Pliosaur Stomach Contents from the Oxford Clay

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Abstract: A new specimen of pliosaur from the Lower Oxford Clay of Peterborough, Cambridgeshire, contains stomach contents, including cephalopod hooklets and gastroliths. The specimen is associated with organic matter thought to be derived from the decomposing carcase, and shows some indication of soft tissue preservation in the region of the thorax. This is the first pliosaur from the famed reptile beds of Peterborough to be scientifically excavated.

Pliosaurs are an important element of the Lower Oxford Clay (Middle Callovian, Middle Jurassic) marine reptile fauna. They were the top carnivores of the food web, and at that time displayed a diversity of dental morphologies, presumably reflecting a variety of trophic specializations (Tarlo, 1960; Massare, 1987). However, direct evidence of diet is rare. In this paper I report a new find from the Peterborough district in which stomach contents and some soft tissues are preserved associated with a partial, partly articulated example of a young pliosaur, tentatively identified as (cf.) *Liopleurodon* sp.

The new pliosaur was discovered in a waste disposal site at Dogsthorpe, Peterborough, in 1990 by workmen of Shanks and McEwan (Waste Services) Ltd (Dawn, 1991). The site was formerly a quarry operated by the London Brick Company (X in Fig. 1), and is known for its well preserved vertebrate fossils (Martill 1985, 1986a; Martill and Hudson, 1991). The pliosaur is registered as PETCM R.296 (Peterborough City Museum and Art Gallery, Priestgate, Peterborough PE1 1UA). It was placed on temporary display in 1991, and the specimen and its excavation were described in a popular booklet (Duff and Chancellor, 1991).

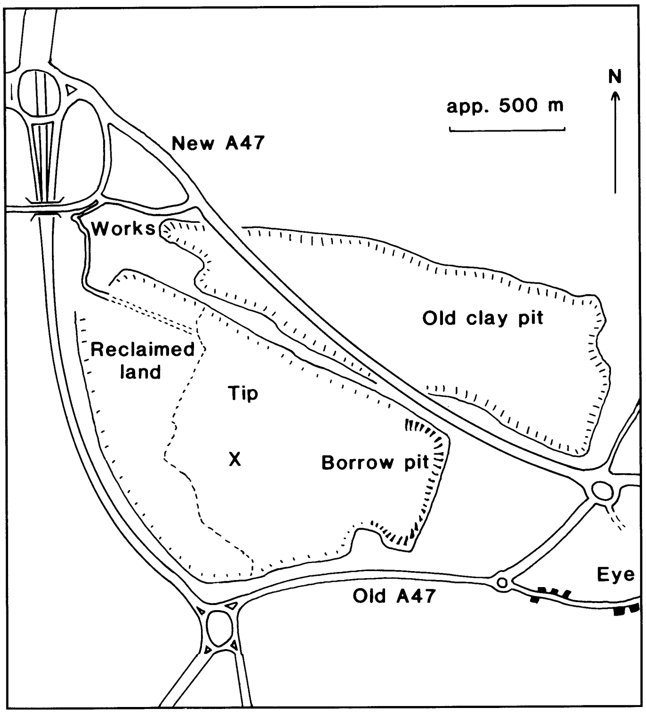

Fig. 1. Map showing location of the new pliosaur discovery, and the final outline of the now abandoned Dogsthorpe clay pit.

Stratigraphic horizon and material

The specimen occurred wholly within bed 10 (following the bed numbering of Callomon, 1968) of the Lower Oxford Clay (Fig. 2). This bed lies within the *jason* Subzone of the *jason* Zone, Middle Callovian, and is a highly fossiliferous, organic-rich, fissile mudstone, that is frequently well exposed in the bottom of the brick pits of the Peterborough district. The bed is rarely more than 0.2m thick, but is particularly well known for fossil vertebrates including fish and reptiles. Large (up to 3m diameter × 0.3m thick) carbonate concretions rich in

