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The Preservation of Marine Vertebrates in the Lower Oxford Clay (Jurassic) of Central England

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The preservation of marine vertebrates in the Lower Oxford Clay (Jurassic) of central England

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[Plate 1]

Fossil vertebrate remains are found throughout the Lower Oxford Clay (Callovian, Middle Jurassic) in the Peterborough (Cambridgeshire) area, but occur more frequently in the Jason Zone at the base of the sequence. Five types of vertebrate preservation can be distinguished, most of which are lithologically restricted. Predation, scavenging and bacterial decomposition are responsible for the break-up of corpses. Current activity, storm events, firmness of substrate and oxygen content of sediment pore waters are factors affecting preservation.

1. Introduction

Fossil marine vertebrates are frequently found in bituminous shales and, in some formations, can be a major element of the nekton. While most palaeontologists are familiar with the often beautifully preserved marine reptiles from the European Jurassic bituminous shales, such as occur at Holzmaden, West Germany, Lyme Regis, Dorset, and Whitby, Yorkshire, such specimens occur infrequently compared with the numerous isolated bones and fragmentary skeletons that are also found at these localities. A detailed examination of the vertebrates from the Lower Oxford Clay (Middle Jurassic, Callovian) of central England shows that a broad spectrum of preservational styles can be recognized. Each of these styles is dependent on a variety of taphonomic, sedimentological and diagenetic factors.

Kauffman (1981) has shown that taphonomic studies on marine vertebrates can yield important palaeoecological and sedimentological data. He examined the fish and marine reptiles of the West German 'Posidonienschiefer' (Lower Jurassic, Toarcian) and drew conclusions about the level of oxygenation at the sediment–water interface. Unfortunately the material examined occurs mainly on large slabs of indurated shale which have been prepared from below, prohibiting examination of the upper surface of the specimen. In the Lower Oxford Clay it is usually possible to free the fossils from the matrix completely and examine all aspects of the specimens simply by washing.

Although extensive collections of Lower Oxford Clay vertebrates exist in museums throughout the world, most of these collections lack detailed field data, especially with respect to stratigraphic position and *in situ* attitude of the specimen. It became clear that to undertake a detailed study of marine vertebrate taphonomy and preservation, it would be necessary to collect fresh material so that intimate relationships between fossil and substrate could be recorded.

2. LOCALITIES

Most of the collecting for this study was undertaken in the large clay pits of the London Brick Company p.l.c. in the neighbourhood of Peterborough, Cambridgeshire (figure 1). Fieldwork was centred mainly on the Dogsthorpe brick pit to the northeast of Peterborough at National Grid reference TF 219019, with pits at Yaxley, National Grid reference TL 178932; Norman Cross, National Grid reference TL 173916; Whittlesey, National Grid reference TL 237970 and Orton, National Grid reference TL 165937 supplementing the collecting.

During this study the chance discovery of an ichthyosaur by a site workman near Milton Keynes, Buckinghamshire, at National Grid reference SP 892352, was also brought to my attention, and a systematic excavation undertaken. Material in the following museums has also supplemented this work: British Museum (Natural History) (BM(NH)); University of Leicester, Department of Geology collection (LEIUG); and Buckinghamshire County Museum (BCM).

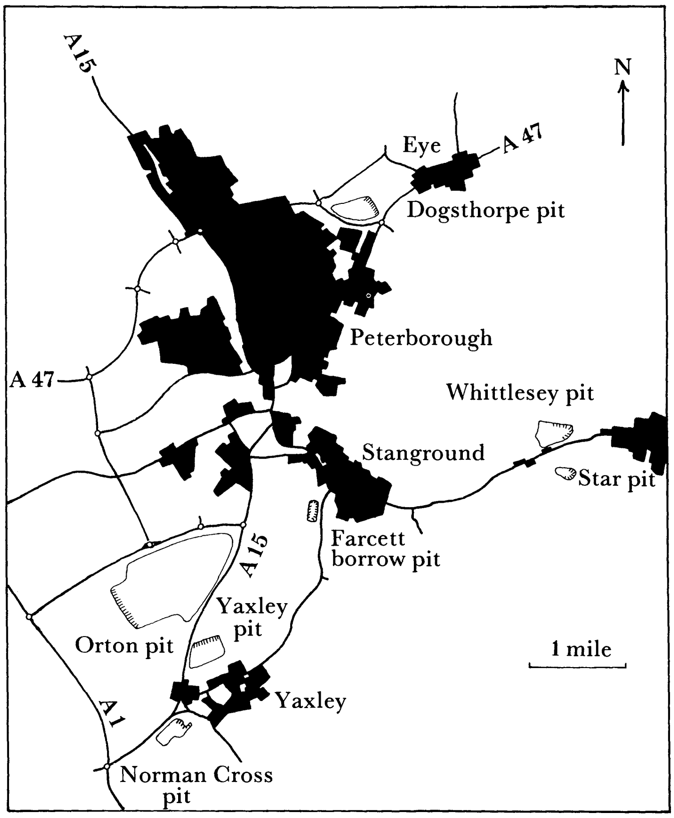


FIGURE 1. Map showing main vertebrate-yielding localities in the Lower Oxford Clay of the Peterborough area.

