

THE GASTRIC CONTENTS OF AN ICHTHYOSAUR FROM THE LOWER LIAS OF LYME REGIS, DORSET

by JOHN E. POLLARD

ABSTRACT. The partial skeleton of a small ichthyosaur associated with the gastric mass is described from the Lower Lias of Lyme Regis. The gastric mass was oval in shape and composed of minute dibranchiate cephalopod hooklets in random orientation. Four distinct types of hooklet are recognized in these gastric contents.

Examination of published records and museum specimens suggests that gastric contents composed of cephalopod remains are more commonly preserved than those of fish remains. A study of ichthyosaur coprolites shows a predominance of defecated fish remains and an absence of hooklets from these structures. The diet, mode of feeding, and digestive mechanism of Liassic ichthyosaurs, in comparison with a teuthophagous cetacean, the sperm whale, are considered.

IN April 1963 the skeleton of a small ichthyosaur was found in the shales of the Lower Lias on the foreshore west of Lyme Regis, Dorset. Unfortunately due to the exposed location of this specimen, in soft shaly-mudstone at about the half-tide level, only a short time was available for its extraction. Only the anterior part of the skeleton could be recovered consisting of parts of the skull, pectoral girdle, vertebral column, and ribs. Careful preparation of this material showed that the skeleton was crushed and slightly dismembered, but that the stomach contents were preserved as a dark discrete area underneath the vertebral column and ribs. Such occurrences are fairly well known, but the good state of preservation and lack of dispersal of the stomach contents of this specimen make them worthy of detailed description, quantitative analysis, and discussion in terms of the feeding habits and digestive mechanism of the Liassic ichthyosaurs.

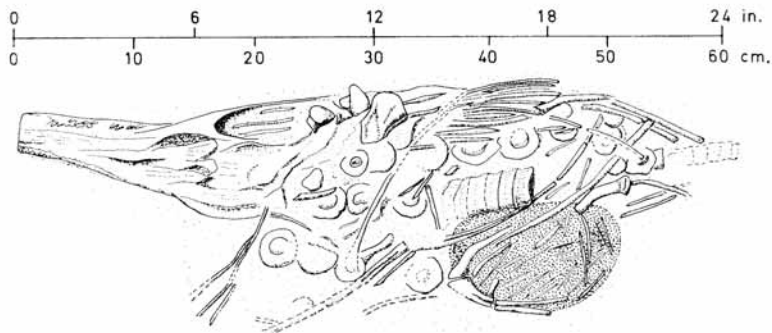
DESCRIPTION

Horizon and locality. The specimen was collected from the shales of the lower part of the *Psiloceras planorbis* Zone of the Lower Lias (Woodward and Ussher 1911, p. 38), at the south-east corner of Pinhay Bay, two miles west of Lyme Regis (National Grid Reference: SY 325907). The enclosing sediment was a poorly fossiliferous silty and shaly mudstone, which was interbedded with thin limestones and shales containing *Liotrea liassica*, *Hemicidaris* spines, and rarely *Plagiostoma gigantea* and *Psiloceras planorbis*. No other vertebrate remains or coprolites were observed at this horizon.

Skeletal remains. The partial skeleton of the ichthyosaur extracted was 2 ft. (60 cm.) in length and consisted of the skull and parts of the vertebral column, pectoral and pelvic girdles, rib cage, and a paddle. (The specimen is now preserved in the collections of the Geology Department, University of Manchester, registration number SF.1.) Text-fig. 1 is drawn from a field photograph of the specimen *in situ*, and shows the relative positions of the bones and the gastric mass from the dorsal aspect. The prepared skeleton can be examined both dorsally and ventrally, Plate 72, figs. 1 and 2, and enables the individual bones to be identified.

[Palaeontology, Vol. 11, Part 3, 1968, pp. 376-88, pls. 72-73.]

The skull is 10 in. (25 cm.) long, crushed dorso-ventrally and twisted sinistrally. The anterior part of the snout is missing, but the premaxilla and eleven upper jaw teeth and thirteen lower jaw teeth on the right side of the mouth are visible on the upper surface (Pl. 72, fig. 1). On the under surface of the skull both dentary bones are present and twenty-three upper jaw teeth, and sixteen lower jaw teeth, from the left side of the mouth (Pl. 72, fig. 2). The teeth appear to be well formed typical ichthyosaur teeth, up to 13 mm. in length exposed, with smooth apices and bifurcating grooves on the crown. The form of the tooth crown is close to that of *Ichthyosaurus communis* Conybeare as figured by Owen (1881, pl. 24, fig. 5). The anterior part of the right orbit was present dorsally



TEXT-FIG. 1. Ichthyosaur skeleton *in situ* in the Lower Lias west of Lyme Regis, showing the relationship of the various bones to the gastric mass. Widely spaced fine stippling represents the shale matrix, while the closely spaced coarser stippling represents the gastric contents.

(text-fig. 1) but no sclerotic plates were seen. The hind part of the skull is badly crushed, and the only other bones clearly recognizable are displaced fragments of the articular and basioccipital (Pl. 72, fig. 1).

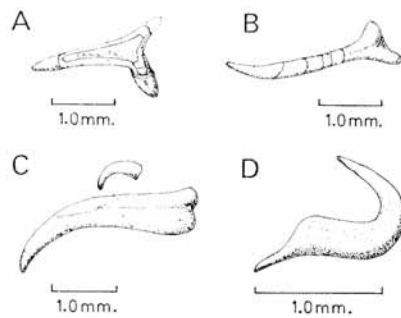
The post-cranial skeleton is represented by a total of twenty-eight vertebrae and numerous fragments of single and double ribs. On the upper (dorsal) surface of the specimen, Pl. 72, fig. 1, seven thoracic vertebrae occur in a row from 4 to 8 in. (10–12 cm.) behind the skull, and bound the gastric mass dextrally. The dorsal left boundary of the gastric mass is formed by a series of parallel double ribs (text-fig. 1 and Pl. 72, fig. 1), while a complex of complete and broken double and single ribs are elsewhere compressed into the gastric mass dorsally.

