left elytron. (× 30.)
Figure 15. *Micropeplus* species?, thorax. (× 30.)
Figure 16. *Stenus brunnipes*, aedeagus. (× 100.)
Figure 17. *Rhynchaenus quercus*, aedeagus. (× 40.)
Figure 18. *Rhynchaenus quercus*, head. (× 40.)
Figure 19. *Xestobium rufovillosum*, left elytron. (× 20.)
Figure 20. *Ataenia* cf. *brevicollis*, right elytron. (× 20.)
Figure 21. *Brachytemnus submuricatus*, head. (× 30.)
Figure 22. *Brachytemnus submuricatus*, left elytron. (× 20.)
Figure 23. *Brachytemnus submuricatus*, apex of left elytron. (× 30.)
Figure 24. *Ochthebius bicolon*, thorax. (× 30.)
Figure 25. *Platypus cylindrus*, apex of elytron, ♂. (× 30.)
Figure 26. *Platypus oxyurus*, apex of left elytron, ♂. (× 40.)
Figure 27. *Platypus oxyurus* (modern), apex of left elytron, ♂. (× 40)


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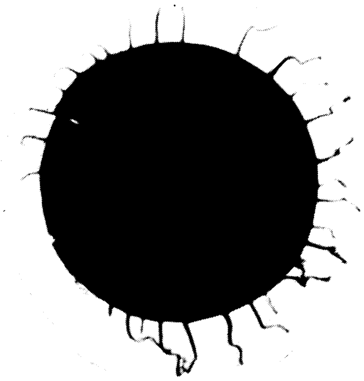
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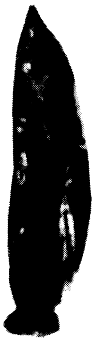
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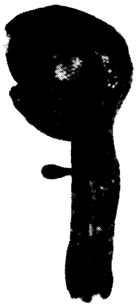
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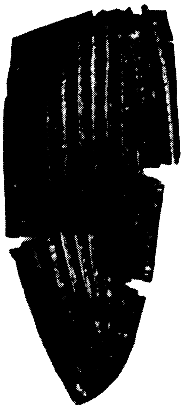
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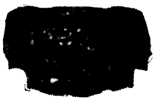
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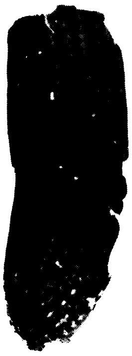
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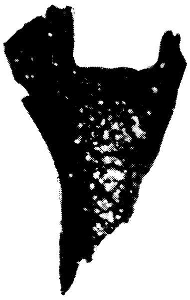
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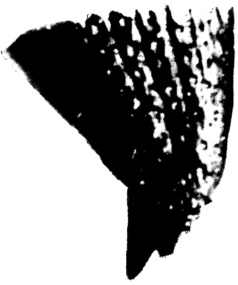
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(*Facing p.* 362)

The second group comprises 4 heads, 14 elytra and 2 metasterna which cannot be distinguished from and probably are *riparia* but which, being unaccompanied by pronota, are not absolutely definitive.

The third group, of 3 pronota and 12 elytra, obviously are not *riparia* but the parts are either insufficient or too badly preserved to allow specific identifications.

Reference may be made to the remarkably well-preserved aedeagus of *H. riparia* dissected from a male abdomen. It is figured as a drawing from a photograph in figure 2*a* and may be compared with a figure similarly prepared from a modern specimen (figure 2*b*). In the latter the parameres have been drawn in an unnaturally divergent position so as not to conceal the median part of the organ. The aedeagus of this species was described by Balfour-Browne (1958) as one of the most complex in beetles. Attention may be drawn particularly to the two nearly similar-sized parameres with the left carrying a semicircular hollow bounded by a thickened rim, the long fringing hairs and the thick central organ with its peculiar anvil-shaped extension from which rises a thick spiral bristle. All these features are meticulously reproduced in the fossil dissection. Balfour-Browne expressed his belief that *H. riparia* is now parthenogenetic, because the aedeagus is too complicated to be functional. We need only point out that, if this is so, the same situation must have held about 250000 years ago and that, since then there has been no atrophy in this postulated functionless organ.

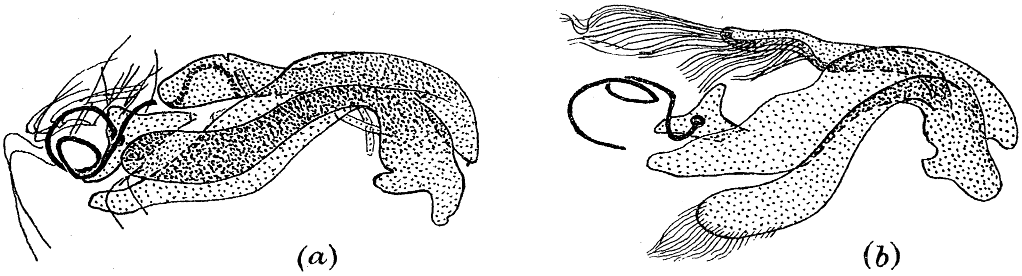


FIGURE 2. *Hydraena riparia*. *a*, Aedeagus from a Nechells specimen, traced from a photograph; *b*, aedeagus from a modern specimen, traced from a photograph but with the parameres diverged to show the central organ (both × 150).

Micropeplus caelatus (figure 14, plate 30). One left elytron having four ridges between suture and shoulder, with the spaces between the punctures shining instead of shagreened and dull as in *porcatus*.

M. staphylinoides. Two right elytra, strongly punctured, with three ridges between suture and shoulder and having the short length which separates this species from *fulvus*.

M. fulvus. A single left elytron with punctures and only three ridges, but not of the abbreviated length of *staphylinoides*.

Micropeplus sp. (figure 15, plate 30). There is one pronotum whose sculpture does not match exactly with any British species, nor with any species examined by us in the British Museum. It appears closest to *staphylinoides* but is slightly larger, more shining, and the pattern made by the ridges is different.

Stenus spp. Skeletal fragments of *Stenus* are quite common, but specific identification of isolated parts is only possible where the species possesses some unique character or combination of characters. Thus, the head of *bimaculatus* is wider than any other British species, it is crossed by two deep longitudinal grooves which delineate a broad elevated central ridge, and it is coarsely punctate with moderate micro-reticulation on the spaces between the punctures. On these characters, we have no hesitation in saying that a single head from II N. *d* matches exactly modern specimens of *S. bimaculatus* and no other British species. It is therefore given this name on the basis that where a specimen exactly matches a modern British species, it can legitimately take its name. *Stenus juno* is represented by one head, three right elytra and one left elytron. As a very large form, it can only be compared with a few British species. The head is distinctive in its size, shape and ornament, but even more specific are the elytra, where in the centre of each, the spaces separating the coarse punctures become transformed into strong ridges which form a rough spiral. *S. cicindeloides*, another large form, is identified on an elytron which shows the characteristic features of large but sparsely distributed punctae separated by wide and very smooth flat spaces.

S. brunnipes is identified on two male abdomens. The size, shape and puncturation of the tergites and sternites alone reduce the choice of name to a group of about three including *brunnipes*. In both examples the aedeagus was dissected out and in each case it conformed to *brunnipes*. A photograph of one of these (figure 16, plate 30) will allow comparison with modern dissections or illustrations thereof (e.g. Tottenham 1954, fig. 157).

In addition to the specimens mentioned above, there is a residue of 10 heads, 1 pronotum and 16 elytra which we are unable to name.

Reichenbachia impressa. This species is represented by one right elytron. The diagnostic character is the presence of an extra pore between the bases of the two striae.

Adelocera murina. Many fragments of the species were found, amongst which were 3 heads, 1 pronotum, 3 prosterna, 2 pygidia and numerous pieces of underside and elytron. All showed the characteristic ornament consisting of very deep, straight-sided punctures and very faint micro-reticulation on thick black integument. The shape of the prosternum, head and posterior angles of the pronotum are also diagnostic.

Melanotus rufipes. The single occurrence of *M. rufipes* consisted of fragments of elytra, probably only two elytra being represented. The shape of the apex and the strong interstrial puncturation, with the narrow band of very close punctures round the outside apical edge, were characteristic.

Prosternon tesselatum. One head and one prosternum of this species were found. The shape and puncturation of the prosternum, the form of the ridges over the antennae and the puncturation of the head, together with the size of the fragments, were regarded as definitive.

Dalopius marginatus. A single small prosternum was found. Amongst the British Elateridae the only species that this will fit exactly is *D. marginatus*. The size, shape and punctuation of this part are characteristic.