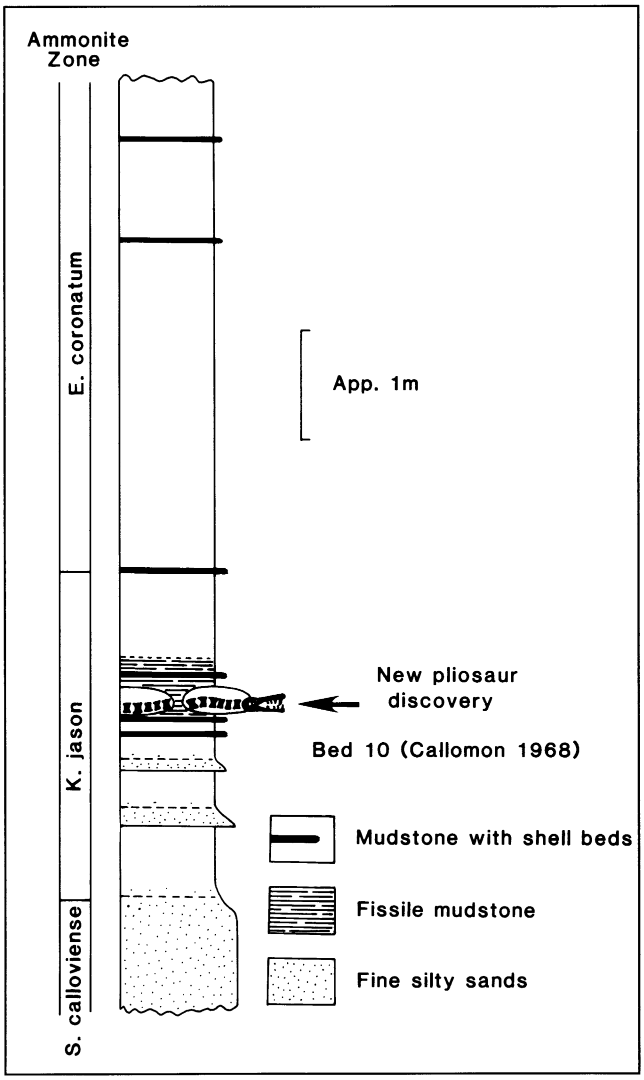

Fig. 2. Stratigraphic section for the Dogsthorpe clay pit with the position of the new pliosaur skeleton, PETCM R.296.

pyrite occur in this bed. They are of early diagenetic origin (Hudson, 1978) and one such concretion enclosed the skull, while another concretion enclosed part of the thoracic region of the skeleton. These concretionary masses protected both the skull and the stomach area from severe damage by compaction. The concretion containing the stomach region was particularly interesting as it displayed a thin band of shiny dark material on a fractured edge.

Bed 10 contains abundant vertebrate fossils (Martill, 1985), and was deposited under conditions of high organic productivity during the early stages of a marine transgression (Hudson and Martill, 1991). Even more vertebrates (but generally less well preserved) occur in the overlying bed 11. This elevated abundance may be the result of storm winnowing of a formerly thicker sequence in bed 10 (Martill, 1986b).

The preservation of vertebrates in bed 10 is particularly good, in that skeletons are usually complete, and are often articulated. This condition is thought to be in part due to the sinking of dense carcasses into a soupy substratum, removing the carcase from damaging macro-scavengers, epizoans and epiphytes (Martill, 1987).

Preservation 1. The skeleton

Many skeletal elements enclosed by shale were disturbed by digging machinery and the bone bearing concretions were bulldozed to a nearby spoil dump before the fossil was discovered. However, it was possible to record the *in situ* attitude of a considerable portion of the skeleton, and to infer the position of the bone-containing concretions by the shape of the remaining holes in the ground (see Fig. 3). Bones not found *in situ* were simply bagged up and collected. Bones found *in situ* were numbered and their position recorded in the field on an acetate sheet at a scale of 1 to 1.

The postcranial skeleton lay on its ventral surface, and the skull on its left side. The teeth are still set in their sockets, and the lower jaw remains articulated with the skull. The mouth is closed.

