

STOMACH CONTENTS OF A LOWER TRIASSIC ICHTHYOSAUR FROM SPITZBERGEN

Marie-Céline BUCHY¹, Philippe TAUGOURDEAU² & Philippe JANVIER³

¹ Universität Karlsruhe, Geologisches Institut, Postfach 6980, D-76128 Karlsruhe, Germany.
mcbuchy@compuserve.com

Current address : Geowissenschaftliche Abteilung, Staatliches Museum für Naturkunde, Erbprinzenstrasse 13,
D-76133 Karlsruhe, Germany.

² 5, Villa Murat, F-75016 Paris, France.

³ Laboratoire de Paléontologie, Muséum national d'Histoire naturelle, 8, rue Buffon, F-75005 Paris, France.

Abstract : The stomach contents of a Lower Triassic ichthyosaur from Spitzbergen are here described for the first time. The stomach contents themselves are now lost, and the description relies on unpublished photographs and a description made in the 70's. The specimen is a juvenile that was previously identified as *Grippia longirostris*, but the re-examination of the specimen and original literature contradicts this attribution. It is here provisionally assigned to cf. *Merriamosaurus hulkei*. Its stomach contents consist of black hooks identified as the remains of belemnoid cephalopods and annelids, which have never before been described in this context. The hypothesis that these annelid remains represent the gastric contents of the preyed cephalopods is discussed. The specimen would then represent one of the rare examples of a partially preserved Mesozoic marine trophic web.

Key words: Ichthyosauria, Lower Triassic, diet, cephalopod hooks, annelids, stomach contents

Le contenu stomacal d'un ichthyosaure du Trias inférieur du Spitsberg

Résumé : Nous décrivons ici le contenu stomacal d'un ichthyosaure du Trias inférieur du Spitsberg. Ce contenu stomacal est aujourd'hui perdu, et la description est basée sur des photographies et descriptions datant des années 1970. Le spécimen est un individu juvénile, précédemment attribué à *Grippia longirostris*, mais le réexamen du spécimen et de la littérature originale contredisent cette identification. Il est provisoirement rapproché de cf. *Merriamosaurus hulkei*. Son contenu stomacal est composé de crochets noirs attribués à des céphalopodes belemnoides, et des restes d'annélides, qui n'ont jamais été décrits dans ce contexte. Nous discutons l'hypothèse que ces restes d'annélides représentent le contenu stomacal des céphalopodes ingérés. Le spécimen serait alors l'un des rares exemples d'un réseau trophique marin du Mésozoïque partiellement préservé.

Mots clés : Ichthyosauria, Trias inférieur, régime alimentaire, crochets de céphalopodes, annélides, contenu stomacal

INTRODUCTION

At the end of the 70's, two of the authors (Ph. T. and Ph. J.) observed a whitish deposit sprinkled with small black elements in the abdominal region of an ichthyosaur, coming from the Scythian of Mount Ibsen, Spitzbergen (specimen number SVT 203, Muséum national d'Histoire naturelle, Paris [MNHN]) then assigned to *Mixosaurus* sp., as most Triassic ichthyosaurs of this origin were pending further investigation. The study and identification of the

pieces that constitute the gastric contents proved to be delicate, some recalling scolecodonts, others cephalopod hooks, and the manuscript prepared at that time was not published.

Later, Mazin (1981) assigned this incomplete specimen to *Grippia longirostris* Wiman, 1929. Here we refer the specimen to the recently erected taxon *Merriamosaurus (Rotundopteryx) hulkei* (Maisch & Matzke, 2000 ; Maisch & Matzke, 2002 ; 2003) as is discussed below in detail.