3. STRATIGRAPHY

Within the Peterborough district some 16 m of bituminous clays and fissile paper shales with thin sands and shell beds, make up the Lower Oxford Clay. The complete sequence can only be seen easily in the pits at Yaxley and Whittlesey. The Lower Oxford Clay has a diachronous base with the underlying Kelloways Sand (Callomon 1968), but at Peterborough this corresponds to the base of the Enodatum Subzone. The top of the Lower Oxford Clay is probably also diachronous with the overlying Middle Oxford Clay. At Peterborough the upper boundary lies somewhere within the lower part of the Athleta Zone. Figure 2 shows the main vertebrate-bearing horizons within the Lower Oxford Clay. All the vertebrate fossils from the Peterborough area south of the Tinwell–Marholm fault come from the Lower Oxford Clay and are therefore Callovian (Middle Jurassic) in age. Because of the confusion between lithostratigraphic (formation) names and stage names, many museum specimens have been erroneously labelled as Oxfordian.

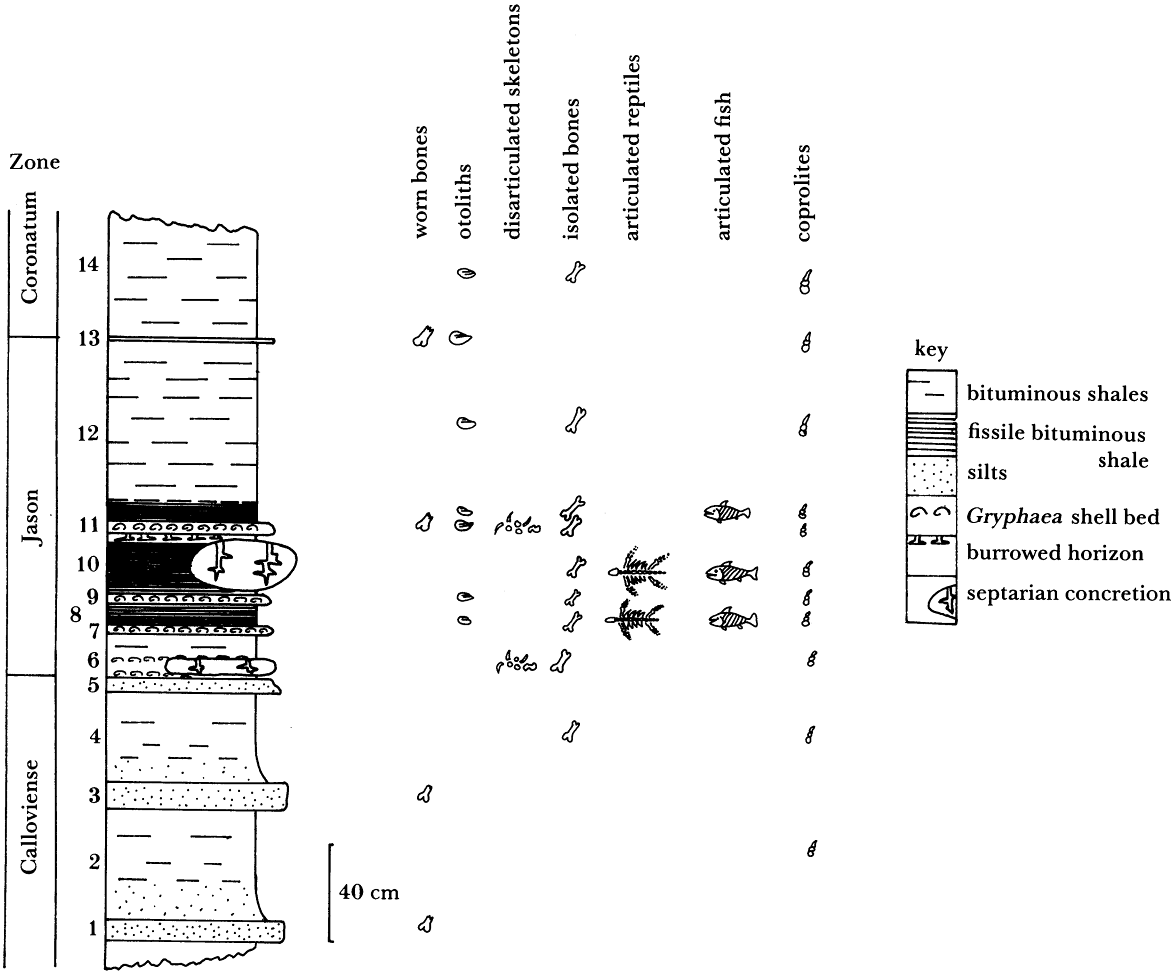


Figure 2. Generalized section through the basal beds of the Lower Oxford Clay of the Peterborough area showing the distribution of different preservational styles. Bed numbers correspond to those of Callomon (1968).