The anterior boundary of the gastric mass on the ventral side of the specimen is formed by the bones of the pectoral girdle (Pl. 72, fig. 2). Parts of the left coracoid, humerus, and scapula are clearly recognizable and are impressed into the gastric mass ventrally. The interclavicle is present, and fragments of fifteen phalangeal bones of the left anterior paddle were found just beyond the humerus. The only other recognizable bones collected were a displaced pubis and three phalangeal bones of a posterior paddle, Plate 72, fig. 1, all occurring postero-dextrally of the gastric mass.

The nature and arrangement of these skeletal remains suggest that there had been a fair amount of displacement of the bones during burial and that the gastric mass must

have been trapped in an unusually anterior position, crushed between the anterior-dorsal thoracic rib cage and the pectoral girdle.

Gastric mass. The gastric mass of this specimen, text-fig. 1, was broadly oval in shape, compressed dorso-ventrally, 13.5 cm. long from anterior to posterior, and 8.5–9.0 cm. wide from right to left of the skeleton. Only the anterior part of the mass (8 cm. anterior to posterior by 7 cm. right to left) was collected and prepared for further study (Pl. 72, fig. 1; Pl. 73, fig. 1). Estimates of the dorsal area of the stomach mass, measured from the field photograph vary from 85.5 to 95.5 sq. cm. or approximately 90 ± 5 sq. cm. The depth or thickness of the dorso-ventral cross section of the gastric mass was measured accurately on the prepared specimen (Pl. 73, fig. 1), using a travelling microscope, and varied from 0.25 to 0.75 cm., with a mean value of about 0.33 cm.



TEXT-FIG. 2. Cephalopod hooklets from the Lias. Types A, B, and C are all drawn from hooklets in the gastric contents shown on Plate 73, figs. 1 and 2, while type D is drawn from specimen OUM.J.14800, in mudstone from the Upper Lias at Dumbleton, Gloucestershire.

on the dorsal surface, but occurring in considerable concentration in patches of the ventral surface of the mass (i.e. at point X on Pl. 72, fig. 2).

Three, or possibly four, distinctly shaped types of hooklet can be recognized in these contents, types A, B, C, and D of text-fig. 2. Type A is relatively short straight spinose form with a strongly bifid base, rather like an odontaspid shark's tooth in shape. Type B is longer and more slender than type A, with a less pronounced base and a gentle curve along its length. Type C is broader bladed than types A and B, has distinct lateral flattening, and a strong, nearly 90° hook. The base of type C is much less pronounced than on types A or B, but this character may be suppressed due to lateral flattening. Type D of text-fig. 2 is extremely rare in the gastric contents, about 1 mm. or less in size, and a specimen from a different horizon and locality is figured here for comparative purposes, the significance of which will be discussed later. Each of these hooklet types

EXPLANATION OF PLATE 72

Fig. 1. Dorsal view of prepared ichthyosaur skeleton preserved with gastric contents. Lower Lias, Planorbis Zone, Lyme Regis, Dorset. SF.1. Geology Dept. Collections, University of Manchester. *a.*, articular; *v.*, vertebra; *r.*, rib; *sc.*, scapula; *pd.*, paddle; *pub.*, pubis.

Fig. 2. Ventral view of ichthyosaur specimen SF.1. Symbol 'X' indicates the region of the ventral surface of the gastric mass with a concentration of quartz grains. *d.*, dentary; *sa*, supra-articular; *icl.*, interclavicle; *cor.*, coracoid; *hum.*, humerus.

in the gastric contents shows considerable size range, for instance in terms of length, type A varies from 1.0 to 1.90 mm. (10 measured), type B from 0.70 to 3.00 mm. (16 measured), and type C from 0.9 to 2.90 mm. (22 measured). Types B and C appear to be commoner than type A in the mass.

All these hooklets seem to be composed of a jet black and very brittle organic, possibly chitinous, material. They are all hollow although sometimes filled with crystalline calcite. Due to their brittle nature and hollow centre, most of the hooklets are cracked and partially crushed and splinter if any attempt is made to separate them from the mass.

In an attempt to determine the approximate number of hooklets on the dorsal surface of the gastric mass, the distribution of the hooklets in an area 2 cm. square was plotted from the enlarged photograph, Plate 73, fig. 2. The frequency of hooklets on this surface varied between 450 and 540 per sq. cm., with a mean of about 500 per sq. cm. This number represents only those hooklets that could be clearly identified and is, therefore, a minimal estimate. The total number of hooklets on the dorsal surface of the gastric mass, area 90 ± 5 sq. cm., is about $45,000 \pm 7,000$ (i.e. $90 \pm 5 \times 500 \pm 50$).

It has proved very difficult to estimate the total number of hooklets in the gastric mass due to their being crushed and randomly orientated. The cross-sectional diameter of a number of hooklets of various sizes, uncrushed on the dorsal surface, varied from 0.20 to 0.50 mm. The mean depth of the gastric mass is 0.33 cm., so that allowing for parallel packing and no crushing, the hooklets would be from approximately 16 (3.30/0.2) to 7 (3.30/0.5) layers deep. Making an allowance for crushing and random packing, from 6 to 14 or 10 ± 4 layers deep, would seem to be a reasonable estimate. Therefore, the total number of hooklets in the gastric mass is $45,000 \pm 7,000 \times 10 \pm 4 = 478,000 \pm 250,000$ or $478,000 \pm 53$ per cent. Such a large error is unavoidable in such approximate calculations, but the figure gives some idea of the correct order of magnitude.