Today, the area where the stomach contents were located is still visible, but the black structures are piecemeal and no longer identifiable. A sample observed with optical microscope and SEM provided no further information. Acidic etching was also unsuccessful. Therefore, the photographs taken in the late 70's by Ph.T. (now hold by M.-C.B.) remain the only evidence for the existence of the gastric contents. Despite the loss of the contents and the poor quality of the original photographs, no other material yielding information on the diet of Lower Triassic ichthyosaurs has yet been discovered, while stomach contents of later ichthyosaurs are well known and have long been studied (Moore, 1857; for reviews see Pollard, 1968 and Böttcher, 1989). Moreover, they contain the possible remains of annelids, which have never been described in this context. The aim of this paper is therefore to document a unique specimen which would otherwise be lost for ever.

TAXONOMY

The genus *Grippia* with its type species *G. longirostris* was erected by Wiman in 1929 [the original description was printed 1928 in the volume of the Bulletin of the Geological Institution of the University of Upsala for the years 1927-1930 and actually published in 1929, hence some confusion in the date of erection of the new taxon. We here keep the publication year 1929 as subsequent authors did (Mazin, 1981; Maisch & Matzke, pers. comm.)] on the basis of a fragmentary skull and propodials, preserved in a calcareous nodule ("Konkretion 1", or "Gripps Exemplar" of Wiman, 1929, 1933) from the Sticky Keep Formation (Lower Triassic) of Spitzbergen. Later, Wiman received fifteen more concretions discovered during two Norwegian expeditions in Spitzbergen in 1929 and 1930, and described the material as referred specimens of *Grippia longirostris* (Wiman, 1933). Although coming from different localities, this material comprises both cranial and postcranial elements, some nodules with cranium and rostral postcranial elements, others with rostral postcranial and more caudal postcranial elements, and altogether provided a quite complete overview of the osteology of the species (Wiman, 1933, provides an exhaustive list of the concretions and their contents).

Unfortunately, the type material kept in Hamburg was destroyed during World War II (Maisch & Matzke, 1997; pers. comm.). In 1969, a French CNRS / MNHN expedition to Spitzbergen collected three nodules containing ichthyosaurian fragments (MNHN, specimens SVT 201, 202 and 203) coming from two different localities. First assigned to *Mixosaurus* sp., these specimens were later identified by Mazin (1981) as belonging to *Grippia longirostris*, on the basis of SVT 201 and 202 which comprise skull fragments similar to the type material of Wiman (1929, 1933). The third nodule, SVT 203, consists of seven aligned dorsal vertebrae, ribs, a femur, partial pelvic girdle, a tibia or fibula, metapodials, and the gastric contents described herein. This nodule was the basis of the latest re-description of the postcranial osteology of the species by Mazin (1981). Yet, the nodule lacks cranial parts that could be referred to the holotype of *Grippia longirostris*, and the femur, pubis and ischium of SVT 203 as preserved and depicted by Mazin (1981: figs. 8, 9) differ from the referred material of Wiman (1933: pl. II, figs. 6-9). The pubis of SVT 203 shows a caudally open obturator recessus (Mazin, 1981: fig. 8), whereas the pubis of *Grippia longirostris* as described by Wiman (1933: pl. II, figs. 7, 8) on the basis of referred material possesses an obturator foramen. Mazin (1981) interprets this difference as either individual variation or related to the young individual age of SVT 203. Yet, in their phylogenetic analysis of the Ichthyosauria, Maisch & Matzke (2000) observed an obturator foramen in early ichthyosaurs, like for example in *Grippia*, *Utatusaurus*, *Chaohusaurus*, and *Mixosaurus* while the obturator recessus is seen in later ichthyosaurs, like *Besanosaurus*, *Shastasaurus* or *Shonisaurus*. Moreover, *Mixosaurus* is the only Triassic genus for which juvenile specimens are known sufficiently well, which also show the closed condition (Maisch & Matzke, pers. comm.). The attribution of the isolated specimen SVT 203 to *Grippia longirostris* (Mazin, 1981) is therefore inconclusive and is not followed here.