Dascillus cervinus. The identification of this species was made on two heads and a number of fragments of elytra. The heads have the Y-shaped mark with a shining triangle at the fork, the fine puncturation and the large antenna holes typical of *D. cervinus*; the elytra have an interstrial ornament consisting of numerous fine, punctured granules to which, in life, the scales are attached.

Ten mandibles were also found which do not fit those of any other species known to us but which match those of *D. cervinus* exactly. They are large, curved, have a tooth about one-third from the tip and the basal area is thickly punctured. Having regard to this match and the fact that *D. cervinus* was obviously present in some numbers, they have been confidently assigned to that species.

Elmis maugei. Two pronota in which the lines down the sides do not reach the base but turn in towards each other. In size and sculpture they agree closely with *E. maugei*, but we have no means of knowing whether they represent the variety *aenea* now found in these islands.

Esolus parallelopipedus. This species is represented by 3 heads, 12 pronota and 9 elytra. The heads were all found still joined to their pronota.

The chief features are the small size and elongate shape, the fact that the lines on the pronotum reach the basal margin, and the presence of a single line on each elytron similar to those on the pronotum.

Limnius troglodytes. The species of this genus have lines on the pronotum which reach the hind margin, and on the elytra are three lines of crenulations reaching from the base in the shoulder region, to the apex. The outer margin is also crenulate.

The species *troglodytes* differs from *tuberculatus* in size and in being much more evidently punctured, particularly on the pronotum. The most significant difference between *troglodytes* and *rivularis* lies in the different spacing of the three crenulate lines on the elytra, those of *rivularis* being equally spaced but the interval between the first two is wider than that between the second and third in *troglodytes*. In *rivularis* the lateral lines of the pronotum are more or less sinuate towards the base, whereas in *troglodytes* they are much more nearly straight.

Thirty-three pronota, 13 elytra and 2 heads were found, both the heads being associated with pronota.

Brachytemnus submuricatus (figures 21 to 23, plate 30). This non-British species was represented by 7 heads, 6 pronota and 20 elytra, as well as several underside parts.

The main diagnostic characters used were the very short rostrum and position of the scrobes, and the rasp-like sculpture on the declivity of the elytra.

Rhynchaenus quercus. The heads, of which 61 examples were found, were the main source of characters for the identification of this species (figure 18, plate 30). The chief diagnostic points were: the very narrow space between the eyes, the 'parting' in the puncturation behind the eyes, the length and shape of the scape and its place of insertion on the rostrum. The length and ornamentation of the rostrum were also helpful. Four out of the 22 pronota found were joined to heads.

The elytra were of the right size, shape, colour and ornament for *quercus* so that it was felt safe to assume that with them belonged the very numerous pronota. One aedeagus was dissected and matched that of a modern *R. quercus* exactly (figure 17, plate 30) whilst several femora with the characteristic teeth of *Rhynchaenus* were also recovered.

R. avellanae. As with *R. quercus*, the characters exhibited by the head of *R. avellanae* were found to be the most useful. The small scapes set very close to the head, and the sculpture of the rostrum were most important. Seven heads, 16 pronota and 25 elytra were found, 3 of the heads and pronota being joined together. All the pieces were black and shining and in a much better state of preservation than the brown *R. quercus* fragments.

Rhynchaenus sp. close to *pilosus*. Two heads of a *Rhynchaenus* were recovered which obviously belonged to neither *quercus* nor *avellanae*. The nearest match amongst the British species is *R. pilosus* but from this the Nechells specimens differ in the sculpture of the rostrum and the width and puncturation of the space between the eyes.

Rhamphus pulicarius. This species is included on the strength of one head. The rostrum is bent under the head, flattened and widest at its apex. The eyes touch and the antennae are inserted at the base of the rostrum. These characters, coupled with its very small size, are enough to put the specimen into the genus *Rhamphus*. It agrees in all details of its micro sculpture with our *R. pulicarius* but has not been compared with the few continental species.

Platypus cylindrus (figure 25, plate 30). Although only a small fragment of elytron of this species was found, it was a part that was quite characteristic. When the striae of *P. cylindrus* reach the elytral declivity they culminate in a row of teeth, and, further down the declivity, there is a large spike-like projection. Both these characters are to be seen on the Nechells example.

P. oxyurus (figures 26, 27, plate 30). The male of this non-British species is characterized by having the apices of the elytra prolonged into two serrated points, a feature of a most unusual kind. It was such an apex and a part of the elytron from the junction of the apex and main part that were found in the Nechells deposit. The latter fragment bears precisely the same ornament as the corresponding part of a modern specimen, but it is the unique apex which makes identification certain.

Mollusca. We are indebted to Mr B. W. Sparks for the identification of these. It is notable that only one species—*Bithynia tentaculata*—is represented by actual shell and then only by its opercula. The other records are provided by internal casts of pyrite from which the shell has been removed. The possible significance of this restricted distribution of molluscs, the absence of coiled shells of *Bithynia*, and the very limited vertical distribution of pyritized remains (affecting also the ostracods) will be discussed later.

Cristatella mucedo. Only one modern European fresh-water polyzoan produces statoblasts of the type illustrated in figure 11, plate 30. There seem to be no characteristics by which the fossils differ from the modern specimens, whose name has therefore been applied even in the absence of the adult colonies.

Complete statoblasts are not abundant—the majority have split and either the dorsal or ventral disk, edged with its hooked spines, is preserved. When these disks are measured, it is possible to assign most of them to either the ventral (larger) or dorsal (smaller) side. Measurements of modern specimens (as figured, for example, in Toriumi 1941, 1942, 1943) provide a mean ratio for the diameter of the whole statoblast, the ventral disk and the dorsal disk of 1:0·74:0·65. From this it is possible to say that the size-range for all but a very few of the hundreds from Nechells lies between 850 and 1060 μm. This is very normal, since at the present day the limits of variation seem to be about 700 and 1250 μm. The number of hooked spines in our specimens varies between 20 and 52 on a single disk but there seemed to be no correlation between the number of spines and the diameter of the disk as there apparently is in modern specimens where the dorsal side of the disk usually has fewer than its ventral counterpart.

Collections from IN2 contained a few (not included in the figures given above) which stood out as conspicuously large. Measurements indicated diameters for the complete statoblasts between 1120 and 1160 μm and this is clearly a distinct variety. Kraepelin (1887) attempted to distinguish a large variety with more spines (*idae*) from a small one with fewer spines (*gunuina*) and on grounds of size only, these few examples would fit into *idae*; but Toriumi (1943) demonstrated clearly that the varietal distinction was invalid, both varieties being part of a continuous series in which the spine number was not correlated to size. Our large specimens nevertheless have other features which differentiate them from the common type. In particular, the hooked spines are much longer and stouter (cf. figure 3*a* with figure 3*b*) and the end branching is different. Normally the spines carry four hooks, less commonly more than this or three or two, and nearly all our fossil specimens have four which branch off simultaneously (as in figure 3*b*). In the few specimens from IN2, however, each spine terminates in a long T-piece which then divides at its ends into two tiny hooks (figure 3*a*).

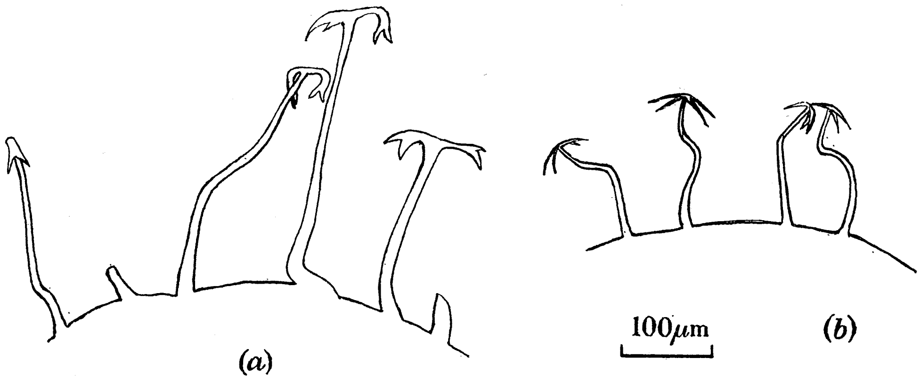


Figure 3. Hooked processes on the rim of the disks of *Cristatella* statoblasts. (*a*) The abnormal large form from the top of IN2; (*b*) typical *C. mucedo* which occurs throughout.

Whilst putting this variety on record, it is not yet possible to say if its limited occurrence has any significance in relation to the environment.