The first four cervical vertebrae are articulated with the skull. The remaining cervical vertebrae are enclosed within concretionary limestone, and so are not clearly visible. Fifteen dorsal vertebrae are partially articulated, but appear to be detached from the cervical vertebrae by a gap of some 600mm. The caudal vertebrae are loosely associated and appear to be continuous with the

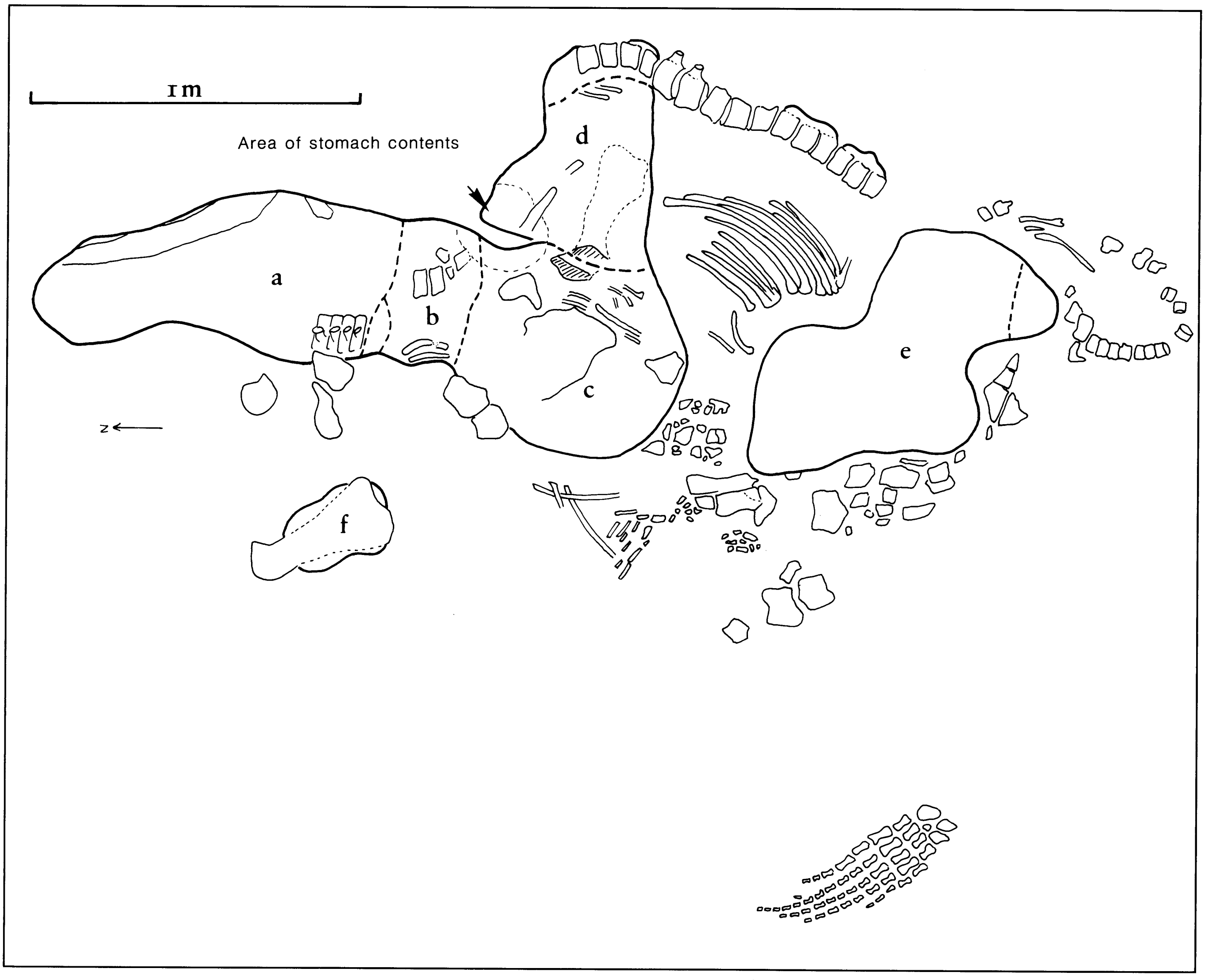

Fig. 3. Plan of the skeletal elements of the new pliosaur, as found. Data recorded by Mr. Ron McKenna.