The femur of SVT 203 (Mazin, 1981: fig. 9) resembles unpublished material of the recently described *Merriamosaurus hulkei* (Maisch & Matzke, 2000) from the Sticky Keep Formation of Spitzbergen, except for its small size compared to that of the type and referred material (Maisch & Matzke, 2000; 2002;

2003 pers. comm.). *Merriamosaurus hulkei* was erected on the basis of redescribed material collected during the two CNRS / MNHN expeditions in Spitzbergen of 1964 and 1969. Hence, assuming the size difference is due to the young age of individual SVT 203, this specimen is here referred to as cf. *Merriamosaurus hulkei*, pending further investigation.

DESCRIPTION

The specimen SVT 203 is preserved in a phosphatic limestone nodule (Mazin, 1981). Because of the hardness of the matrix, most of the bones were removed in order to obtain casts (Mazin, pers. comm.). Therefore, only their external moulds remain today on the two parts of the open nodule. The bones are a little dislocated (fig. 1). The skeletal elements were described and figured by Mazin (1981). The gastric contents are located in the abdominal region, among the ribs, cranial to the pelvic girdle. They appear as a whitish deposit, formerly containing numerous black hooks (fig. 2). Today, this deposit is still sprinkled with small black elements, but they do not present any identifiable shape.

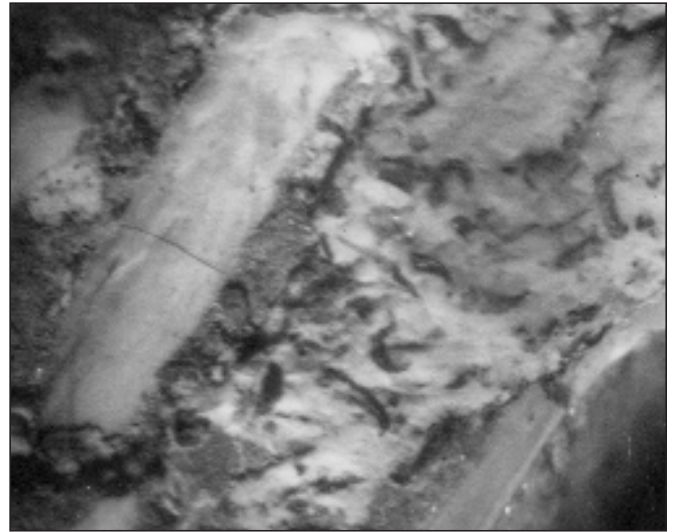


Figure 2 : Original photograph from the unpublished manuscript by Taugourdeau & Janvier. Detail view of the stomach contents of SVT 203, among ribs, magnified 15 times.

Figure 1: Schematic drawing of the specimen SVT 203 from the Lower Triassic of Spitzbergen, as preserved today. The stomach contents are shown in dark grey, the samples taken in light grey. Ph: phalanx; mt: metapodial. Scale bar 10 mm.