VI. General discussion of the fauna

The faunal list consists predominantly of insects and within these, beetles predominate. This coleopterous fauna is the earliest of any size to have been systematically examined within the British Pleistocene. The beetles from the Wolvercote Channel (Blair 1924; Sandford 1924) may belong to a time not much later, but the list is comparatively small. It should be stressed that the palynological and stratigraphical evidence at Nechells both point unequivocally to a Mindel/Riss Interglacial age dating back to the order of a quarter of a million years. It would not therefore have been surprising had the insects differed from those of present-day England in three respects,

(*a*) by containing species which have evolved, with obvious change, into those of the present day;

(*b*) by having species which have become extinct; and

(*c*) by including species which have now left England and migrated elsewhere.

The third condition is satisfied, but the other two are not. We have found nothing which is demonstrably an extinct species, though admittedly it needs more perfect and complete material to demonstrate that such is present than to recognize a living species. We have repeatedly been able to equate skeletal fragments with modern species because of the identity of the smallest structural details present in both fossil and modern examples, so that in these cases no detectable change has taken place. Essentially the Nechells fauna is a modern British one. This is an important if unspectacular conclusion, for it encourages the belief that future work can be done on earlier Pleistocene deposits with every hope that most of the insects can be identified by comparison with living forms when they still exist, or by failure of such comparison, adjudged to be extinct species.

VII. The fauna in relation to ecology

The general picture of the environment which Kelly (1964) derives from the lithology and palynology is that of a lake, probably ice-dammed at first, but becoming normal and shallower and passing eventually to an alluvial plain with small scattered pools and a sluggish river. Concurrently the climate changed from glacial to temperate but there is little preserved evidence of the return half of the cycle. The small animals found at Nechells throw additional light on the nature of the interglacial environment.

The fish remains are interesting, since they represent an order of animals that is not well documented from Pleistocene deposits. It is notable that not only have the fossils been referred by Dr P. H. Greenwood to five modern British species but the assemblage is one that might now be found in any lake or canal. The absence of fish from zones higher than IIN.*a* is discussed later, but in the lower zones their presence is strongly suggestive of the presence of still water.

Even more strongly suggestive of a lake are the ostracods which have been examined by Professor Sylvester-Bradley. The small assemblage is a lacustrine one but for the dominant species, *Cytherissa lacustris* (figure 12, plate 30), a large, deep and also a cold body of water is called for. Perhaps no other modern ostracod could point so clearly in this direction. It confirms Kelly's conclusion that during IN, the stage of glacial damming and in early IIN.*a*, there was a large lake with water which could have been up to 75 ft. in depth and was about 30 ft. at the close of IN, figures which were based on the lateral extent and height variation of the varved sediments and not in any way on the included organisms.

Throughout most of the sequence, from IN1 up to IIN.*c*, remains of the head capsules of larval chironomids are present and often common and these diptera are clearly amongst the earliest of colonizers of water after a glaciation (figure 4). As a group they also point to still though not necessarily deep water. It will be seen from figure 4 that there is a succession of genera as the fauna builds up. *Microtendipes* and *Tanytarsus* are the first to appear, closely followed by *Pentaneura*, *Anotypina* and *Chironomus*. *Microtendipes* and *Chironomus* build up to appreciable numbers compared with the others by the end of IN but at this point there is complete disappearance of all but *Chironomus*. The latter, however, persists, and increases to a maximum of abundance in IIN.*b*2 and IIN.*b*3. At the same time *Cryptochironomus*, *Dicrotendipes* and *Glyptotendipes* which had not been recognized in Zone IN, appear sporadically and in very small numbers at various points in IIN.

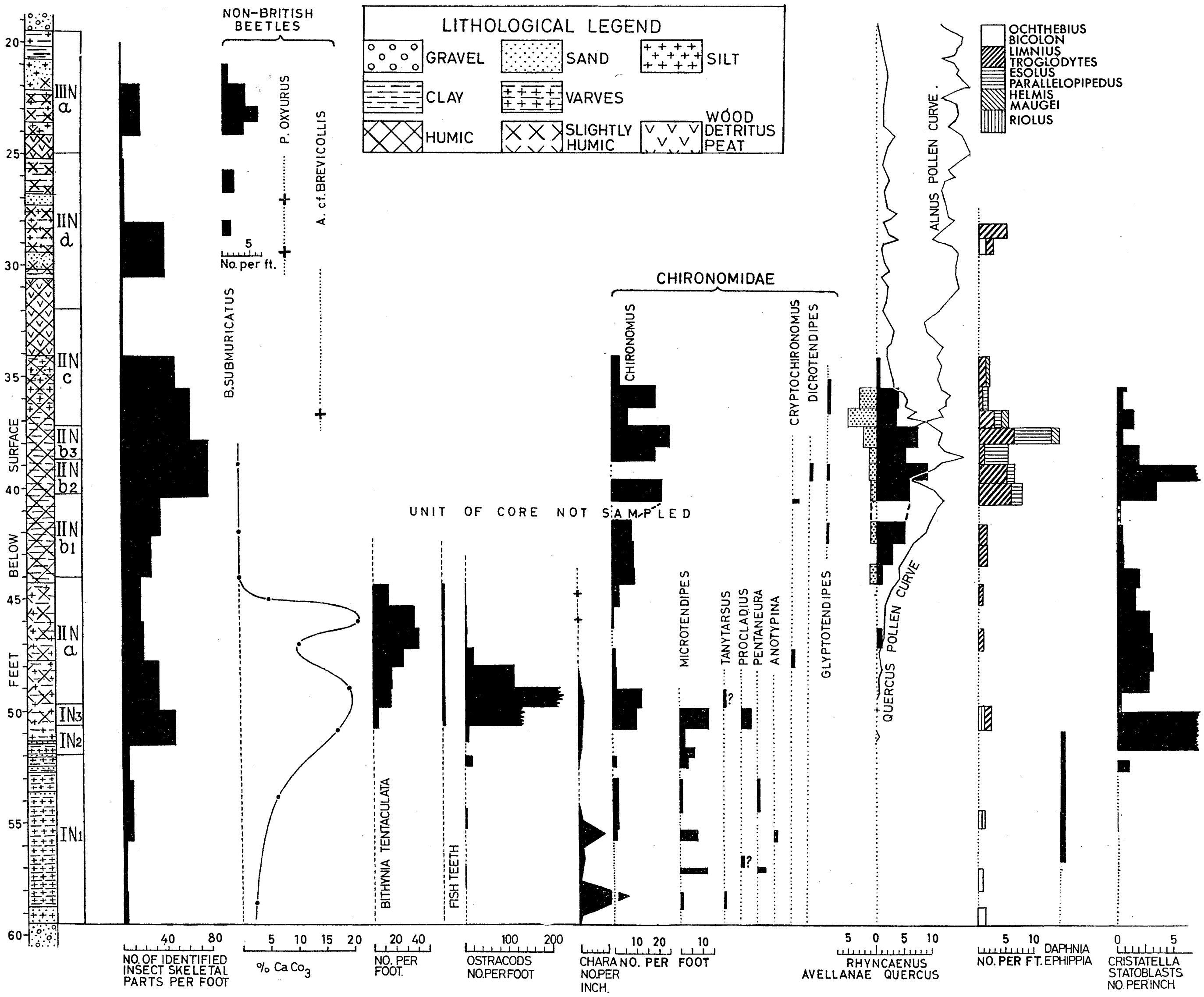


FIGURE 4. Distribution of various organisms in the Nechells borehole.

All the Chironomids disappear when the brushwood peat deposit occurs in IIN.*c* and thereafter there is no trace of them even in silty deposits of apparently suitable lithology. This may well represent the change from permanent lake to the conditions of sporadic flood plain pools.

Welsh (1935) and Thienemann (1954) have discussed the relation between chironomid larvae and the characteristics of the lake water in which they live. Recently Bryce (1962) has examined the chironomid content of a series of cores from the region of Malham Tarn, Yorkshire ranging in age from late III of the Late-glacial through parts of the Post-glacial. There should be a relation between the feeding habits of the chironomids and the organic content of the water and its bottom sediments for the *Chironominae* are predominantly detritus eaters, the *Orthocladiinae* live on algae and detritus which they scrape from other plants and stones, and the *Tanypodinae* are mainly carnivorous. At Nechells only the *Chironominae* and *Tanypodinae* have been recognized and it is perhaps significant that all of the latter (*Pentaneura*, *Anotypina* and *Procladius*) are restricted to the oligotrophic lime-rich sediments of Zone I N. Although *Chironomus* is also present in Zone IN, it achieves its great expansion in Zone IIN where the sediments indicate full eutrophic conditions, and it is accompanied by other newly appearing genera of the *Chironominae*.