thoracic vertebrae. The distal elements of the caudal skeleton are disarticulated. The general attitude of the backbone is one of a sigmoidal curve with a displacement to the left anteriorly. The thoracic ribs have been displaced somewhat from the vertebral column, but remain associated. It remains to be established whether or not this displacement was due to skeleton collapse after the decomposition of ligamentous tissue, to predation, or to scavenging.

The pectoral girdle is partly contained within concretionary limestone and has yet to be prepared. Consequently its position relative to the skeleton is not yet precisely established. However, it lies in approximately the correct position behind the skull. The pelvic girdle also lies within a concretion, but is sufficiently well exposed to show that the ?right ilium, ischium and pubis are superimposed on as yet unidentified pelvic girdle elements of the other side.

The appendicular skeleton comprises the right humerus in approximate articulation with the pectoral girdle, and a possible left humerus which was discovered lying close to the pectoral girdle, but rotated through 90 degrees. It is not clear whether this bone was *in situ* when discovered. The articulated digits and some tarsals of the ?left hind limb lay approximately 1 metre from the concretion containing the pelvic girdle. Missing limb elements, including at least two propodials, a radius and an ulna, may yet prove to be present within the main body of the concretion.

The general appearance is of a partially articulated skeleton that may have arrived on the sea floor as a partly dismembered carcase held together by ligaments and other resistant tissues.

Preservation 2. Soft tissues

Only rarely are soft tissues found preserved in the Lower Oxford Clay. The best known examples are phosphatized muscle fibres from teuthid cephalopods of Christian Malford, Wiltshire (Allison, 1988; Page and Doyle, 1991), although Martill (1987) reported organic coatings associated with an ichthyosaur skeleton from Buckinghamshire which he interpreted as bacterial autolithified tissue *sensu* Wuttke (1983).

The pliosaur discussed here is particularly noteworthy for the presence of preserved tissue lying between the thoracic ribs. This takes the form of a thin (few microns thick) layer of blackish-brown or grey material with a fibrous aspect. The long axes of the fibres are parallel to the length of the ribs (Fig. 4a). Unfortunately at higher magnifications little detail is revealed (Fig. 4b). A lack of clear evidence of the nature of the preserved tissue makes it difficult to identify its structure and function. Three possibilities are considered: *(i)* It represents a part of the integument of the pliosaur. *(ii)* The fibres are poorly preserved intercostal muscle fibres. *(iii)* They represent an as yet unrecognised sheet of elastic connective tissue. The black material that preserves the soft tissue is currently being analysed, and results will be reported elsewhere.

Black organic material is also associated with what are interpreted as the stomach contents. Two types are present. One perhaps represents breakdown products of the wall of the alimentary tract, and appears amorphous, while the other represents the massed remains of cephalopod hooklets, and has a distinctly coaly (bright) aspect.

The stomach contents 1. Food

The stomach contents are dominated by hooklets from teuthoid cephalopods. The hooklets are generally in the size range of 2 to 10mm, and are elongate, recurved hooks with slightly expanded bases. Such hooklets have been reported in the gut regions of crocodilians (Martill, 1986b) and long necked plesiosaurs (Andrews, 1910-1913) from the Oxford Clay, and commonly from Liassic ichthyosaurs (Pollard, 1968; Bottcher, 1989). The hooklets from the new specimen resemble closely those of the teuthid *Belemnotheutis antiquus* Pearce, the phragmocones of which are abundant in the Lower Oxford Clay. A specimen of *Belemnotheutis* from the Lower Oxford Clay of Christian Malford in which the entire animal is preserved has a body length (including tentacles and phragmocone) of 190mm. The hooklets of this specimen are between 1 and 4.5mm in length. In addition to cephalopod hooklets, a single indeterminate reptilian tooth with a well developed