4. Marine vertebrates as palaeoecological indicators

Vertebrate skeletons are internal multicomponent systems usually composed of a single mineral phase, unlike most invertebrates which have external skeletons, usually consisting of only a few elements and can be made of a variety of mineral phases; for example, calcite or aragonite. Only the echinoderms can be compared with the vertebrates in a taphonomical study, but here the low magnesium calcite of their tests makes them prone to syntaxial overgrowths of diagenetic calcite and possible removal from the fossil record due to dissolution.

Vertebrate remains can, therefore, be useful as palaeoecological indicators, especially where invertebrates are absent due to diagenetic processes. As the vertebrate skeleton is internal, except for teeth and some types of dermal armour, it is not possible for the skeleton to be encrusted by epibionts until the animal has died, and the flesh decomposed sufficiently to expose the bones. Therefore, any encrusting of a bone must take place on the sea floor, and indicates the presence of oxygenated sea water. This avoids the argument that ensues with encrusted ammonites as to whether encrusting occurred while the ammonite was alive, or was *post mortem* on the sea floor (Seilacher 1981). The amount of encrusting of a skeleton allows estimates to be placed on the rate of deposition. If the encrusting epibionts, usually serpulid annelids and oyster-like bivalves, are large, it follows that the sedimentation rate must have been slow.

5. THE LOWER OXFORD CLAY VERTEBRATE FAUNA

Vertebrates have been recorded from the Lower Oxford Clay for well over 100 years. The fauna is diverse, consisting mainly of marine reptiles and fishes, although a poorly represented, but nevertheless diverse, terrestrial fauna of dinosaurs is known. There is also a single record of a pterosaur from this formation (Leeds 1956).

The marine reptiles are the most abundant and are now very well known, due largely to the industrious collecting undertaken by Mr Alfred Leeds at the turn of the century, which led to their being described in a two part monograph by Andrews (1910, 1913). This work has formed the basis for all of the more recent reviews of the fauna (Tarlo 1960; Appleby 1956; Brown 1981). The dinosaur fauna was described during the latter part of the last century and early part of this century (Woodward 1905), but reviews of some of the terrestrial elements of the fauna have appeared in more recent years (Charig 1980; Galton 1980).

The fish fauna is less well known, and was mainly described at the turn of the century (Woodward 1897). Fieldwork undertaken for this study has resulted in the discovery of several new fishes, including a new palaeoniscid and a giant pachycormid. Thies (1983) has discovered several new species of neoselachian sharks, based on fossil teeth from shell beds in the Lower Oxford Clay of Bedfordshire.

The often beautiful preservation of some of the fish and reptile specimens has been commented upon by Andrews (1910), but has received little attention from other palaeontologists, and has been virtually ignored by palaeoecologists and sedimentologists. In recent years, vertebrate palaeontologists have begun to realise the potential of taphonomic studies on vertebrate remains. Increasingly, papers are now appearing in which taphonomy forms at least a part of the discussion (Camp 1980; Milner 1980). Studies on the taphonomy of recent aquatic vertebrates (Schäfer 1972; Wuttke 1983) have shown that the decomposition and break up of carcasses is a complex process, and requires detailed observation. Attempts to do this with fossil marine reptiles from a bituminous shale have been made by Keller (1976) and Brenner (1976) on ichthyosaurs from the South German Posidonienschiefer.

6. VERTEBRATE PRESERVATION IN THE LOWER OXFORD CLAY

An examination of several *in situ* sauropterygians, crocodilians, ichthyosaurs and fish reveals that even in a seemingly monotonous sequence of clays, slight perturbations of current activity, oxygen level, firmness of substrate and rate of sedimentation can dramatically affect the style of preservation of the animals.

Although the range of preservational styles forms an almost continuous spectrum, it is convenient to recognize five preservational categories based on taphonomic and sedimentological criteria. These categories can be further subdivided by using diagenetic and compactional criteria, but the effects of these are not discussed here. Figure 3 shows five preservational styles recognized in the Lower Oxford Clay.

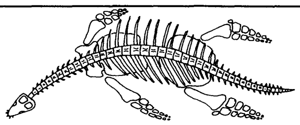
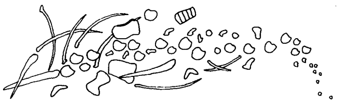
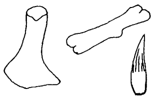
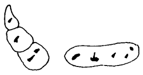
classification	pictorial representation	
articulated skeletons		all bones in true position
disarticulated skeletons		all or most bones moved
isolated bones and teeth		bones dropped from drifting carcasses
worn bones and teeth		eroded or biologically degraded
coprocoenosic accumulations		small bones in coprolites and etched otoliths

FIGURE 3. Table showing types of vertebrate preservation in the Lower Oxford Clay, with some of the characteristic features.