DISCUSSION

In order to understand the significance of the gastric contents previously described, and the precise nature of the dibranchiate remains they contain, a search has been made in the literature and other specimens have been examined in several British museums. The author does not intend this as an exhaustive treatment of the subject, but more as a spur to examination and comment by other workers.

Other Liassic ichthyosaurs with gastric contents. Ichthyosaur remains with associated gastric contents preserved have been known for more than a hundred years from the Liassic shales of Lyme Regis and Whitby in England, and Holzmaden in Germany. Buckland in the *Bridgewater Treatise* (1836) is among the earliest English records. He described and figured (pl. 13 and 14) two ichthyosaur specimens from Lyme Regis that contained a coprolite mass with fish scales, preserved within the abdominal cavity. These specimens are in the collections of the Oxford University Museum and will be discussed later in this paper.

Probably the earliest description of the preserved cephalopod hooklets associated with ichthyosaur bones is that of Coles (1853). He describes a layer of carbonaceous material made up of 'minute black points'—hollow and filled with calcite, that was found

adhering to an ichthyosaur vertebra from the Lias of the Tewkesbury district. His excellent figures (pl. 5, figs. 2 and 13) show shape, size, and crack patterns identical to the hooklets described and figured in this paper (Pl. 73, fig. 2 and text-fig. 2). This material was wrongly identified by Coles (1853, p. 81) as 'setiform or bristly scales' of the ichthyosaur integument, and was reported by him to be known associated with ichthyosaur skeletons from the Lias of Lyme Regis and Ilminster as well as Tewkesbury. Cole's error was corrected by Moore (1856), who reported finding stomach contents composed of cephalopod arm hooklets in sixteen out of twenty-three Liassic ichthyosaur skeletons he had prepared for his museum. Moore examined the gastric contents further, and suggested that they consisted of the desiccated ink and arm hooklets of naked Jurassic cuttle-fish allied to *Onychoteuthis*.

Buckman (1879), when describing a new species of fossil dibranchiate *Belemnoteuthis montefiorei* from the Lower Lias of Charmouth, mentions the frequent occurrence of ichthyosaur stomach contents and coprolites full of cephalopod arm hooklets. Similar general statements recording gastric contents composed largely of cephalopod hooklets have been made by several workers studying ichthyosaurs from the Holzmaden Lias (Seeley 1880, Branca 1908, Drevermann 1914, Huene 1922, Hofmann 1958, and Augusta 1964). Wurstemberger (1876) described a Holzmaden specimen of *Stenopterygius quadrisissus*, with head 50 cm. long, vertebral column 240 cm. long, where a large stomach mass of fish and cephalopod remains was found only 20 cm. behind the head. This unusually anterior thoracic position of the stomach is very similar to that of the specimen described here. Williston (1914, p. 123) refers to an ichthyosaur skeleton in the Stuttgart Museum that has preserved in its stomach contents the remains of more than 200 belemnites. Dr. K. D. Adam (pers. comm.) informs me that no such specimen exists in the Stuttgart Museum, but Williston's comment is probably a mistaken reference to a well preserved specimen of the shark *Hybodus* from the Upper Lias of Holzmaden described by Brown (1900) and later Shimanskiy (1949). The gastric contents of this shark contain over 250 belemnite rostra.

Many British museums possess in their collections ichthyosaur skeletons with well preserved gastric contents. On other specimens the gastric contents have obviously been cleaned off in the preparation of the skeleton, and so it would appear that these contents are of much commoner occurrence than the literature would suggest. The ichthyosaurs figured by Buckland (1836, pls. 13 and 14) are preserved in the Oxford University Museum, numbered specimens J.13587 and J.13593 respectively. Re-examination of these specimens by the author confirms that Buckland's figures and descriptions are extremely accurate and that the gastric contents consist largely of scales and spines of the Liassic fish *Pholidophorus* sp., set in a matrix of a pale buff coprolitic clay. The larger specimen J.13593 (Buckland 1836, pl. 14) does have a very sparse scattering of type C hooklets over the whole dorsal surface of the gastric mass. Three other specimens

EXPLANATION OF PLATE 73

Fig. 1. Dorsal view of the gastric mass and associated bones of ichthyosaur specimen SF. 1 (compare with Pl. 72, fig. 1). Scale of 1 cm.

Fig. 2. Magnified view of part of the dorsal surface of the gastric mass of specimen SF. 1 showing the various types of cephalopod hooklets present. (This field of view may be orientated on Pl. 73, fig. 1, by the arcuate row of five large quartz grains in the lower half of the picture.) Scale of 1 cm.

of Liassic ichthyosaurs from Lyme Regis in Oxford University Museum, J.12125, J.13592, and J.10348, all contain patches of gastric material, composed of types A, B, and C hooklets, in the thoracic or anterior abdominal regions. The gastric mass in each case is identical to the specimen described here, just hooklets without any matrix of the coprolitic clay seen in Buckland's specimens.

Specimens of various species of ichthyosaur from the Lower Lias at Lyme Regis on display in the public galleries of the British Museum (Natural History) show gastric contents of densely packed hooklets devoid of matrix (e.g. BMNH 36256, BMNH R1614, BMNH R1072, BMNH 38523, BMNH 43006, and BMNH R1896). In the Manchester Museum an excellent specimen from the Upper Lias at Whitby has a large gastric mass containing A, B, and C type hooklets, just posterior to the pectoral girdle.

The conclusion to be derived from a study of these listed, and other specimens, is that gastric contents of densely packed dibranchiate cephalopod hooklets are much commoner in prepared specimens than the fish remains in a matrix of coprolite clay described by Buckland. The gastric contents of many Jurassic plesiosaurs are also known to be composed largely of dibranchiate hooklets (Juravlev 1943, Hekker and Hekker 1955, and Tarlo 1959), but here large gastroliths usually occur as well (Seeley 1877, Brown 1904, and Williston 1904). Gastroliths have not been found preserved in ichthyosaur stomach contents.