It should be emphasized, however, that a change from oligotrophic to eutrophic conditions is not the only variation represented by the sediments. Subzones IN and IN2 represent an ice-dammed lake with the seasonal release of cold ice-melt waters; whereas late in Zone IN3 and Zone IIN there must have been some amelioration towards more temperate if by no means warm, conditions. Only future work will determine whether climate exercises a control on the distribution of chironomids at generic level. It is significant, however, that Bryce (1962) records a striking complementary fluctuation in the abundance of *Tanytarsus* and *Chironomus* which is clearly related to relative oligotrophy and eutrophy in a series of deposits which cover a period of consistently warming climate, the opposite trend to that which we have been considering at Nechells.

Molluscs are comparatively rare and are restricted to IN2, IN3 and IIN.*a*, but they too point to lacustrine conditions. It is notable, however, that only one species, *Bythinia tentaculata*, occurs in any quantity and this is represented entirely by the small, thick operculum and not by the large thin-walled spiral shell. It appears that even in the lake we must allow for currents sufficiently strong to winnow these two parts of the external skeleton after death.

Molluscs and indeed all organic remains are extremely rare in the earliest deposits (Zone IN1), reflecting the cold climate of the period immediately following the Mindel glaciation. These deposits are also calcareous, as would be expected of sediments derived from unleached tills. This calcareous content persists over the lowest 15 ft. and then declines rapidly to nothing at the top of IIN.*a*. This coincides with a sudden change from a small to a rich humic content in the fine-grained sediment. Clearly the IIN.*a*/*b* junction marks a significant change in the bottom conditions with an alkaline environment giving place to an acid one. It is significant that this same level marks the disappearance of all calcareous organisms—molluscs, ostracods and the oogonia of *Chara*—and also of fish teeth (see figure 4). We interpret this as a secondary effect. It seems unlikely that fish would disappear from the lake because its water had become acid, when it still clearly carried a supply of food in the form of plants and insects and in particular of chironomid larvae. To explain the complete absence of fish remains we must invoke post-depositional solution of bones and teeth in the acid bottom sediments, a process which would also remove any molluscs and ostracods if these existed.

In using animal remains to interpret the contemporary ecology, it must be borne in mind that the recorded fauna will divide into four portions. These are:

(*a*) the inhabitants of the water (which must be still or sluggish when fine sediments occur) at the place of deposition;

(*b*) the aquatic population of tributary streams which feed the water at the site of deposition. Remains of these will periodically be transported downstream;

(*c*) the inhabitants of the mud flats, sand banks and fringing vegetation which border streams and lakes. These, as a result of floods, have a high chance of incorporation in any subsequent deposits;

(*d*) the fauna of the 'dry' land—predators and feeders on dung, carrion, tree trunks, leaves, herbs and fungi—whose incorporation will be a matter of highly variable chance.

All these four elements are present and there is no marked trend of change in their relative proportions throughout the succession, except perhaps for those that indicate standing water. Kelly (1964) postulated that lacustrine conditions persisted until the close of II N.*c* but even during the riverine conditions of II N.*d* and III N.*a*, the intermittent deposition of fine sediment would only take place during times of flooding, with standing water. Hence we find that as far as water beetles alone are concerned, there is nothing which points clearly to this change of conditions; but if we take into account also the occurrence of ostracods, *Daphnia*, the mollusc *Bithynia tentaculata* and larvae of *Sialis*, caddis flies and chironomids, there is a marked diminution in the total lacustrine element after II N.*c*.

Contrasted with the normal water beetles are those like *Ochthebius bicolon* and the helmids which live attached to stones in fast-flowing streams. The distribution of these has been plotted on figure 4, and they are obviously unusually abundant in the upper part of II N.*b*, II N.*c* and II N.*d* (except for the unusual deposit of brushwood peat at the II N.*c*/*d* junction). Clearly the contribution of tributary streams becomes more important in the later phases of the Nechells sequence.

It would be expected that there would be a correlation between the occurrence of phytophagous beetles and the evidence for the presence of the appropriate food plant. This is usually so, with the first indication of the plant appearing often before the insect, as might be expected in view of their relative chances of preservation. In the case of *Platypus oxyurus*, however, the reverse is the case. This beetle now lives on the submontane slopes of southern Europe, feeding on the bark of the silver fir, *Abies alba*. Apart from a record of the cork oak, it would appear to be restricted to this one food tree. It is interesting that the beetle has been found twice in II N.*d*, yet *Abies* pollen does not appear until III N.*a* (and then only in trace quantities) and does not become abundant until III N.*d*. This latter zone does not, of course, occur in Borehole 7, so that there is no question of the specimens of *Platypus oxyurus* being drilling contaminants from above. Either *Abies* had already established itself in sheltered corners at II N.*d* time despite its failure to appear in the pollen diagram, or the beetle fed under the bark of another kind of tree.

Of the phytophagous beetles, only *Rhynchaenus quercus* and, to a less extent, *R. avellanae* occur abundantly enough to allow their distribution in time to be compared with that of their food plant. *R. quercus* feeds exclusively on oak, *avellanae* mainly on this though hazel (*Corylus*) is an alternative food. On figure 4 we have plotted the vertical variation in abundance of both species against the *Quercus* pollen diagram of Kelly. The beetle numbers are those of 'minimum individuals', that is, one head, one left elytra and one right elytron would only count as one, whereas two left elytra would indicate that two individuals must be represented. It will be noted how the beetles appear very soon after there is evidence of the advent of oak, and then increase in abundance sympathetically with the trees' own increase; but clearly the decline and disappearance of *Rhyncaenus* from the Nechells record is not to be similarly correlated with the disappearance of *Quercus*. After II N.*b*, oak pollen ceases to be one of the most dominant forms, but it is present in appreciable amounts up to the close of the borehole record. There must then be another explanation for the disappearance of *Rhyncaenus*.

We have indicated (following Kelly) on figure 4 how alder pollen achieves a great burst in abundance from the beginning of IIN.*c* and the decrease of oak pollen is partly due to the local influence of newly developed extensive alder swamps pushing the oak into the background. The disappearance of *Rhyncaenus* from the Nechells record, unlike its appearance, is not to be correlated with the presence or absence of its food plant but rather on the proximity of the latter to the site of sediment deposition. This factor must always greatly affect the apparent abundance of insects that feed on land plants. If insects eventually demonstrate their value in Pleistocene stratigraphy as pollen grains have done, the useful species will be those that live in water and at the water's edge, rather than on drier land.

VIII. The fauna in relation to climate

From a number of sites, Pleistocene insect faunas have been described in which clear evidence of some degree of colder climate is provided by the occurrence of species which now live wholly north of the site and in many cases are north-European and non-British (Coope, Shotton & Strachan 1961; Coope 1962; Pearson 1962).

A few species have been recognized, like *Diachila polita*, *D. arctica* and *Agonum sahlbergi*, which have now most restricted distributions in the Arctic. Yet although the lowest part of the Nechells sequence must from geological and palynological evidence represent really cold conditions, there are no insects which point clearly to this fact. There are, indeed, virtually no beetles at all from IN1 and IN2 where the scarce insect fauna is represented by larvae of chironomids, *Trichoptera* and *Sialis*. In IN3 there are records of *Dyschirius globosus*, *Ochthebius minimus*, *Limnius troglodytes*, *Riolus cupreus*, *Apion subulatum* and (?) *Dascillus cervinus*. All these now occur in Britain at least up to south Scotland, but the species of *Limnius*, *Riolus* and *Apion* do not seem to occur in the extreme north of the country. Their northernmost distribution in Scandinavia ranges from Lapland in the cases of *Ochthebius minimus* and *Dyschirius globosus*, to Denmark and southern Sweden for *Limnius troglodytes* and *Riolus cupreus*. It appears likely, therefore, that although the climate of IN3 could have been cooler than now, it must have passed out of the period of Arctic severity.

The abundance and diversity of insects are to some extent a reflexion of climate. On figure 4 we have plotted the total number of insect skeletal parts of all kinds, as a rough measure of the insect population. It will be seen that in the Mindel Late-Glacial phase represented by the varved clays of IN1 and the lower half of IN2, the number is small but it increases rapidly in upper IN2, reaches a maximum in the upper half of IIN.*b* and then to some extent declines. Superimposed on this general trend are two periods of exceptional paucity of remains (at the IIN.*c*/*d* and IIN.*d*/IIIN.*a* junctions) which have an explanation largely in terms of sedimentation. They occur in places where brushwood peats are extensively preserved—materials which, unlike the organic silts and muds, were deposited rapidly with consequent great attenuation of frequency of the preserved insect remains.