(*a*) *Articulated skeletons*

Articulated skeletons are those in which all of the bones of the skeletons are present, and lie in positions showing true bone-to-bone relationships with adjacent elements of the skeleton. Teeth are usually present within the jaws, and in some cases coprolitic material may be present within the gut region. In exceptional cases there may be evidence of soft-part preservation.

Such beautifully preserved specimens are rare, and restricted lithologically to only a few horizons within the Lower Oxford Clay. Most notably they occur within fissile highly bituminous shales of the Jason Zone, at the base of the Peterborough succession. These bituminous shales are interbedded with *Gryphaea* shell beds, which also yield large vertebrates. Within the fissile shales large sauropterygians, BM(NH) R 8621, (Charig *et al.* 1971), LEIUG 90988, figure 4*a*; crocodilians, LEIUG 90987 and LEIUG 90985, figure 5*a*, have been found, beautifully articulated, along with fish, a small *Lepidotes macrochierus* Woodward, BM(NH) P. 61398; *Asthenocormus* sp. BM(NH) 61563; and *Hypsocormus* sp. BM(NH) P. 61397.

The fish all display perfectly articulated tails, fins and scales, and each specimen contains coprolitic material within the body wall. In the case of BM(NH) P. 61398 only the lower surface of the fish is articulated, the scales of the upper surface (right side of the fish) having been disturbed slightly, probably due to the escape of decomposition gases.