Contents of coprolites from Lower Lias. Well-preserved coprolites, usually assigned to ichthyosaurs or plesiosaurs, have been known from the Lower Lias at Lyme Regis since before Buckland's classic paper of 1835. Most of these coprolites are assumed to have been formed by ichthyosaurs, on account of their similarity in composition to material described by Buckland (1836) from within the ichthyosaur abdominal cavity. Other workers (Fraas 1891 and Woodward 1917) have questioned the assignment of these coprolites to ichthyosaurs. They argue that spirally folded coprolites are rarely found associated with ichthyosaur skeletons and are more likely to have been formed by the spiral intestine of Liassic sharks than by the typical reptilian intestines which the ichthyosaurs probably possessed. The following analysis shows that the majority of Liassic coprolites do not have well-formed spiral folds but have faunal, lithological and chemical features identical to the ichthyosaur gastric contents described by Buckland. Moreover, the hybodont sharks, suggested by Woodward (1917) as probable producers of the coprolites, are believed on account of their dentition (Romer 1966, p. 40) to have been benthonic or necto-benthonic scavenger feeders, and not nectonic fish feeders as were the producers of the Liassic coprolites.

Buckland (1835) showed that Lower Lias coprolites contain fish remains, bones of young ichthyosaurs, and possibly the sucker rings of fossil cuttle-fish. He did not observe or describe any dibranchiate hooklets. The matrix of these coprolites, which I have called 'buff coprolitic clay', was shown by Buckland to be phosphatic material derived from the digestion of fish and reptile bones. Buckland suggested that the strong spiral involutions frequently seen on coprolites indicate that the small intestine of the ichthyosaur was ribbon like and twisted into a spiral. Firtion (1938) analysed the contents of coprolites from the Lower Lias of Alsace. He found that the undigested contents were mainly crinoids, gastropods, or pelecypods with less abundant foraminifera, ostracods, fish remains, and brachiopod shells. These coprolites rarely had spiral folds and were

obviously formed by a benthonic feeding animal. However, he assigned them to ichthyosaurs, although stomach contents of the above composition are unknown in ichthyosaurs. Such coprolites could as easily belong to teleosaurs or plesiosaurs (Drevermann 1914). Ager (1963, p. 120) mentions that a study of coprolites suggests that Mesozoic ichthyosaurs included belemnites in their diet, but he does not refer to any actual records of this fact.

Fifty well-preserved coprolites from Buckland's collection in the Oxford University Museum have been examined by the author. These specimens vary from 1 to 6 in. in length, mainly 2–3 in. long, and their contents can be examined on the cleaned surface, or internally where they have been sectioned and polished. Forty-five specimens contain recognizable fish remains, mainly scales, fin rays, and spines of *Pholidophorus* sp., less commonly remains of *Dapedium* sp. and *Lepidotus* sp. Two specimens, those figured by Buckland (1835, pl. 29, figs. 2, 3, 4, and 5), contain reptilian bones and fifteen specimens have well-formed spiral involutions. None of these coprolites contain visible remains of dibranchiate hooklets and the possible sucker rings figured by Buckland (1835, pl. 30, figs. 1, 2, and 3) are considered to be transverse sections of fin rays and small vertebrae of fish. Examination of sixteen well-preserved coprolites in Manchester Museum and Geology Department, University of Manchester, shows that all these contain fish scales and spines, none contain reptilian bones, and only four specimens have well-formed spiral folds. One of the Manchester Museum specimens has a small patch of shale matrix with type B and C hooklets adhering to its surface, but they are not contained in the adjacent coprolite material. Lydekker (1889, pp. 114–17) lists sixty-six coprolites from the Lower Lias in the British Museum collections, but only mentions fifteen containing fish scales, only two with reptilian bones, and only one showing well-formed vascular impressions.

From this survey it is suggested that ichthyosaurs from the British Lower Lias primarily defecated fish remains in their coprolites. Undigested cephalopod remains have not been seen in these coprolites, so it may be inferred that they accumulated in the stomach, as their predominance in gastric contents would suggest. The commonest form of fish eaten, *Pholidophorus*, is presumed to have been a nectonic or necto-benthonic form, not a deep bodied benthonic fish like *Dapedium* or *Lepidotus*. The possible significance of this latter observation will be discussed later.

Nature of the cephalopod remains. Throughout the preceding part of this paper the hooklets found in the gastric contents of the ichthyosaur have been broadly described as belonging to Liassic dibranchiate cephalopods. It is of some importance to establish the precise nature of the dibranchiates possessing these hooklets before discussing their relationship to their ichthyosaur predators.

As well as occurring in gastric contents of ichthyosaurs, these hooklets are known preserved in their life position on the arms of predominantly soft bodied dibranchiates that are rarely found in Liassic and other Jurassic argillaceous sediments. Pearce (1842) named one of these soft-bodied dibranchiates with arm hooklets from the Oxford Clay as *Belemnoteuthis*. The arm hooklets of *Belemnoteuthis* were figured by Owen (1844, pl. 6, fig. 2) and Mantell (1852, fig. 4) as all possessing elongated pointed bases, and one form similar in shape to type D of text-fig. 2.

It has already been mentioned that Coles (1853) seems to have been the first person

to describe the hooklets from the Lias, although he was in error about their nature. The suggestion of Moore (1856), that these hooklets belonged to naked dibranchiates allied to *Onychoteuthis*, does not seem to be supported by any earlier published records of specimens of this genus from the Liassic rocks of Britain. Huxley (1864) was the first person to unquestionably associate these forms with belemnoid arm hooklets. He figured (1864, pl. 1, fig. 5a) forms identical with the types A, B, and C of text-fig. 2 when he described two specimens of belemnites from the Lias (BMNH 74106 and BMNH 39855), where soft parts were preserved in association with the guard, phragmocone, and proostracum. One of these specimens, BMNH 74106, must be interpreted with some caution as it has been restored in preparation. Dr. K. A. Joysey (pers. comm.) has informed me that one such specimen (J42835) in the Sedgwick Museum, Cambridge, is a 'well intended' forgery by a preparator, for the belemnite guard has been artificially shaped to improve its appearance before being set in an artificial matrix in association with a genuine group of hooks. However, Huxley's interpretation appears to be correct and has been accepted by such later workers as Crick (1907), Naef (1922), and Jeletsky (1966).