It has already been said that the Nechells insect fauna is very 'British' and because of this it seems likely that the climatic optimum represents conditions not very different from those of today. There are nevertheless three species which are certainly not British. On the single elytron (figure 20, plate 30) which we have compared with *Ataenia brevicollis* we should not place much stress. It is certainly an aphodiid not now occurring in this country and it closely resembles and indeed could be *A. brevicollis* which now occurs, as far as we have been able to find out, in the Canaries and Madeira; but it would be wrong to draw any conclusions about climate from such a disputable identification.

Much more conclusive are the identifications of *Platypus oxyurus* and *Brachytemnus submuricatus*, the latter of which is quite abundant. From figure 4 it will be seen that both appear late in the Nechells sequence. (We have neglected a single elytron of the second species which was found between 49 and 50 ft. and is so removed from all the others that it must surely be a contaminant.)

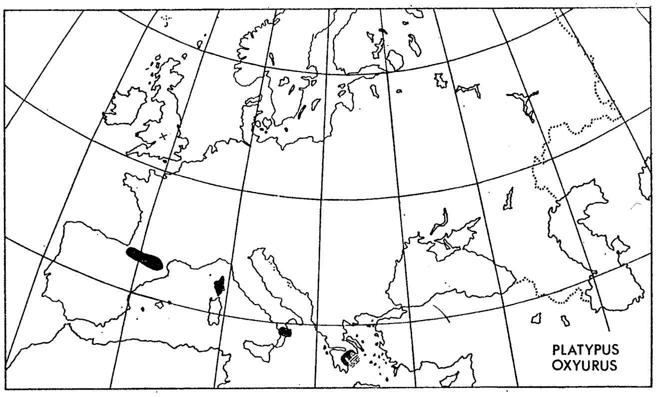
Platypus oxyurus now has a very discontinuous distribution in southern Europe which is shown on figure 5. It is an uncommon beetle feeding under the bark of *Abies* and, according to Eggers (1906), also under cork oak bark. It is known from the French side of the Pyrenees, the Plasencia province of Spain, Corsica, Calabria in southern Italy and parts of Greece including some of the islands. Although it has also been said to occur farther east in Turkey, Persia and India, Dr Karl E. Schedl doubts whether these records are correct. The scattered occurrence of this insect is to some extent due to the fact that it occurs at considerable height following the distribution of *Abies*, but there are many places where this tree occurs (for example, the Apennines of Italy, Switzerland, Austria and Germany) and where the beetle is unknown. In view, however, of its modern height distribution, its occurrence at Nechells cannot be taken as an indication of a really warm climate.

The third non-British species, *Brachytemnus submuricatus*, is another bark beetle. It is well represented in numbers and ranges from IIN.*a* to IIIN.*a*. Its foodplants are *Populus nigra* and *Salix alba*. The distribution of this species in Europe (figure 6) is as disjunct as that of *Platypus oxyurus* and is not dissimilar in pattern, but it may be very poorly known. It is the best indicator of what may be the climatic optimum of the interglacial in IIIN.*a*

The record of one British beetle, *Micropeplus caelatus*, from either IN3 or lower IIN.*a*, is worthy of mention. Its occurrence at Nechells is clearly associated with a climate which cannot have been more than cool–temperate, yet nowadays its British occurrence is restricted to S.W. Ireland, the most Atlantic part of the British Isles. On the continent its distribution is poorly known, but it is known to occur in Zealand and the extreme south tip of Sweden and in northern, central and south Germany (figure 7). Such a distribution appears to have no simple climatic control.

Of the animals other than insects, the ostracod *Cytherissa lacustris* is perhaps the best indicator of cold conditions, for as Professor Sylvester-Bradley points out in the appendix, it is characteristic of large bodies of cold water. It is restricted to IN2, IN3 and IIN.*a*, with its peak of abundance very marked at the IN3/IIN.*a* junction.

Occurring abundantly in IN1 and IN2 are the purse-shaped ephippia of *Daphnia*. We were unfamiliar with the technique of isolating fragments of the Cladocera (Frey 1960) until the raw material had been destroyed, though Dr Frey examined a residual



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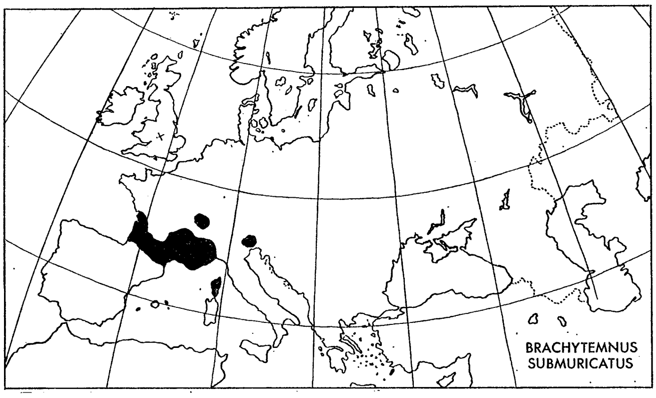

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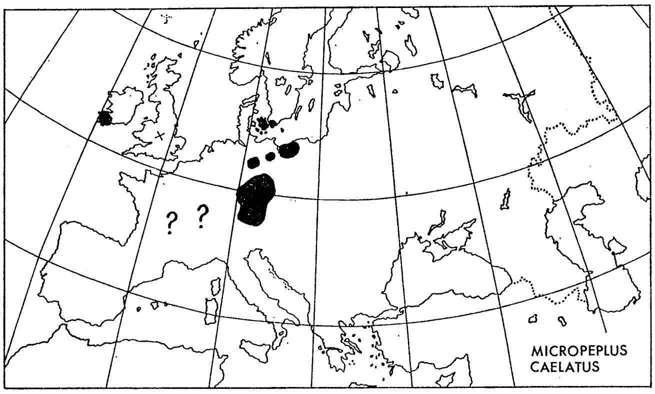

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FIGURES 5 to 7. Present-day distributions.

specimen of varved clay from low down in IN1 but found no evidence of these Crustacea. *Daphnia* as a genus is widespread in pools over a great range of latitude and so are several individual species. The only conclusion to be drawn from the ephippia is that there were marked seasons so that the animal found it necessary to produce resting eggs for its survival; but this it does now in latitudes ranging from Arctic to sub-Tropical. The restriction of ephippia to IN1 and IN2, which from other reasons discussed earlier is clearly the Glacial-Lake stage, cannot be explained simply by climatic factors. It is inconceivable that the climate was not strongly seasonal after IN2 and indeed throughout the sequence, and it is noticeable that another animal, the bryozoan *Cristatella mucedo* which develops statoblasts for overwintering, does this throughout the succession up to IIN.*c* (figure 4). The limited occurrence of *Daphnia* ephippia must have an explanation, but it is clearly not one that is simple. It is possible that the species represented is an Arctic one, but this cannot be deduced from the ephippia only.

It was hoped that the statoblasts of *Cristatella*, which occur from the extreme top of IN1 to IIN.*c*, would prove useful as indicators of climate. Toriumi (1943) claimed that both the capsule size and the number of spines varies sympathetically with the temperature of the water in which the statoblasts develop. He did not provide any temperature figures, but associated with the measurements on 1954 specimens were the dates on which the collection of material was made (from June to December). The variation of monthly isotherms in the Sendai area of Japan is as much as 21°C (from a July/August maximum to a January minimum) and Toriumi's measurements on both the diameter and number of spines are very clearly correlated with the seasonal temperature variation. Unfortunately, when we measured the Nechells specimens no systematic trend of variation in either of the factors was apparent even though the statoblasts occur through a succession in which the conditions must change from Late-Glacial to Temperate. It is possible, of course, that any reaction to a long-term climate alteration might be masked by a change in the time of the year at which maximum statoblast liberation took place.

We are indebted to the following who have identified specimens: Dr P. H. Greenwood (fish), Professor P. C. Sylvester-Bradley (ostracods), Dr D. Bryce (chironomids) and Mr B. W. Sparkes (molluscs). With Mr J. Balfour-Browne, Dr D. G. Frey and Dr G. R. Coope we have had stimulating discussions, and we have had helpful advice from Dr K. E. Schedl in Austria. To the British Museum (Natural History), the Hope Department of Entomology at Oxford and the Birmingham City Museum, we are indebted for repeated access to their insect collections. In the practical matter of drilling the borehole and manufacturing the special core tool, much help was given by C. Isler and Co., Ltd., and the Talbot Stead Tube Co., Ltd., while the Birmingham Corporation Engineer's Department gave access to temporary sections. Finally, the sinking of the borehole was financed by a grant in aid of research from the Royal Society and general support for the study of Pleistocene insect faunas is provided by a research contract with the Department of Scientific and Industrial Research.