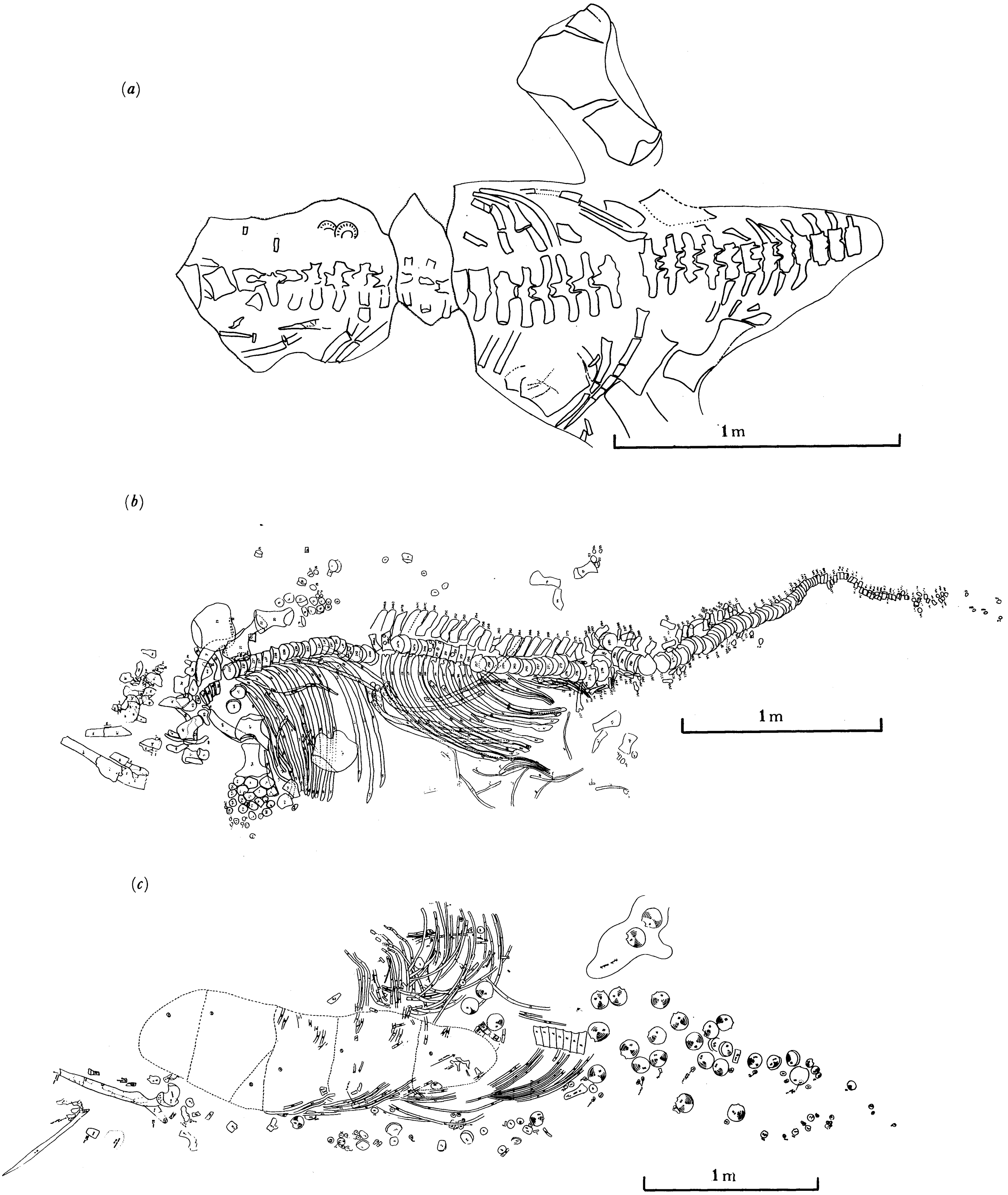


FIGURE 4. Outlines of articulated and partly articulated skeletons of marine reptiles from the Lower Oxford Clay. Solid and dotted lines outline septarian concretion. (*a*) Sauroptergyian cf. *Cryptoclidus* sp. LEIUG 90988, in concretion from bed 10. This specimen is fully articulated and shows true bone to bone relationships. (*b*) *Ophthalmosaurus* sp. from the Coronatum Zone at Peterborough. This specimen is almost completely articulated except for a few of the smaller elements of the paddles, the ventral rib cage, proximal caudal vertebrae and the skull. Many of the bones are encrusted with epibionts. (*c*) Partly articulated *Ophthalmosuarus* sp. from the Coronatum Zone at Milton Keynes. BCM 1001.1983. Only the disarticulated portions of the skeleton are encrusted with epibionts. The undersides of the articulated portions show evidence of soft-part preservation.

(*b*) *Disarticulated skeletons*

The degree of disarticulation between specimens can vary considerably. Skeletons may be completely disarticulated, but with all the bones present and in association, or may be only partly disarticulated with more coherent parts of the skeleton, such as interlocking vertebrae, remaining articulated. Owing to the large range covered by this category, there is less restriction lithologically, but there is a positive correlation between grain size and degree of disarticulation.

The *Gryphaea* shell beds within the Jason Zone represent non-deposition and reworking events and frequently yield large reptilian skeletons. These are always disarticulated partly as a result of reworking of articulated specimens from the underlying shale, and partly owing to storm activity upon specimens deposited during the event. A partly disarticulated *Ophthalmosaurus* sp. LEIUG 90984, from Dogsthorpe brick pit, and a juvenile plesiosaur cf. *Cryptoclidus* sp. LEIUG 90983, also from this pit, were found within the same shell bed. Figure 5*c* shows the position of the skeleton of *Ophthalmosaurus* sp. LEIUG 90984 and shows that parts of the skeleton, such as the shoulder girdle and a part of the rib cage, are articulated, but detached from the skeleton. This can be attributed to scavenging on the sea floor. The juvenile plesiosaur, LEIUG 90983, figure 5*b*, shows no articulation of the skeleton. This may be due to scavenging and perhaps storm activity. Higher within the sequence the deposit feeder bituminous shales, *sensu* Duff (1975), also yield disarticulated skeletons. The rare occurrences of vertebrates in the slightly calcareous shales of the Middle and Upper Oxford Clays are also usually disarticulated (Leeds 1956; C. Forbes, unpublished data). Figure 4*c* shows the skeleton outline of a large ichthyosaurian *Ophthalmosaurus* sp. BCM 1001.1983 from the deposit feeder bituminous shales of the Coronatum Zone at Milton Keynes, Buckinghamshire. This specimen is partly articulated, mainly on its left side, and partly disarticulated, especially towards the distal end of the vertebral column, the right side of the rib cage and the limbs. This should be contrasted with LEIUG 90984 in figure 5*c*. The Milton Keynes specimen BCM 1008.1983 remained partly articulated because the skeleton sank part of the way into the muddy sea floor, the enclosing sediment, therefore, holding the skeleton together after the integument had decomposed.

Figure 5*a*, shows part of the skeleton outline of a large *Metriorhynchus* sp. LEIUG 90985, which was discovered lying partly in fissile shales and partly in an overlying *Gryphaea* shell bed. The parts of the skeleton within the fissile shales, trunk, proximal part of the tail, shoulder girdle and limbs, remain fully articulated. The body cavity contains abundant cephalopod hooklets, presumably the gut contents. The parts of the skeleton that were found in the overlying shell bed, distal part of the tail only, were disarticulated, but very closely associated. This indicates that the carcass or skeleton had been completely buried by the fissile shale sediment, but partly re-exposed by storm activity rather than strong current activity. If current activity had been responsible for the reworking, the smaller elements of the tail (small vertebrate and chevrons) would have been washed some distance from the site of the articulated skeleton.

Here it is clear that the last two specimens mentioned lie both in category one and category two, but for different reasons: the first owing to a soft substrate and slow sedimentation rate, the second because of rapid sedimentation rate and reworking.