Buckman (1879) described a specimen of a head of hooked arms from the Lower Lias, which he named *Belemnoteuthis montefiorei*. This specimen is in the collection of the British Museum (BMNH C5026) and the hooklets are identical with the types A, B, and C described here. However, in affinity this specimen seems to be *Belemnites* as suggested by Crick (1902) and not the *Belemnoteuthis* of Pearce (1842).

The most complete study of the arms of Liassic and other Jurassic dibranchiates is undoubtedly that of Crick (1907). He examined seventeen specimens of 'belemnite' arms in the British Museum collections and described and figured six of these specimens in detail in his paper. Crick concluded that the belemnites possessed six arms bearing rows of hooklets with swollen bases, as types A, B, and C, while *Belemnoteuthis* (= *Acanthoteuthis*) had eight or ten arms bearing hooklets with pointed bases. This latter form of hooklet is characteristic of fossil dibranchiates known from the Upper Jurassic Oxford and Kimmeridge Clays in Britain, and the lithographic stone of Solenhofen in Germany (Pearce 1842, Owen 1844, Mantell 1852, Crick 1897 and 1907).

Several of the standard textbooks on palaeontology (Zittel 1913, Woods 1946, and Piveteau 1953) figure dibranchiate cephalopod hooklets from Mesozoic sediments but give little idea of possible affinities of the various forms. Naef (1922) in his authoritative work on fossil dibranchiates figures and discusses various forms, including types from the Upper Lias of Holzmaden similar to types B and C of this paper, but is uncertain of any definite correlation of hooklet form with type of dibranchiate. Both Naef (1922, p. 219) and Jeletsky (1966, p. 138) disagree with Crick's (1907) interpretation of six-arm belemnites and suggest that they had eight or ten arms in common with the belemnoteuthids. Jeletsky (1966, p. 138) believes that all members of the order Belemnitida possessed arm hooklets.

From a detailed study of the literature and museum specimens it is here suggested that some broad association of hooklet form with three major groups of Mesozoic dibranchiate cephalopod may be possible. Members of the Belemnitidae may have had hooklet types A, B, and C as described here, characterized by a gentle curved shape and a swollen bifid base. Such forms are known mainly from the Lias (Huxley 1864, Crick 1907, Naef 1922, and Jeletsky 1966). Dibranchiates of the family Belemnoteuthidae may

have had gently curved or recurved hooklets with an elongate obliquely pointed base. This hooklet type is known from Upper Jurassic specimens (Pearce 1842, Owen 1844, Mantell 1852, Crick 1897, 1907, Hekker and Hekker 1955). Genera of the order Phragmoteuthida probably had hooklets of a belemnite type (Jeletsky 1966, p. 31). Separated hooklets of a variety of shapes are frequently found in microfaunas of Jurassic and Cretaceous age and are known as '*Onychites*' sp. (Quenstedt 1885, Naef 1922, Piveteau 1953, Hekker and Hekker 1955). Such hooklets probably belonged to other little-known members of the order Belemnitida as fossil teuthoid squids and sepoid cuttle fish seem to have been devoid of arm hooklets in Mesozoic seas (Jeletsky 1966). Therefore, the types of hooklets described in the earlier part of this paper would seem to have belonged to dibranchiate cephalopods of the family Belemnitidae, and not the family Belemnoteuthidae or the order Phragmoteuthida.

TABLE 1

Arms and arm hooklets of fossil belemnoids from the Lower Lias. Details from Woods (1946, fig. 169) and Crick (1907, pl. 23, figs. 1, 3, and 5).

Specimens	Number of arms	Total no. of hooklets	Hooklets per arm		Number of hooklets per arm of lengths		
			mean	max.	> 40 mm.	> 30 mm.	> 20 mm.
SM. J37812	8	211	29	34	32 (5)	0	17 (3)
BM. C3007	6	143	24	28	26 (3)	21 (3)	0
BM. 82895	4	123	31	36	31 (4)	0	0
BM. 47020	6	156	25	30	26 (2)	26 (2)	24 (2)
Approx. 'mean'	6	c. 150	27	32	29	23	20

Examination of published figures and museum specimens of 'belemnite' arms with hooklets (e.g. Woods 1946, fig. 169, and Crick 1907, pl. 23, figs. 1 to 6) has enabled observations to be made regarding the number of hooklets per arm, the total number of hooklets per belemnite individual, and the arrangement of hooklet types along the arms.

The varied state of preservation of specimens with arms from the Lower Lias makes detailed analysis very difficult. Crick (1907) showed that of the seventeen specimens in the British Museum collections only six were worthy of description, and of these six only three are considered sufficiently complete by the present author for detailed analysis (Table 1). Crick (op. cit.) showed that the belemnite arms varied in length, and that the hooklets were arranged in two parallel rows on the inner surface of the arms. In many of the known specimens the arms are either incompletely preserved or superimposed, so that it is impossible to be certain of the original arrangement of the arm hooklets. The specimens listed in Table 1, although varying in the number of arms, all possess arms that appear to be complete, as the hooklets are arranged in parallel rows, and are largest in the mid-length of each arm, gradually diminishing in size towards each end (Crick 1907, p. 271). From Table 1 it appears that the number of hooklets per arm varies with the length of the arm, but about thirty (fifteen pairs) hooklets per arm is an average number. Specimen SM. J37812 possesses eight distinct arms, and therefore confirms that there must have been eight or more arms in the belemnites in agreement with Naef (1922) and Jeletsky (1966). There must have been, therefore, at least 300 hooklets on an individual ten-armed belemnite in Liassic times.