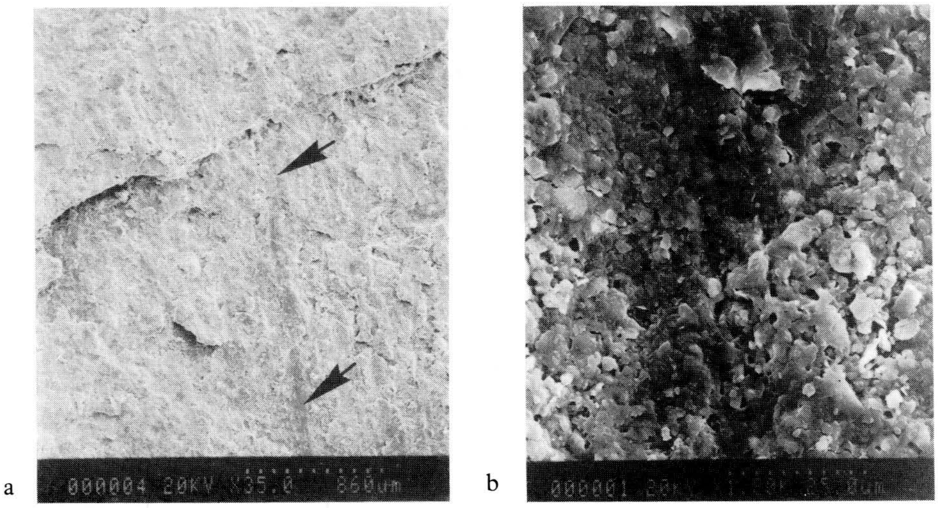

Fig. 4. Possible soft tissues. A fibrous surface associated with a black organic layer. This material occurs on the surface of the thoracic ribs and on the intervening shale. a, Low magnification electron micrograph showing fibrous aspect, × 35. b, Higher magnification electron micrograph suggesting material is amorphous organic material retaining little of the original structure, × 1200.

resorption scar was found, as well as rarer small fish teeth, vertebrae and other indeterminate fish bones. Larger bony material is otherwise absent.

Throughout the "stomach" contents are scattered patches of brown, phosphatic material containing subspherical bodies of quite unknown affinities. These patches sometimes have well defined edges, but some are strung out in wisps (Fig. 5b, 5c). A number of ammonites (mainly *Kosmoceras jason*) occur within the concretion containing the stomach contents (Fig. 5b), but they appear to be chance associations rather than a part of the stomach contents as they occur in other parts of the concretion where cephalopod hooklets are absent.

The stomach contents 2. Gastroliths

Four pebble-sized stones (20-40mm diameter) and a considerable, but unmeasured, quantity of sand and grit are present within the concretion, in intimate association with cephalopod hooklets. This material is concentrated in a thin layer running through much of the thoracic concretion and is considered to have lain within the gut of the pliosaur. There appears to have been some mixing of the surrounding sediment and gut contents, and small patches rich in sand and others more rich in cephalopod hooklets occur. Sand and pebbles have been reported from a wide variety of marine vertebrates but their function remains a matter of debate. Taylor (1981) suggested that stones in the guts of marine reptiles, some mammals and penguins are possibly for buoyancy regulation, while other authors have suggested such stones may be for grinding food to smaller pieces, or even increasing the reactive surface area on which adsorbed enzymes can operate (Davenport *et al.*, 1990). There is little or no data available in the new specimen which lends support to any of these hypotheses. It can be said, however, that the cephalopod hooklets are in very good condition despite their delicate nature, and retain sharp points, suggesting that grinding was not the role of the gastroliths in this case.