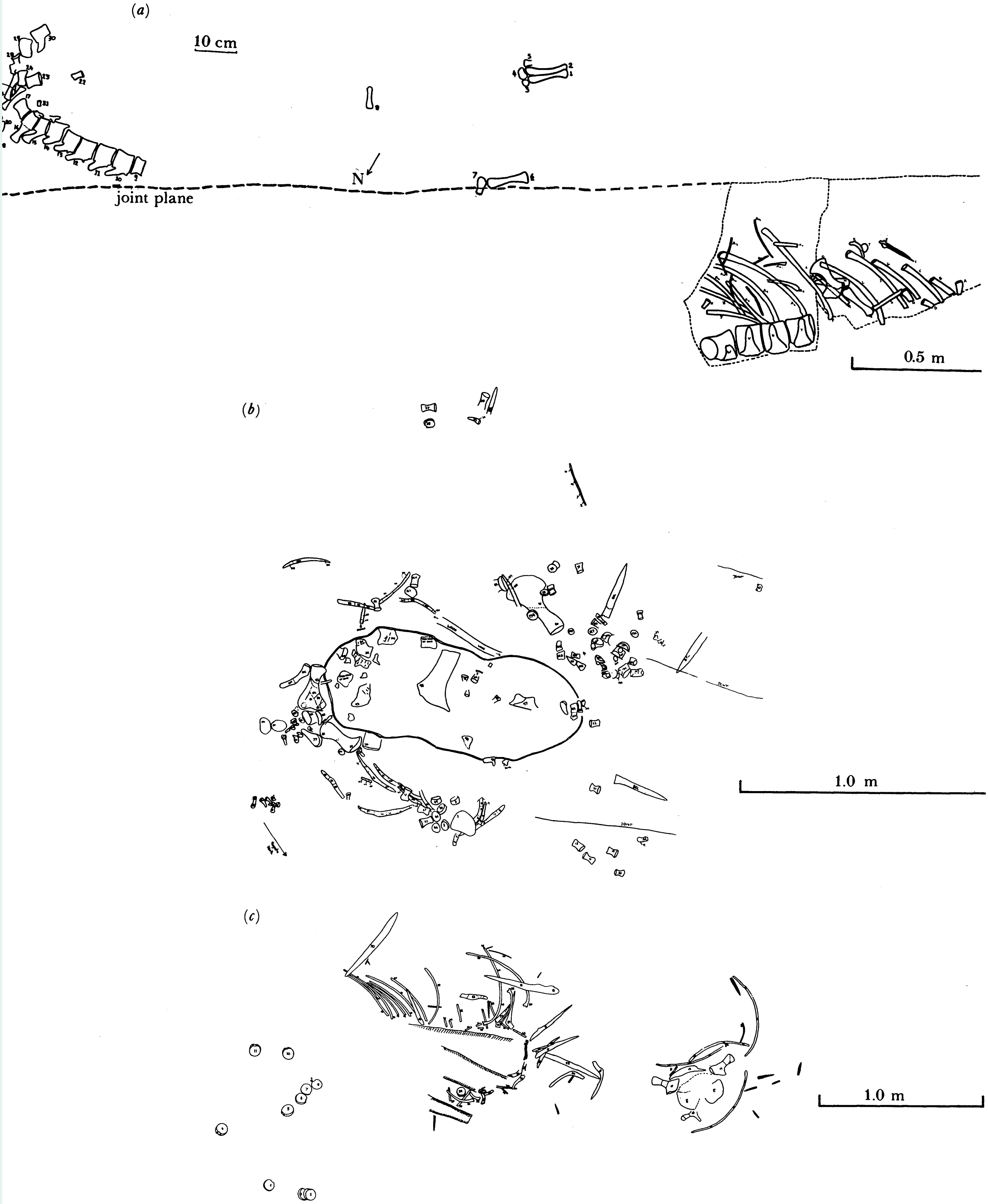


FIGURE 5. Disarticulated skeletons. (*a*) *Metriorhynchus* sp. LEIUG 90985, from Peterborough. The main, articulated, part of this specimen was found in fissile shales of bed 10, but the distal part of the tail was within the shell bed above (bed 11). Field numbering of bones to record position when collected. (*b*) Skeleton of juvenile plesiosaur from bed 11 at Peterborough (LEIUG 90983). (*c*) Skeleton of *Ophthalmosaurus* sp. LEIUG 90984, showing shoulder girdle detached due to scavenging. Grooves on surface of bed made by excavator indicated by solid lines with hatch marks.

(*c*) *Isolated bones and teeth*

Isolated bones and teeth of fish and reptiles occur frequently throughout the Lower Oxford Clay sequence. Many are perfectly preserved. Isolated bones probably dropped from decomposing carcasses floating in the water column (Schafer 1972), although some may have been derived from carcasses on the sea floor by scavengers. The most likely explanation for the occurrence of isolated teeth is that they were shed while the animal was still alive, as in present-day reptiles, or like the isolated bones they may also have dropped from drifting carcasses. In the Lower Oxford Clay this category does not appear to be lithologically restricted.

(*d*) *Worn bones*

Worn and eroded bones are common within the *Gryphaea* shell beds, nuculacean shell beds and the fine sands and silts that occur at the Kelloways beds–Lower Oxford Clay transition. These bones have been worn by attrition by comminuted shell fragments and fine sand. In the fine sands and silts at the base of the sequence the eroded bones are usually a pale yellow or buff colour on their surfaces, suggesting prolonged exposure to weathering on the sea floor. It is possible that some of the erosion may be due to biological activity, as some echinoderms and bacteria are known to feed on fish bone (Brongersma-Sanders 1949). Echinoid remains have been found in some of the shell beds.