The detailed arrangement of the hooklets along the arms can only really be seen on two of the specimens included in Table 1, Wood's fig. 169 (SM. J37812) and BMNH 82895 (Crick 1907, pl. 23, fig. 3). On these specimens the proximal hooklets are seen to be small examples of types A and B. The hooklets at mid-length of the arms are large examples of types B and C which decrease in size towards the distal end. This broad pattern of hooklet arrangement can be seen to a lesser extent on other less well preserved specimens (e.g. Crick 1907, pl. 23).

Significance of the gastric contents

(a) Feeding habits

Diet. The evidence of the gastric contents and coprolites suggests that Liassic ichthyosaurs fed mainly on fish and/or dibranchiate cephalopods. Among fish-eaters stomach contents were rarely preserved while coprolites are commonly found. A reverse situation possibly exists regarding dibranchiate eating forms, stomach contents being commonly preserved but coprolites rarely. Both these diets suggest that ichthyosaurs in Liassic seas were predators on nectonic not benthonic animals. If at least two distinct dietary habits were established amongst Liassic ichthyosaurs, they could be explained by either selective predation, or feeding at different levels in the sea as in the sperm whale (Clarke 1962, p. 186). Drevermann (1914, p. 42) has suggested that in Upper Jurassic seas, virtually toothless ichthyosaurs like *Ophthalmosaurus* may have fed exclusively on naked cuttle fish. The suggestion put forward in an earlier section of this paper that some Liassic ichthyosaurs fed mainly on belemnoids is made with some reservation, as the known fossil belemnoids from the Lias where arm hooklets and hard parts occur in association are few and none too well preserved. The similarity of the ichthyosaurs in mode of life and diet to odontocete Cetacea, especially the sperm whale, has been suggested by several workers (e.g. Buckland 1835, p. 227, Kukenthal 1892, Branca 1908, and Wiman 1946).

Volume of food eaten. In the previous sections it has been shown that the gastric contents contain $478,000 \pm 250,000$ hooklets, and that each belemnite probably had about 300 arm hooklets. The gastric contents described here, therefore, could represent between 760 and 2,430 digested individual belemnites. The undigested organic hard parts of these belemnites accumulated in the stomach, much in the same way as arm hooklets and beaks of modern dibranchiates accumulate in the stomach of the sperm whale. Akimushkin (1955) records 28,000 squid beaks, representing 14,000 squids, and Clarke (1962) records 4,000 beaks plus 28 undigested squids, representing 2,160 squids, found in the stomachs of sperm whales caught in the North Pacific and Atlantic respectively. The length of time of accumulation of these belemnoid hooklets in the ichthyosaur stomach is impossible to ascertain. It could represent several meals or a lifetime's accumulation. Judging from the length of skull and relative size of the various bones it is probable that the ichthyosaur described was only a young specimen. In this particular specimen, therefore, the gastric contents might represent a lifetime's accumulation.

Mode of feeding. Several workers (i.e. Buckland 1836 and Seeley 1880) have suggested that the ichthyosaurs were voracious feeders, where the prey was swallowed whole without mastication, as in the sperm whale (Clarke 1956 and Clarke 1962). In the

teuthophagous whales the presence or absence of teeth makes very little difference to the efficiency of feeding (Clarke 1956). If a parallel situation existed amongst dibranchiate-eating Jurassic ichthyosaurs, the presence or absence of teeth could not be explained purely in terms of diet as suggested by Drevermann (1914). The sperm whale frequently has facial scars from squid tentacles (Clarke 1956), suggesting that the squids were swallowed head first. If belemnoids were eaten in this manner by Liassic ichthyosaurs, biting of the heads would cause separation of the hooked arms from the body with hard parts. Further significance of this comment is discussed below.

(b) *Digestive mechanism*

The ichthyosaurs appear to have swallowed their prey whole into a large expandable stomach where all the digestive breakdown took place (Buckland 1836). Chyme, including softened fish and reptile bones, passed into the intestine, and then the indigestible material was defecated as coprolites. In outline this digestive process is similar to that of the sperm whale (M. R. Clarke, pers. comm.). Undigested dibranchiate remains, hooklets, and possibly beaks accumulated in the stomach as they could not be passed on. The reasons for this accumulation are difficult to understand. Possibly the process was a defence mechanism on the part of the ichthyosaur to protect the delicate tissues of the posterior part of the digestive system from damage by the sharp undigested hooklets. The gastric contents could represent a gravity accumulation of indigestible material on the ventral side of the stomach in a very fluid chyme, produced by the digestive breakdown of cephalopod tissue. Such an explanation would account for the pockets of quartz grains found on the ventral side of the gastric mass (Pl. 72, fig. 2). A very fluid chyme might not have been able to transport the undigested matter through the pyrolic valve, as undoubtedly occurred with the viscous chyme produced from the digested fish remains, now preserved as coprolites. A third possibility is that the hooklets gripped in the ventral stomach wall and formed an interlocking network, trapping the quartz grains. This last suggestion could explain why the gastric contents of this specimen were not dispersed before burial, despite the slight dismembering of the skeleton.

The accumulation of such remains raises a number of problems for the ichthyosaur which can only be answered by further analogies with the sperm whale. Did these remains accumulate to the detriment of the animal, perhaps blocking the digestive tract and causing death? In the sperm whale the accumulated squid beaks are periodically vomited from the stomach (M. R. Clarke, pers. comm.). Ambergris frequently contains squid beaks and so may also aid this regurgatory process. Such mechanisms as these may have existed in the ichthyosaurs to clear inconvenient accumulations of hooklets from the stomach.