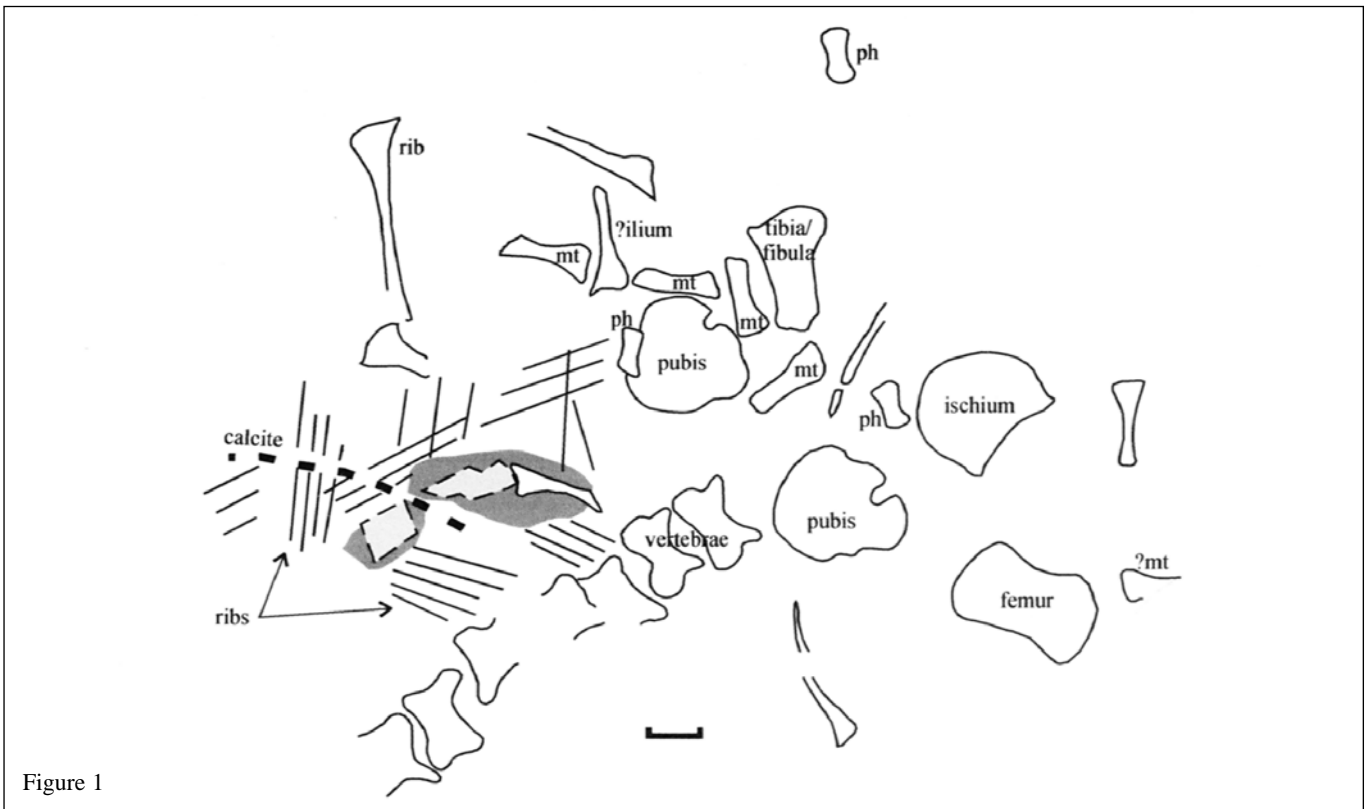


Figure 1

DISCUSSION

Despite its outlines altered by samples taken, the gastric contents still appear to be organised into two oval 10 mm-wide parts, respectively 10 and 30 mm-long, separated by a calcite vein. The partition might be due to this calcite vein.

Six types of elements were recognised inside the gastric contents (Taugourdeau & Janvier, unpublished data). As none could be re-identified, here we translate the original descriptions in French given in the unpublished manuscript by Taugourdeau & Janvier, and present the original photographs accompanying it (figs. 2, 3).

- 1) A 370 μm -long piece, consisting of a straight shaft with a pointed apex, and a rounded curved base as long as the shaft, forming a 45° angle with it; small spur; basal opening hardly visible, extending on the entire length of the base (fig. 3a, arrow).
- 2) Partial assemblage of two hooks at right angle. The 350 μm -long “upper” hook is strongly curved, with a carinated shaft regularly enlarging towards its base. The 250 μm -long “lower” hook is badly preserved, with a similar morphology, except for a possibly bifid base (fig. 3b).
- 3) Fragmented 1 mm-long remains of what was probably a very long element, straight and cylindrical for three-quarters of their length, terminated by a strongly curved conical apex (fig. 3c).
- 4) Triangular element, 600 μm in length, moderately curved in its apical half, with a base at least half wide as the entire height (fig. 3d).
- 5) Subspherical particles, 30 μm in diameter, with a granular surface sculpture, presenting a slight equatorial ridge, apparently in groups of two to three (fig. 3e).
- 6) Partial assemblages, composed of two elongate straight hooks parallel to one another, with a prominent spur. The length of the hooks varies from 550 μm to 400 μm . Between the two hooks is an elevated area being smoother than the surrounding sediment, ornamented with fine veins, some of them apparently anastomosed (fig. 3a star, 3f).