Three large, subspherical, smooth pebbles are exposed at the surface of the concretion enclosing the gut region. Thin sections have been made of these to determine their petrographic nature. Two are fine, grey, sandstone pebbles (Fig. 5a), cemented by poikilotopic calcite. A third pebble is a fine brown sandstone with a pyrite and calcite cement which has weathered to limonite on the pebble's margin. In all of the pebbles the quartz grains are fine and very angular. This is similar to the underlying Kellaways Sand Formation, which is known to have formed sandstone dykes which penetrated the lowest beds of the Lower Oxford Clay (Martill and Hudson, 1989). However, the pebbles are very well cemented and are harder than any Kellaways Sand that I have observed. In addition, the sandstone dykes have a cross cutting relationship with Bed 10 at Dogsthorpe, indicating that this part of the sand body at least remained uncemented during *jason* Zone times. Interestingly, sandstone pebbles are not as popular among animals that contain gastroliths as quartzites and igneous rocks, suggesting perhaps that harder rock types were not available locally.

The sand and grit fraction contains a range of sizes from diameters of three or four millimetres down to fine sand and silt size. Many are medium to well rounded, but a substantial number are angular, with a few being very angular. All have glassy surfaces. The majority of the grains are quartz with some showing strained textures. Microcline feldspars and a few lithic fragments are present, as well as a few small euhedral zircons.

The source of the grains and pebbles is not immediately obvious. Pre-Jurassic sandstones and quartzites are abundant in the UK both temporally and geographically. However, palaeogeographical con-

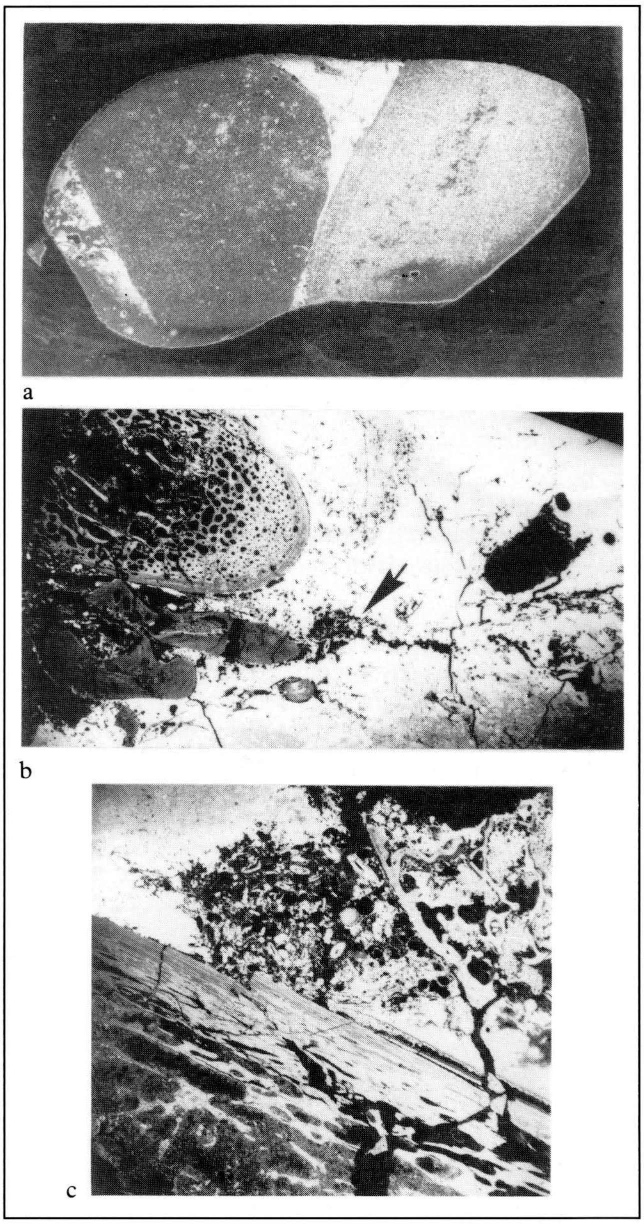

Fig. 5. a, Thin section showing two gastroliths of calcite cemented sandstone from within the gut of the new pliosaur, × 2. b, Thin section through single thoracic rib and the tips of four articulated gastralia showing wispy layer of cephalopod hooklets, × 2. c, Thin section through thoracic rib (lower left of photograph) wedged against an unidentified bone (possibly also a thoracic rib) with small "pocket" of cephalopod hooklets and sand grains trapped between, × 2.

siderations suggest that nearby landmasses such as the Pennines, and perhaps the Belgian parts of the London-Brabant landmass, were exposed during the Callovian. Numerous islands may have existed at the elevated massifs around Nuneaton, Charnwood, the Malverns and elsewhere.