Appendix

On *Cytherissa lacustris* (Sars) and other ostracods from Nechells

By P. C. Sylvester-Bradley

The fauna is dominated by the species *Cytherissa lacustris* (Sars). This species is accompanied by two species of *Candona*, which are at some levels (48 ft. to 49 ft. 11$\frac{3}{4}$ in.) present in numbers about equal to *Cytherissa*. Other ostracods are present in much smaller numbers. Two or three valves of *Cyclocypris* have turned up at several levels (between 48 ft. and 51 ft. 5$\frac{3}{4}$ in.).

Cytherissa lacustris is the characteristic ostracod inhabiting the deeper portions of large bodies of permanent fresh water, and in its present distribution is especially abundant in the more northern latitudes of Europe, Asia and North America (Sars 1925; Klie 1938, 1942; Bronstein 1947; Kazmina 1960; Van Morkhoven 1962, 1963; Staplin 1963; Swain 1963; Benson & MacDonald 1963). Although it occurs Recent in other situations, and has been recorded, for example, from canals (Brady 1868) its presence as the dominant member of the ostracod fauna is strongly suggestive of a large body of deep, cold water. In most localities, *Cytherissa lacustris* is the only species of *Cytherissa* present, but in Lake Baikal it is accompanied by a swarm of endemic species, having apparently taken part in the 'explosive evolution' that is such a feature of that lake (Bronstein 1930, 1939, 1947). Species of *Darwinula* and *Candona* are usually associated with *Cytherissa* as the only other ostracods able to colonize such an environment in Recent lakes (cf. Van Morkhoven 1962, Staplin 1963). It is perhaps surprising that *Darwinula* has not been discovered in the samples from Nechells. Triebel (1941 *a*) has recorded *Cytherissa lacustris* from the Interglacial 'Paludinenbank' of Fürstenberg on the River Oder, and it is there associated with *Darwinula stevensoni*, *Candona devexa* and *C. caudata*, and Staplin (1963) records it from Pleistocene cores from Lake Michigan associated with *Darwinula aurea* and *Candona crogmaniana*. Triebel (1941 *a*, *b*) drew attention to the variation in the strength of the ornament of the carapace of *Cytherissa lacustris*. In his Pleistocene material, 7 well-developed tubercles were characteristic, 3 behind the dorsal sulcus, 4 in front; but some of Triebel's examples were almost smooth, and devoid of tubercles. He pointed out that his material differed in this respect from Recent forms (which Klie 1938, quotes as characterized by only 4 tubercles). He believed the variation was phenotypically controlled. He saw little point in giving such variation nomenclatural expression. The Nechells material also shows great variation in both tuberculation and punctation. Tubercles are most strongly developed in the penultimate instar and most specimens which have tubercles have 5 or 6 in number, 2 or 3 in front of the dorsal sulcus, 3 behind; a few specimens have 7 tubercles, as in Triebel's material; many are almost smooth, especially in the adult stage. Punctation varies from strong to very weak. Recent material in the British Museum in the Norman collection from Britain and Sweden seems slightly larger than that from Nechells, but I can detect no other difference. It is interesting that Swain (1963) has described *Cytherissa*

TABLE 1. RELATIVE ABUNDANCE OF *CYTHERISSA LACUSTRIS* IN OSTRACOD FAUNA

Number of specimens (single valves or carapaces)

depth in core	*Cytherissa lacustris*	*Candona* spp.	other ostracods
44 ft. 3½ in.–45 ft. 3½ in.	1	0	0
45 ft. 3½ in.–46 ft. 3½ in.	1	0	2
46 ft. 3½ in.–46 ft. 5 in.	2	0	0
46 ft. 5 in.–47 ft. 2 in.	2	0	0
47 ft. 2 in.–48 ft. 0 in.	12	1	2
48 ft. 0 in.–48 ft. 9½ in.	27	29	4
48 ft. 9½ in.–48 ft. 11¾ in.	22	27	2
48 ft. 11¾ in.–49 ft. 10 in.	> 100	62	18
49 ft. 10 in.–50 ft. 8½ in.	> 100	8	2
50 ft. 8½ in.–51 ft. 5¾ in.	3	2	2
52 ft. 0 in.–52 ft. 6 in.	6	2	0
54 ft. 4½ in.–55 ft. 3 in.	0	3	0
57 ft. 0 in.–58 ft. 0 in.	0	1	0
60 ft. 3½ in.–60 ft. 10 in.	0	1*	0

*? contaminant

from the Pleistocene Gubik formation of northern Alaska in which the tuberculation seems to be developed even more weakly than in the Nechells material, although it is still clear in immature moults. Swain regarded this form as a distinct species (*C. simplissima* Swain). Van Morkhoven (1962) on the other hand, agrees with Triebel, and contends that such variation in the strength of tuberculation is phenotypically controlled; he compares it with the similar variation found in *Cyprideis torosa*, which is a euryhaline ostracod, almost smooth in brackish water, tuberculate in fresh water. So far as I know, salinity has not been found to control the variation in *Cytherissa lacustris*, a species which seems to be confined to fresh water. Possibly temperature may be a controlling factor. Material described from Post Glacial cores from Lake Erie by Benson & MacDonald (1963) seems very similar to that described by Swain from the Pleistocene of Alaska: the adults show very slight tuberculation, but 'instar stages show considerable shell sculpture in the form of many protuberances and much coarser reticulation than that of the adult' (Benson & MacDonald 1963, p. 22). Likewise, in Europe the adults so beautifully figured by Kollmann (1960) from the Pleistocene of Grosshöflein, Austria, are of the smooth variety.

Males of *C. lacustris* are not known from Europe or America, and Sars (1925) believed the species to be parthenogenetic. Males have been recorded from Lake Baikal (Bronstein 1930) but were subsequently referred to a different subspecies (Bronstein 1947; Kollmann 1960).