Anatomical situation of the gastric contents

The gastric contents of SVT 203 appear to be organised into two parts. Böttcher (1989), on the basis of numerous gastric contents of ichthyosaurs from the German Toarcian, suggests that ichthyosaurs stomachs consisted of at least two chambers. In a first muscular chamber, digestion would have been initiated, and cephalopod hooks separated from digestible parts and accumulated there prior to regurgitation. Described stomach contents of ichthyosaurs (e.g. Pollard, 1968) would correspond to the contents of this first chamber. The digestion would have been completed in a second chamber, preserved as a whitish or yellowish deposit without hooks. As both parts of the gastric contents of SVT 203 preserved hooks, the partition observed on the specimen therefore does not correspond to the anatomical partition described by Böttcher (1989).

Cephalopod hooks and other hook-like structures

Hooks discovered in stomach contents of marine reptiles are always attributed to cephalopods (see Pollard, 1968 for a historical review). Some annelids possess chitinous masticatory pieces, which are usually more complex in shape, with a flat base and denticles (e.g. Taugourdeau, 1968; Zawidzka, 1971; Kozur, 1972; Fauchald, 1977), as are mobile pieces of crustaceans' appendages and gastropods' radulas (Barnes, 1986).

Engeser & Clarke (1988) propose a commented review of recent and fossil cephalopods hooks. The arms of several recent teuthoid cephalopods possess chitinous hooks instead of suckers, yet, the structure and ontogeny of these recent hooks appear different from what can be suggested for pre-Tertiary cephalopods. It is even not clear whether pre-Tertiary hooks were chitinous or not (for a discussion see Engeser & Clarke, 1988). According to the fossil record, hooks were restricted to the arms of phragmo-teuthid, belemnoteuthid and belemnite belemnoid cephalopods. These cephalopods, known from the Devonian to the end of the Cretaceous (Moore, 1962-75), possessed 20 to 100 pairs of hooks per arm. The hooks were hollow, with their base inserted in the soft tissues to a level marked by a scar (Engeser & Clarke, 1988).