(*e*) *Coprocoenosic accumulations*

Coprolitic material is abundant throughout the Lower Oxford Clay, but it is concentrated in the shell beds, mainly as irregular, buff-coloured phosphatic masses and spindle-shaped bodies often several centimetres long. Frequently these coprolites contain small bones and teeth.

The notable occurrence of vast quantities of otoliths in a nuculacean shell bed at the boundary between the Jason and Coronatum Zones at Peterborough may also be included in this category. Here the number of otoliths occurring in samples prepared for micropalaeontological examination far exceeded the number of fish teeth found in the same sample. This can be explained as being due to the concentration of otolith elements in the guts of marine reptiles and fishes. Within the gut of a fish-eating animal, phosphatic elements of the skeleton are preferentially digested by the gastric juices, and are removed from the fossil record, whereas the calcareous otoliths are only slightly etched (Fitch & Brownell 1968). Such a process is known to occur in recent cetaceans and is responsible for concentrating slightly etched sacculiths of a limited number of fish species, often within a very narrow size range. The otoliths found in the nuculacean shell beds are all slightly etched, of a similar size, and there is a greater concentration of drop-shaped otoliths compared with thin plate like-otoliths (figure 6, plate 1).

7. DISCUSSION

The distribution and types of preservation of Oxford Clay vertebrates should be examined in the context of the Callovian transgression as a whole. This is necessary if we are to investigate whether there are any correlations between the style of preservation, and depth of water or proximity of land. Such correlations might enable palaeontologists to predict possible fossil vertebrate occurrences in other formations.

At the start of the Callovian transgression, during deposition of the Upper Cornbrash, vertebrate remains occur only as isolated bones which are frequently worn. As the transgression continues into Kelloways Clay times there is an at present unexplainable paucity of vertebrates. A short period of sandy input into the Midlands basin during Kelloways Sand times sees a return of vertebrate remains. These are always isolated bones and teeth, and as in the Upper Cornbrash are usually worn.

During the transition between the Kelloways Sand and the Lower Oxford Clay vertebrate remains become more abundant, and there is a positive correlation of degree of skeleton articulation with organic carbon content of the sediment. Diversity is also at its maximum at this level.

Although giant marine reptiles occur throughout the Lower Oxford Clay, over most of the outcrop, they are found in greatest abundance in the Jason Zone in the Peterborough area. A diverse and exceptionally well preserved fish fauna is known from Christian Malford, but little is known about the stratigraphic range or abundance of the material. After Jason Zone times there is a drop in the amount of organic carbon in the Lower Oxford Clay to around 4% (Fisher 1983). The number of vertebrate finds in the Peterborough district from these levels appears to be reduced, but it must be emphasized that there is less exposure of the higher beds which may bias this correlation.

The Upper Callovian and Lower Oxfordian Middle and Upper Oxford Clays are non-bituminous, normal clays (Hudson 1982) in which vertebrate remains are exceedingly rare. Although this may in part be due to the lack of exposure at the present day, many pits were operational in these beds at the time that the Leeds collection of fossil vertebrates was amassed. Leeds (1956) only records two partial skeletons from the Middle Oxford Clay.

The increase in abundance of vertebrates in the Lower Oxford Clay correlates closely with the organic carbon content of the sediment, which may be as high as 14%. Such a correlation can also be found in the vertebrate-bearing horizons of the Upper Lias (Toarcian) of Yorkshire (Benton & Taylor 1984). If this correlation reflects high productivity in surface waters, due perhaps to the influx of nutrients from nearby landmasses, it should be possible to predict potential vertebrate fossil Lagerstätten in other thick argillaceous sequences. Palaeontologists should work with sedimentary geochemists to find those parts of clay sequences with high organic carbon content that are punctuated by storm deposits and benthic events which allow vertebrate remains to be concentrated.

I thank the London Brick Company for allowing me to carry out fieldwork in their large pits, and particularly thank their chief geologist Mr J. Horrell who has helped me in the field and given so much general assistance. When excavating large marine reptiles, many hands are needed, and I would like to thank all who helped me in the field, especially Mr A. Dawn and Mr R. Branson. Arthur Meadows drove the Landrover. I would also like to thank Dr R. G. Clements for allowing me to use some of his data, and my supervisor Dr J. D. Hudson for his continued help and encouragement. This work was carried out during tenure of a University of Leicester Research Scholarship.