If Liassic ichthyosaurs frequently ate belemnoid dibranchiates, as has been suggested, another problem arises concerning the digestion of the crystalline calcite guards. Modern teuthophagous cetaceans have little difficulty in digestion of the conchiolinic or weakly calcified 'pens' of squids by solution in the stomach, but densely crystalline guards of the belemnites are much more difficult to destroy, as witnessed by their abundance in Mesozoic elastic sediments. As gastric contents with belemnoid guards are rare, or unknown, in ichthyosaurs three possible explanations are suggested:

1. Heads were bitten off and so guards were not swallowed. This seems an unlikely mechanism as in reptiles and modern teuthophagous cetaceans prey is swallowed whole.

2. The body with guard, phragmocone, and proostracum separated from the head in the stomach and was regurgitated. The habits of the sperm whale give some support for this suggestion as regurgitation of squids frequently occurs on capture of the whales, and in the digestive process in the stomach the bodies and heads of the squids separate at an early stage (Clarke 1956 and Clarke 1962).

3. The guards were dissolved, or broken up by gastroliths and then dissolved, by the chemical environment of the stomach. Difficulties with this possibility are that gastroliths are unknown in ichthyosaurs, and a very acid stomach environment would be necessary to have dissolved dense primary crystalline calcite.

However, of these suggestions processes 2 and 3 would seem to be the more likely. Other possible explanations may simply be that the ichthyosaurs, as modern cetaceans, primarily ate naked dibranchiates, or chemical solution of guard posed no problem for the digestive mechanism of the Liassic ichthyosaur.

Acknowledgements. I thank Dr. F. M. Broadhurst for help in extraction of the specimen and critically reading the manuscript, Dr. K. D. Adam, Dr. K. A. Joysey, and Dr. M. R. Clarke for offering many helpful suggestions, and Mr. P. A. Washbourne for help with photography. Mr. J. M. Edmunds and Mr. P. Powell of the Oxford University Museum gave access to Buckland's original material; the Assistant Keeper and Dr. M. K. Howarth of the British Museum (Natural History) and Dr. R. M. C. Eager of the Manchester Museum allowed me to examine specimens in their collections.

REFERENCES

- AGER, D. V. 1963. *Principles of Palaeoecology*. New York. 371 pp.
- AKIMUSHKIN, I. I. 1955. [The feeding of the Cachalot.] *Dokl. Akad. Nauk S.S.S.R.* **101**, 1139-40. (In Russian.)
- AUGUSTA, J. 1964. *Prehistoric Sea Monsters*. London, 65 pp., 21 pl.
- BRANCA, W. 1908. Nachtrag zur Embryonenfragen bei *Ichthyosaurus*. *Sber. preuss. Akad. Wiss* (1908), **1**, 392-6.
- BROWN, B. 1904. Stomach stones and food of plesiosaurs. *Science*, **20**, 184-5.
- BROWN, C. 1900. Über das Genus *Hybodus* und seine systematische Stellung. *Palaeontographica*, **46**, pp. 163 ff.
- BUCKLAND, W. 1835. On the discovery of Coprolites, or fossil faeces, in the Lias at Lyme Regis, and in other formations. *Trans. geol. Soc. Lond.* (2), **3**, 223-38, pls. 28-31.
- 1836. *The Bridgewater Treatises; Geology and Mineralogy*. London. 2 vols.
- BUCKMAN, J. 1879. On the *Belemniteuthis montefiorei*. *Proc. Dorset nat. Hist. antiq. Fld. Club.* **3**, 141-3, pl. 1.
- CLARKE, M. R. 1962. Stomach contents of a Sperm Whale caught off Madeira in 1959. *Norsk. Hvalfangsttid.* **5**, 173-91.
- CLARKE, R. 1956. Sperm Whales of the Azores. 'Discovery' *Rep.* **28**, 237-98.
- COLES, H. 1853. On the skin of *Ichthyosaurus*. *Q. Jl. geol. Soc. Lond.* **9**, 79-82, pl. 5.
- CRICK, G. C. 1897. *Acanthoteuthis speciosa* Munster. *Geol. Mag.* (4), **4**, 1-4, pl. 1.
- 1902. Note on the type specimen of *Belemniteuthis montefiorei*. *Proc. malac. Soc. Lond.* **5**, 13-16, pl. 1.
- 1907. On the arms of the belemnite. *Proc. malac. Soc. Lond.* **7**, 269-79, pl. 23.
- DREVERMANN, F. I. 1914. Die Meersaurier im Senkenberg Museum. *Senkenberg Naturforsch. Ges. Ber.* **45**, 35-48, 12 figs.
- FIRTION, F. 1938. Coprolithes du Lias Inferieur d'Alsace et de Lorraine. *Bull. Serv. Carte. geol. Als. Lorr.* **5**, 27-43, pls. 4-8.
- FRAAS, E. 1891. *Die Ichthyosaurier der sud-deutschen Trias und jura-ablagerunge*. Tubingen.
- HEKKER, E. L., and HEKKER, R. F. 1955. Ostatki Teuthoidea iz verkhnei yurii nizhnego mela Povolzhya. *Vop. Paleont.* **2**, 36-44, pls. 1 and 2. (In Russian.)