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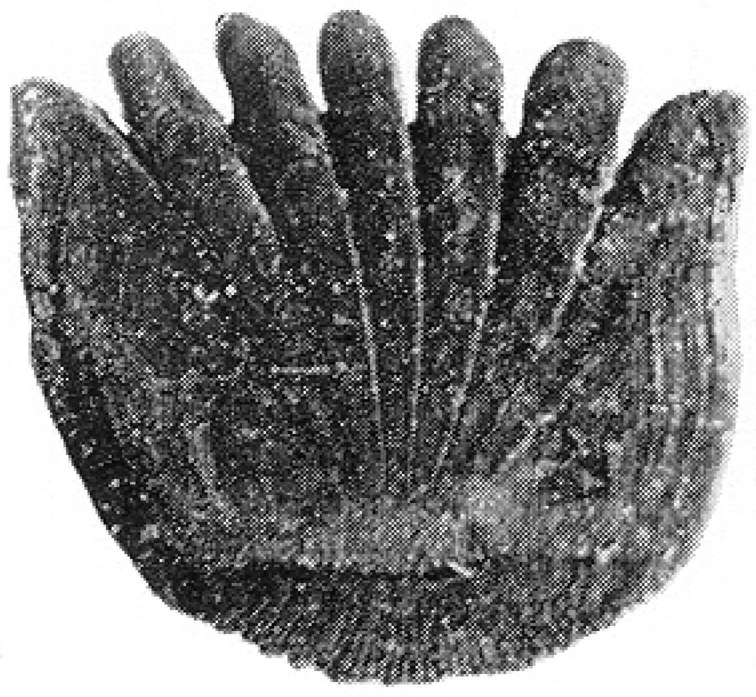
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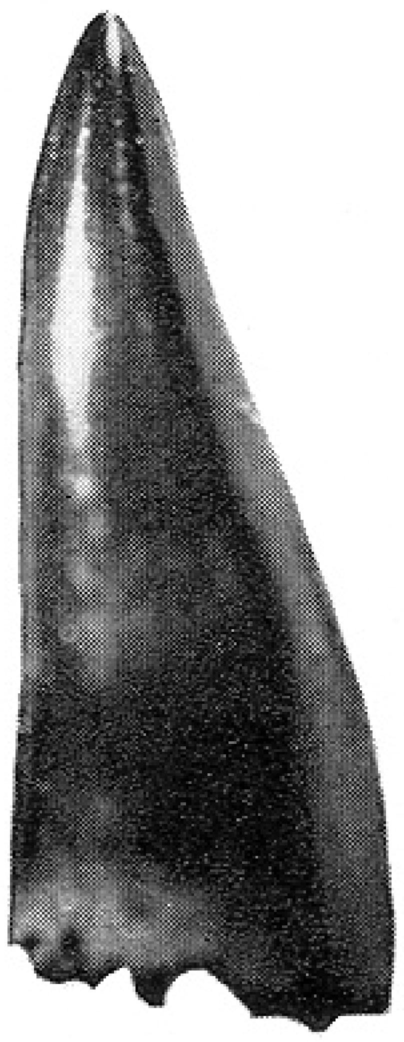
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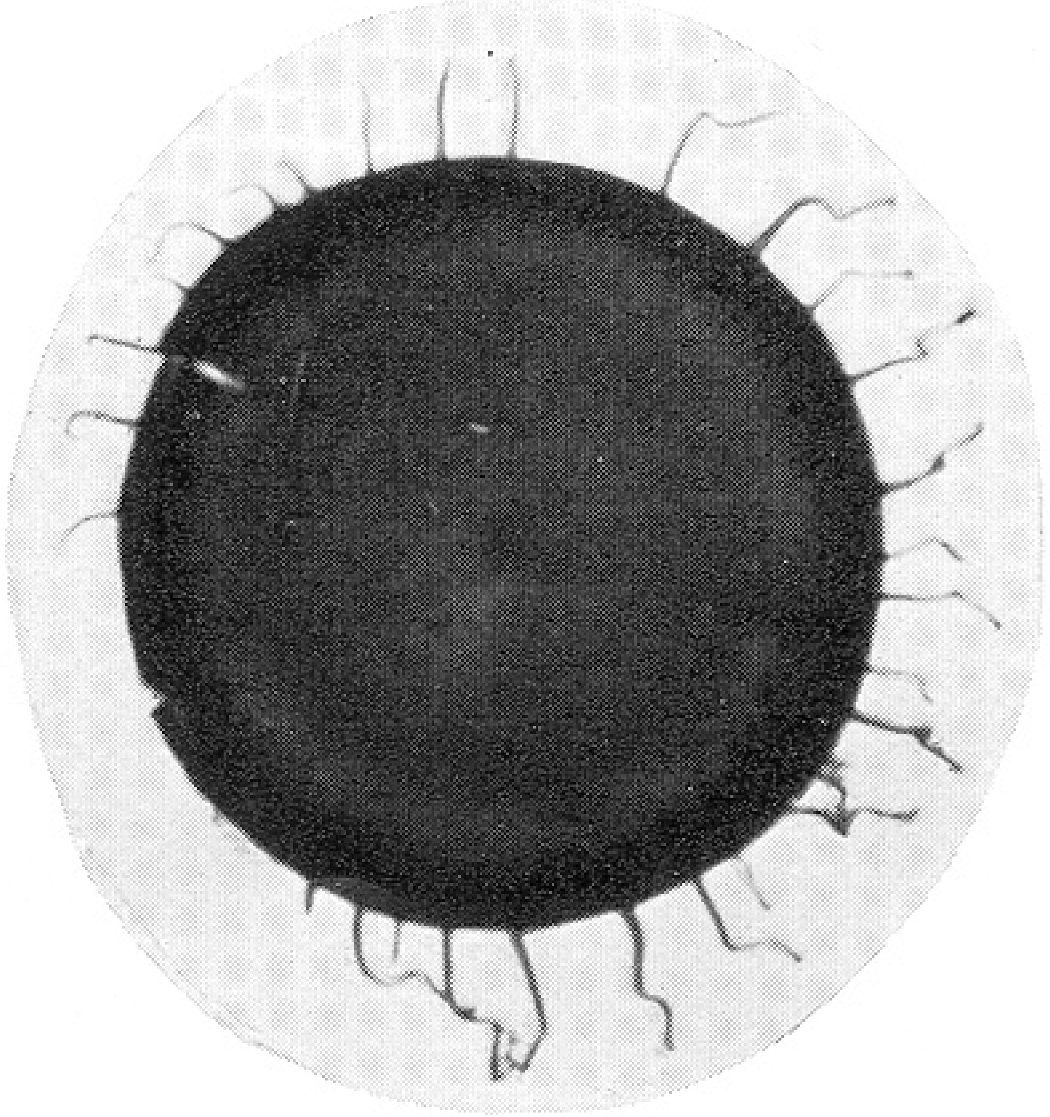
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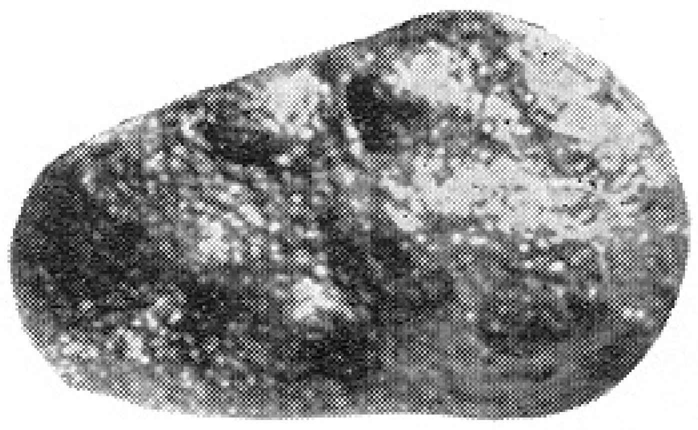
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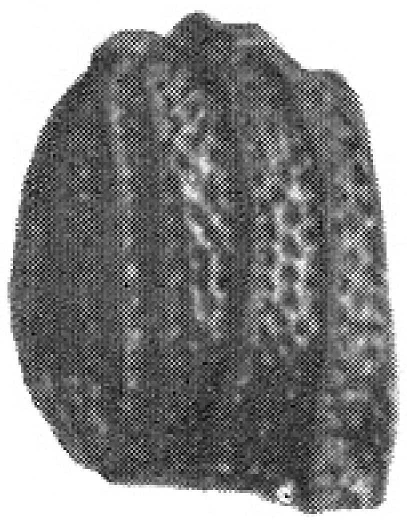
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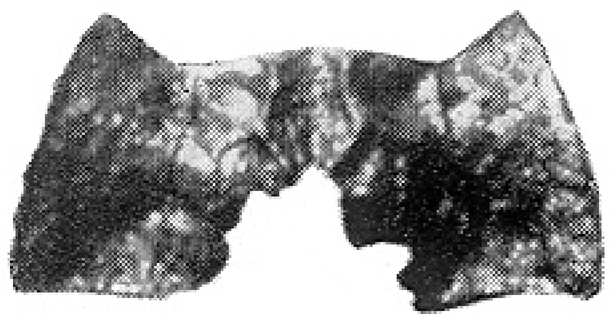
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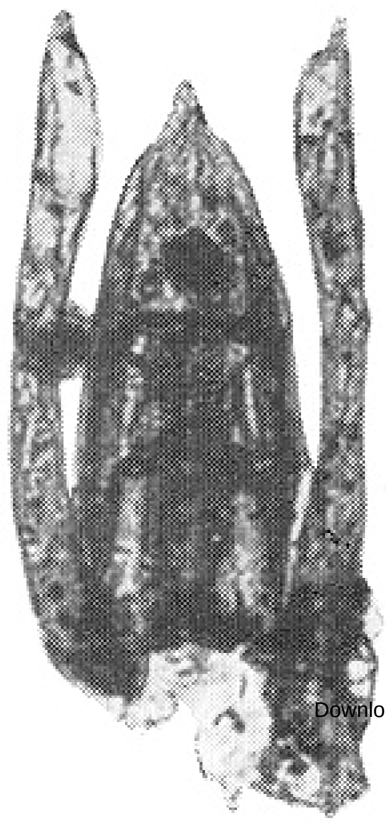
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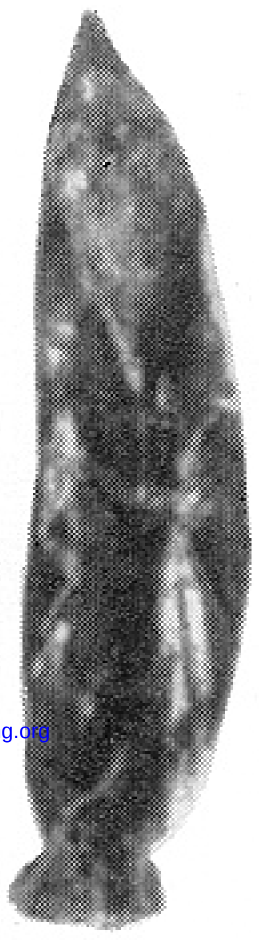