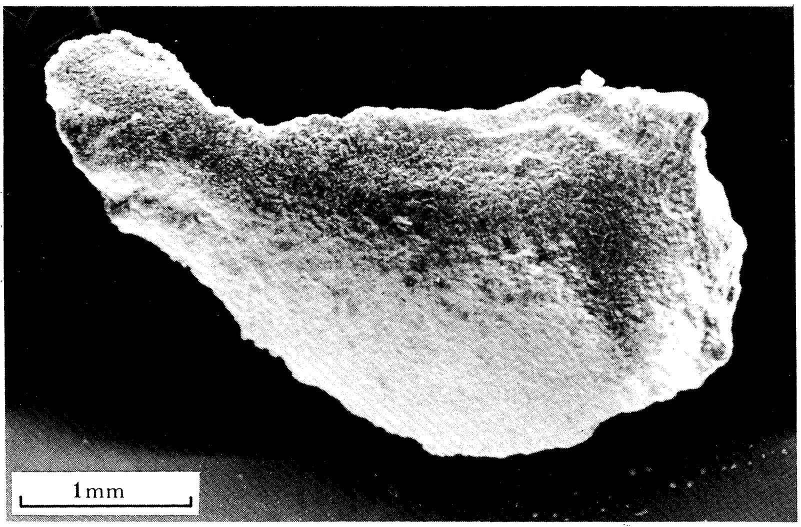


FIGURE 6. Etched otolith of holostean fish from shell bed at top of Jason Zone (bed 13), Peterborough.

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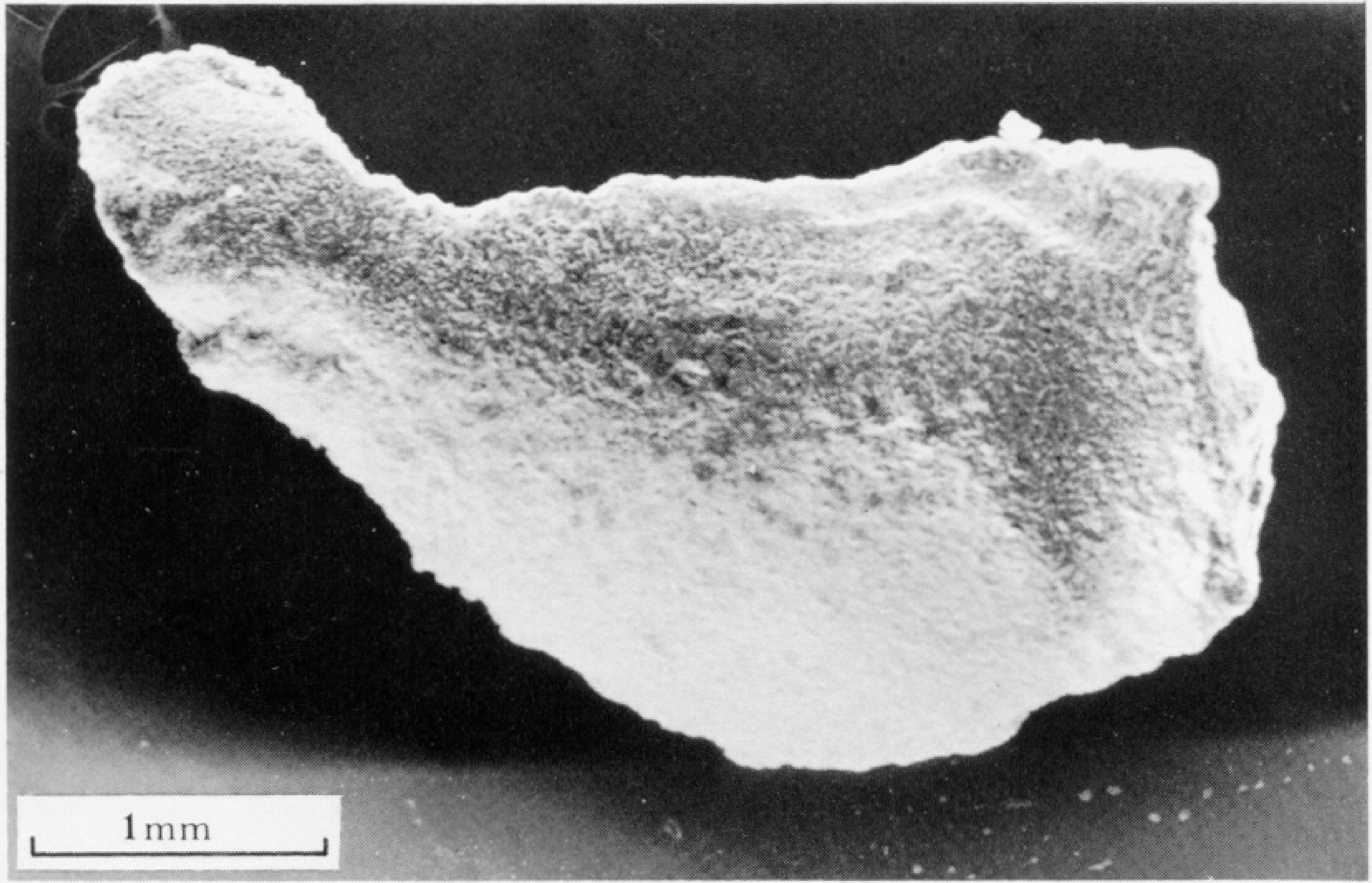

GURE 6. Etched otolith of holostean fish from shell bed at top of Jason Zone (bed 13), Peterborough.