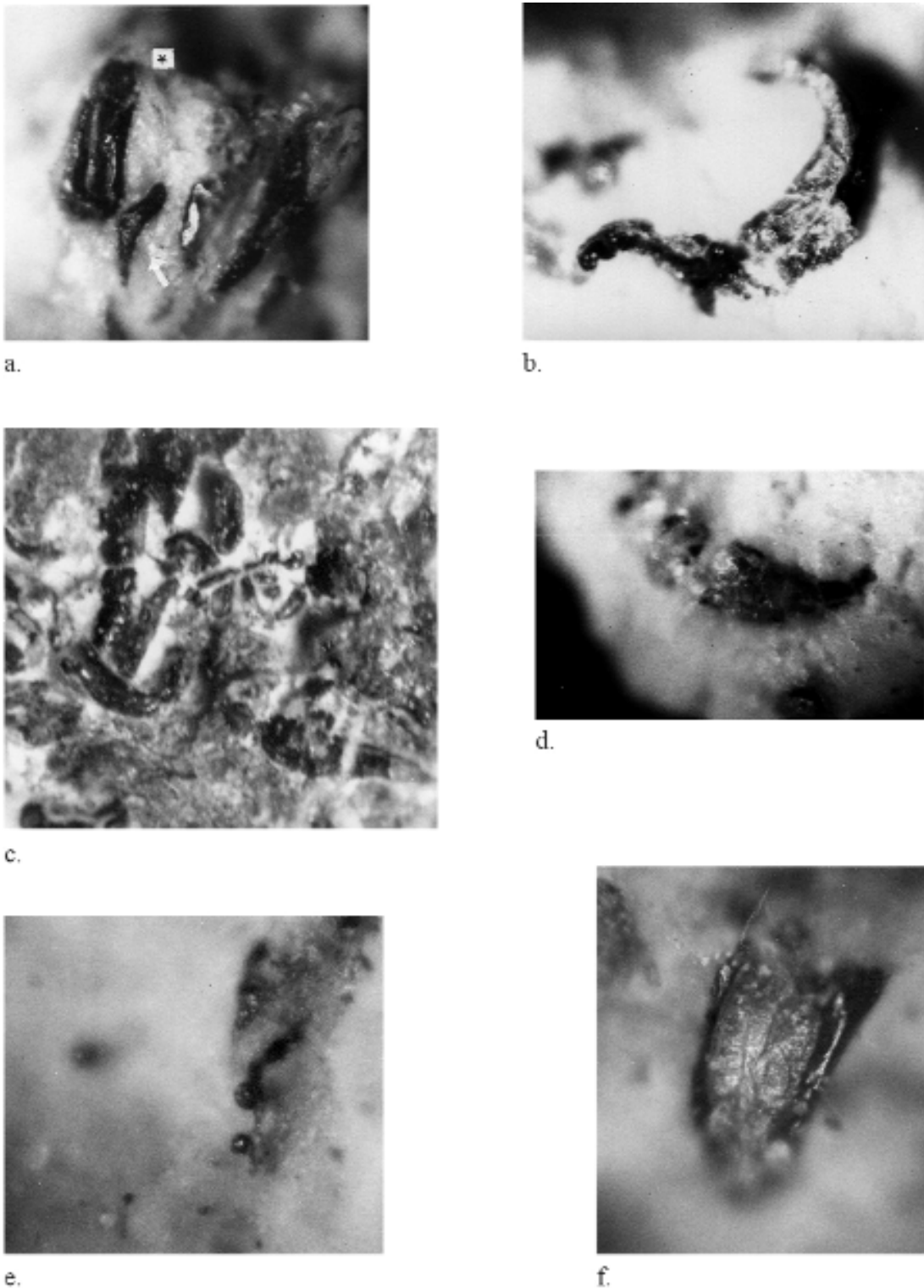


Figure 3 : Original photographs from the unpublished manuscript by Taugourdeau & Janvier. These were taken in the late 70's and no scale was inserted for technical reasons. 3a. Arrow. Undetermined belemnoid cephalopod hook, 370 μm -long. Close to *Cornuncus* Kulicki & Szaniawski, 1972, and "g" type of Engeser & Clarke (1988). 3a. Star. See 3f. 3b. Partial assemblage of two undetermined belemnoid cephalopod hooks. Length of the larger hook: 350 μm , of the smaller: 250 μm . The hooks are similar to the classical type "a" of Engeser & Clarke (1988). 3c. Possible belemnoid cephalopod hook, 1 mm in length, close to *Deinuncus brevirostris* or *Longuncus longus* (Kulicki & Szaniawski, 1972). 3d. 66 μm -long hook, identified either as a belemnoid cephalopod hook or as a scolecodont (see text). 3e. Subspherical particles 30 μm in diameter, interpreted as possible annelid paragnaths (see text). 3f and 3a. Star. Partial assemblage of two parallel hooks, 550 to 400 μm in length. The hooks resemble the type "g" of Engeser & Clarke (1988), while the area between them could be the external mould of an undetermined organ.

Riegraf & Hauff (1983) suggest that one pair of arms in belemnitids was longer, armed with a pair of hooks larger than the others (the onychites, reaching 60 mm in length, Maisch, pers. comm.), while Engeser & Clarke (1988) consider these large hooks as a sexual character, and that the ten arms of belemnitids were of the same length, like those of all belemnoids.

According to Engeser & Clarke (1988), a single arm carries hooks of different sizes. This review mainly takes into account taxa where hooks are associated with soft parts, i.e. 14 taxa, most of them known from incomplete specimens. In one case only, *Acrocoelites (Toarcibelus) rauti*, a belemnitid from the German Posidonia Shales, Engeser & Clarke (1988) recognise two types of hooks along one single arm. Yet, compared to the expected diversity of the group during its geological range, the number of taxa known with soft parts appears too small to conclude that most belemnoids possessed hooks of the same shape on one arm. So, in the case of stomach contents with several types of hooks preserved, it is impossible to judge how many cephalopod taxa were actually preyed upon. Moreover, to our knowledge, no hint exists on the variation of size and/or shape during ontogeny, or on the biological significance of the eight variations of the typical hook morphology recognised by Engeser & Clarke (1988).