- HOFMANN, J. 1958. Einbettung und Zerfall der Ichthyosaurier im Lias von Holzmaden. *Meyniana*, **6**, 10–55, 30 figs.
- HUENE, F. VON. 1922. *Die Ichthyosaurier des Lias und ihre Zusammenhänge*. Berlin. 114 pp., 22 pls.
- HUXLEY, T. H. 1864. On the structure of the Belemnitidae; with a description of a more complete *Belemnites* than any hitherto known, and an account of a new genus of Belemnitidae *Xiphoteuthis*. *Mem. Geol. Surv. U.K. Monogr.* II. 22 pp., 3 pls.
- JELETSKY, J. A. 1966. Comparative morphology, phylogeny and classification of fossil Coleoidea. *Paleont. Contr. Univ. Kans., Mollusca* **7**, 1–162, pls. 1–25.
- JURAVLEV, K. J. 1943. The remains of Upper Jurassic sea reptiles at the Seveljevra shale mine. *Acad. Sci. U.S.S.R. Biol.* **5**, 293–306, 4 figs. (In Russian, English summary.)
- KUKENTHAL, W. 1892. Ichthyosaurier und Wale. *Neues. Jb. Miner. Geol. Paleont. Beil. Bd.* **1**, 161–6.
- LYDEKKER, R. 1889. *Catalogue of fossil Reptilia and Amphibia in the British Museum. Part II. Ichthyopterygia and Sauropterygia*. London. 303 pp.
- MANTELL, G. A. 1852. A few notes on the structure of the Belemnite. *Ann. Mag. nat. Hist.* (2), **10**, 14–19.
- MOORE, C. 1856. On the skin and food of ichthyosauri and teleosauri. *Rep. Br. Ass. Advmt. Sci.* (1856), 69.
- NAEF, A. 1922. *Die fossilen Tintenfische*. Jena. 322 pp.
- OWEN, R. 1844. A description of certain Belemnites preserved with a great proportion of their soft parts in the Oxford Clay. *Phil. Trans. R. Soc.* **134**, 65–85, pls. 2–8.
- 1881. The reptilia of the Liassic formations. Part III. *Ichthyosaurus*. *Palaentogr. Soc. (Monograph)*, pp. 83–130, pls. 21–33.
- PEARCE, C. 1842. On mouths of ammonites and fossils contained in laminated beds of the Oxford Clay, discovered in cutting of G.W.R. near Christian Malford in Wiltshire. *Proc. Geol. Soc. Lond.* **3**, 592–4.
- PIVETEAU, J. 1953. *Traité de paléontologie*. Vol. 2. Paris.
- QUENSTEDT, F. A. 1885. *Handbuch der Petrefaktenkunde*. Tübingen.
- ROMER, A. S. 1966. *Vertebrate Paleontology*. Chicago. 468 pp.
- SEELEY, H. G. 1877. *Mauisaurus gardneri*, an elasmosaurian from the base of the Gault at Folkestone. *Q. Jl. Geol. Soc. Lond.* **33**, 541–7, pl. 23.
- 1880. Report on the mode of reproduction of certain species of ichthyosaurs from the Lias of England and Wurtemberg. *Rep. Br. Ass. Advmt. Sci.* (1880), 68–76, pl. 1.
- SHIMANSKIY, V. N. 1949. O sistematičeskom položzenii rinkolitov. *Trudy Paleont. Inst.* **20**, 199–208.
- TARLO, L. B. 1959. *Pliosaurus brachyspondylus* from the Kimmeridge Clay. *Palaentology*, **1**, 283–91, pls. 51, 52.
- WILLISTON, S. W. 1904. The stomach stones of the plesiosaurs. *Science*, **20**, 565.
- 1914. *Water reptiles of past and present*. Chicago. 251 pp.
- WIMAN, C. 1946. Über Ichthyosaurier und Wale. *Senckenbergiana*, **27**, 1–11, pls. 1–3.
- WOODS, H. 1946. *Palaentology. Invertebrate*. 8th edn. Cambridge. 477 pp.
- WOODWARD, A. S. 1917. The so-called coprolites of ichthyosaurs and labyrinthodonts. *Geol. Mag.* (6), **4**, 540–2, pl. 34.
- WOODWARD, H. B., and USSHER, W. A. E. 1911. The geology of the country near Sidmouth and Lyme. *Regis. Mem. geol. Surv. U.K.*
- WURSTENBERGER, A. R. C. VON. 1876. Ueber Lias Epsilon. *Jh. Ver. vaterl. Naturk. Württ.* **32**, 193–358, pl. 4, figs. 1–16.
- ZITTEL, K. A. VON. 1913. *Textbook of Palaentology*. 2nd English edn. London.

JOHN E. POLLARD
Department of Geology
The University
Manchester 13

Typescript received 19 December 1966



1

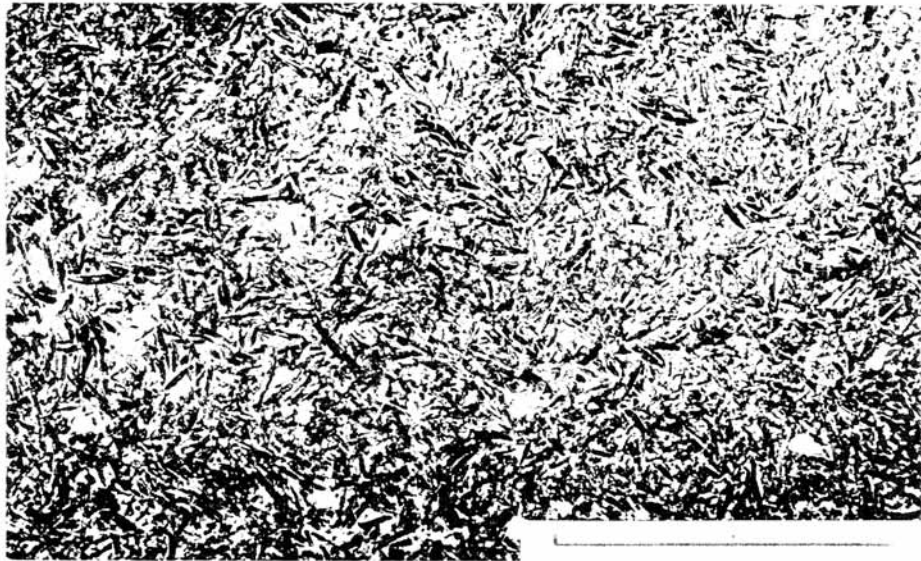


2

POLLARD, Ichthyosaur gastric contents



1



2

POLLARD, Ichthyosaur gastric contents