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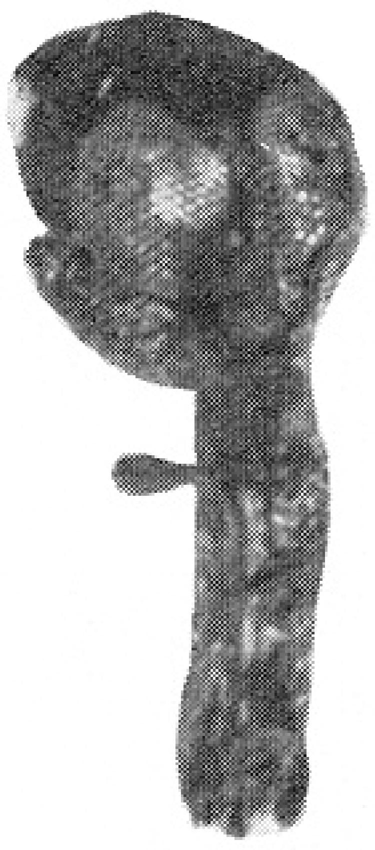
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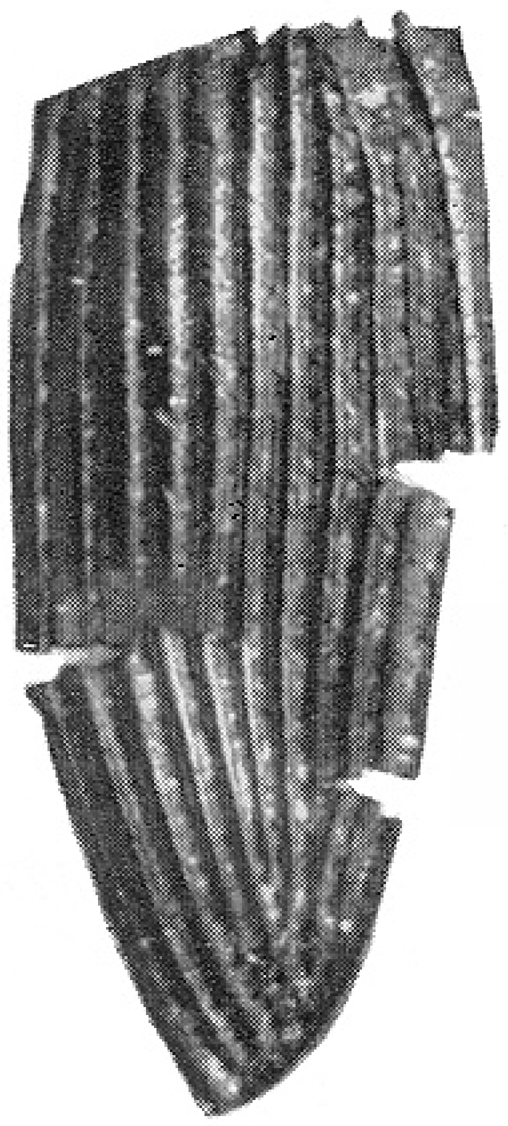
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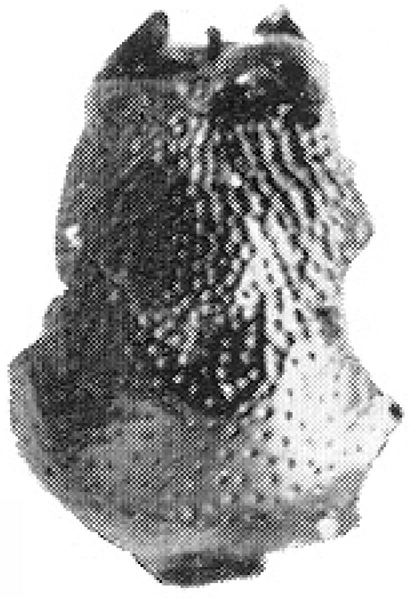
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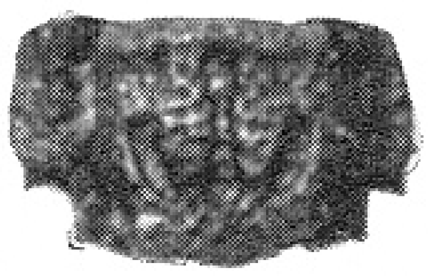
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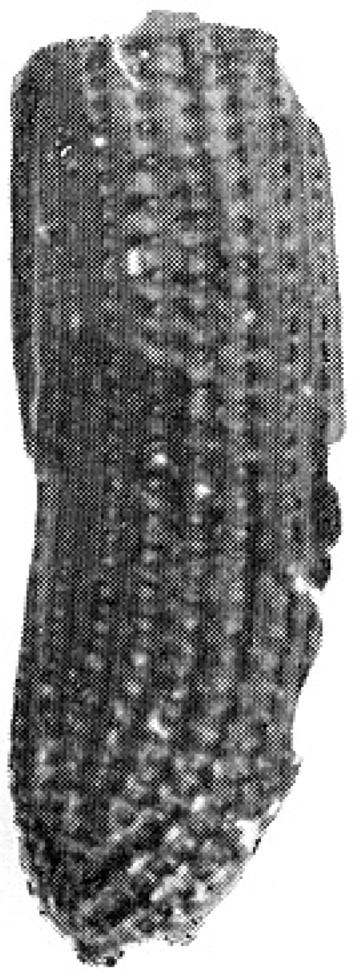
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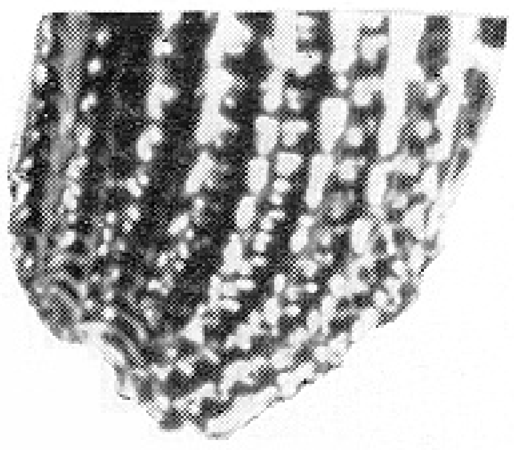
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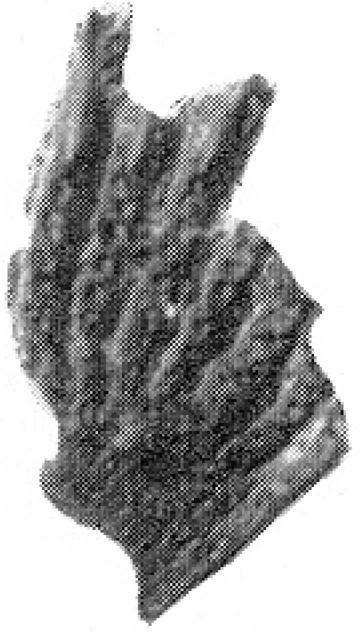
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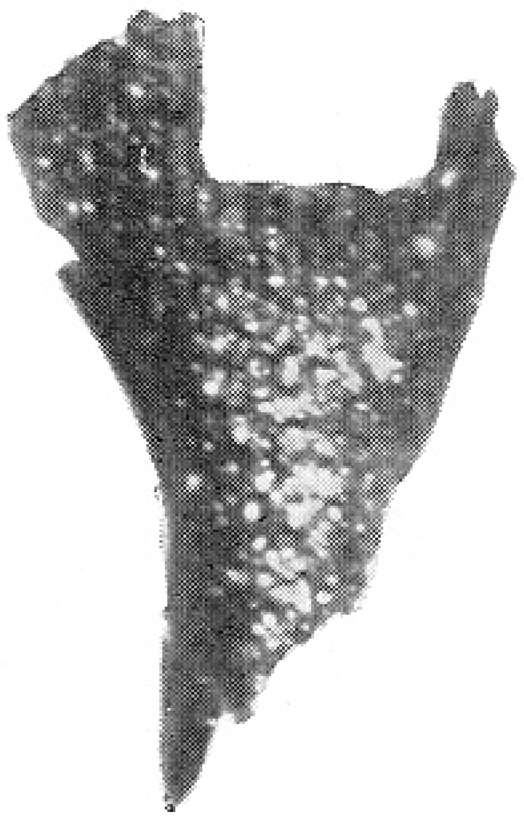
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