When found in the stomach contents of marine reptiles, cephalopod hooks are usually simply mentioned but not properly described (e.g. Keller, 1976; Massare, 1987; Efimov, 1997), preventing any comparison with the hooks described by Engeser & Clarke (1988). In contrast Pollard (1968), Martill (1986) and Böttcher (1989), provide a precise description of the hooks inside stomach contents, respectively of an ichthyosaur (cf. *Ichthyosaurus communis*) from the Lower Lias of Lyme Regis (England), of an indeterminate metriorhynchid crocodylian from the Callovian of Peterborough (England) and of a specimen of the ichthyosaur *Temnodontosaurus burgundiae* (now *T. trigonodon* Maisch, 1998) from the German Toarcian. In all three specimens, several hook types are associated inside the stomach contents, in different proportions, but these studies are concerned only with parts of the contents, and as noticed by Pollard (1968), Martill (1986), Böttcher (1989) and above, it is impossible to draw any conclusion upon

the number of different prey ingested. Pollard (1968) recognises four types, Martill (1986) two, and Böttcher (1989) three. Most of these types can be referred to the classical “a” type of Engeser & Clarke (1988), with the exception of types “D” of Pollard (1968) and “3” of Böttcher (1989), referred with doubt to the type “g” (see below), but which could also represent another group, only known in this context.

Identification of the elements in the stomach contents of SVT 203

From their morphology, having no denticles and an apparently hollow subcylindrical base, three types of elements are here identified as cephalopod hooks (fig. 3a arrow, b, c), even if they are small (some tens of μm) compared to cephalopod hooks as usually described (a few mm long, Engeser & Clarke, 1988). As noted above, it is unknown whether this size difference can be related to the size of the prey, or to different types of prey.

- 1) This hook (fig. 3a arrow) is close to the parataxon *Cornuncus* Kulicki & Szaniawski 1972, from the Middle Jurassic of Poland, despite being wider with a shorter base. This parataxon corresponds to the type “g” of Engeser & Clarke (1988). It is only known as isolated hook, yet identified by Engeser & Clarke (1988) as surely belonging to a belemnoid cephalopod.
- 2) The only mention, to our knowledge, of a carinated cephalopod hook is given by Böttcher (1989). Despite this, the general shape of both associated hooks (fig. 3b) is of the classical “a” type. Several preserved arms of cephalopods exhibit opposed paired hooks (Engeser & Clarke, 1988), and it might also be the case here.
- 3) The apical hooks of these long elements (fig. 3c) resemble the classical type. If the base actually belongs to the hook, then they come close to the parataxa *Deinuncus brevirostris* and *Longuncus longus* (Kulicki & Szaniawski, 1972). These hooks are attributed to belemnoid cephalopods, yet are not taken into account by Engeser & Clarke (1988) because they are only known as isolated elements.

Two of the remaining hook-like structures cannot be identified with such certainty.

The base of the hook in figure 3d appears broken

and/or crushed, it would then correspond to the classical type “a” of Engeser & Clarke (1988). If the base was actually flat as it appears on the original photograph (fig. 3d), it would more resemble a scolecodont, despite the absence of denticles.

The smooth area located between two hooks in figure 3a (star) and 3f was interpreted by Taugourdeau & Janvier (unpublished data) as the external mould of an organ of undetermined nature. The hooks themselves resemble the type “g” of Engeser & Clarke (1988), and depending on the orientation of the camera, it could be a fragment of a belemnoid arm with two opposed hooks.