Discussion

It is at first somewhat surprising that a large pliosaur species such as the one discussed here should have its gut contents dominated by cephalopod hooklets. The only functional analysis of feeding in a pliosaur (Taylor, 1992) was based on comparative studies and a consideration of the biomechanics of feeding in water and this suggested that Lower Jurassic *Rhomaleosaurus* was a top carnivore capable of capturing and despatching large prey items. Likewise, the dentition of *Liopleurodon* is more reminiscent of a predator of large animals rather than squid. However, *Liopleurodon* may not have been a large prey specialist, and may be more comparable with sperm whales in this respect. Sperm whales frequently take large quantities of small prey (usually cephalopods) down to 50mm in length (Clarke, 1980).

A number of possibilities can be considered. Firstly, the diet of this individual may have been dictated by available food supply. Belemnites, ammonites and a number of naked cephalopods were abundant in the Lower Oxford Clay during *jason* Zone times. However, so were fish and other marine reptiles including ichthyosaurs, plesiosaurs and crocodilians.

From a consideration of the biomechanics of pliosaur jaws, and the positioning of the teeth, it is conceivable that pliosaurs could take squids with ease. The mandibular symphysis is elongate, with parallel rows of teeth, and the teeth are sharp, which would make grasping fast-moving, slippery prey easy. However, considering the swimming speeds of pliosaurs (Massare, 1988) it is doubtful if they could actively pursue fast-swimming cephalopods (assuming that they were as fast swimmers as today's squids), but they might take food by stealth rather than pursuit.

Secondly, it is possible that *Liopleurodon* was an opportunistic feeder, and that the cephalopod hooklets represent the preservable, acid resistant residue of a varied diet, the skeletal components of the vertebrates having been lost to the acid environment of the gut. However, thin sections through the gut have not revealed the presence of otoliths which are known to accumulate in the acidic guts of cetaceans (Fitch and Brownell, 1968) suggesting that fish were not an important part of this individual's diet at this location/time/season/age despite the occurrence of some fish bone.

A third possibility is that the pliosaur fed on large prey items which were themselves cephalopod feeders, and that the cephalopod hooks are the residues of the stomach contents of the pliosaur's prey. Martill (1986b) suggested that the marine crocodile *Metriorhynchus* was a cephalopod feeder (but did not consider a secondary origin for the hooklets), and it could be supposed that the Oxford Clay pliosaurs fed on smaller crocodilians, long-necked plesiosaurs and ichthyosaurs. There is however, no firm evidence for this. Evidence for predation on large ichthyosaurs is relatively common in the Kimmeridge Clay, where large pliosaurs are abundant. Bite marks on ichthyosaur vertebrae are common in the Kimmeridge Clay of Dorset and could have been made by pliosaurs or perhaps large crocodilians (Etches, pers. comm.).

In any case, it appears that the new specimen does not itself solve the problems of pliosaur dietary preference. Despite being some four metres long (the skull is 1m long) it is only a young adult. Specimens with lengths up to ten metres are indicated by spectacularly large, but incomplete remains. It is possible that the diet of pliosaurs changed considerably during development. This individual may have been nearing the end of a cephalopod dominated phase.

The presence of stones in the guts of animals has always invited speculation. It is conceivable that the sand fraction present in the pliosaur gut was taken accidentally while the pliosaur was pebble swallowing or taking benthic prey, or represents the acid resistant residue from carbonate cemented sandstone. In addition both the pebbles and the sand fraction may not represent a distinct assemblage, having been acquired from numerous beaches or gravel lags on the sea floor, each with distinct characteristics. Thus the generally immature nature of the sand sample may not be representative of a single sedimentary environment, making any guesses as to derivation highly tenuous (cf. Darby and Ojakangas, 1980).

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