The small globular pieces (fig. 3e) are here referred to polychaete worms, even if their preservational status and isolated condition allow no more precise identification. Among polychaete worms, some members of the family Nereidae possess paragnaths, i.e. chitinous denticles, some tens of μm in size, assembled in clusters on the proboscis (Fauvel, 1958; Fauchald, 1977). The elements in the stomach contents of SVT 203 shown in figure 3e present a similar size and hypothetical chitinous nature, and they are apparently assembled in clusters of two to three, though they are globular whereas typical nereid paragnaths are either conical or rod-shaped (Fauchald, 1977).

Although cephalopod hooks are classically known from ichthyosaur stomach contents (Pollard, 1968; Massare, 1987), annelid paragnaths are described in this context for the first time. One explanation for this absence might be that these small elements were overlooked among stomach contents sometimes consisting of thousands of hooks, most of them, primarily hollow, being crushed (Engeser & Clarke, 1988). The black substance surrounding the hooks in many ichthyosaur stomach contents, interpreted either as coloured by the ink of ingested cephalopods (Pollard, 1968) or remnants of their beaks distorted and partly digested (Engeser & Clarke, 1988), certainly did not help the identification of these small elements. Annelids are a regular component of the diet of some recent cephalopods (Amaratunga, 1983). It appears therefore likely that the paragnaths were present in the digestive tract of the cephalopods ingested by the ichthyosaur. Under this hypothesis, the paragnaths underwent a partial digestion by the cephalopods, prior to digestion by

the ichthyosaur, and mechanical actions of the stomach and other components of the food intake, which would also explain their granular surface even when chitine is not easily affected by gastric juices (Bocherens, 1992). It would also be a reason why certain scolecodonts are not recognised within the stomach contents of SVT 203, or of any other marine reptile. The bases of scolecodonts are flat and thin structures, hence in contact with the gastric acids over a large surface when ingested. Scolecodonts should be more rapidly dissolved, or at least made more quickly unidentifiable, than conical paragnaths which are more massive elements. From their shape, scolecodonts are also more subject to crushing and breakage than paragnaths. This hypothesis would easily explain the rounded shape of the elements in figure 3e, compared to classical conical paragnaths of nereids, the apex of which should be dissolved, abraded or broken first.

Two other explanations for the presence of paragnaths in the stomach contents of SVT 203 would be plausible: the annelids having been directly preyed upon by the ichthyosaur, or a post-mortem association by accident or through scavenging by worms. However the first of these hypotheses would not explain the absence of certain scolecodonts in the stomach contents, under the assumption of a single digestive cycle, while the second would not take into account the poor state of preservation of the paragnaths, having not been digested. It appears more likely that the stomach contents of the ichthyosaur is composed of cephalopod hooks, and of the remains of annelids that the cephalopods in turn preyed upon. SVT 203 would then document a partial trophic web, imprecise at specific levels, only known until now for Mesozoic marine reptiles from an unpublished Australian pliosaur having in the abdominal area an elasmosaur and its gastric contents composed of gastropods (McHenry in prep.; pers. comm.).

A last remark concerns the tooth morphology of the specimen in relation to its diet. The only two fragmentary teeth known of *Merriamosaurus hulkei* are described as “typically ichthyosaurian”, and their preservation prevents any precision (Maisch & Matzke, 2002; 2003). Massare (1987) attributes a grasping function to these ichthyosaurian teeth, and links them with a diet composed mainly of cephalopods. According to the observations of one of

us (M.-C.B.), the tooth morphologies of ichthyosaurs are in fact more diverse, especially concerning features like the massiveness of the crown, the shape of the apex and the ornamentation pattern, differences which have not been taken into account by Massare (1987) in her general review of Mesozoic marine reptiles trophic regimes. Even if SVT 203, which lacks teeth, is actually a juvenile specimen of *Merriamosaurus hulkei*, too little is known about the tooth morphology of the taxon, to determine a functional relationship between the tooth morphology and the diet of the specimen. In a similar way, the functional morphology of the cephalopods it preyed upon cannot be determined either, because of imprecise specific and anatomic identification of both the prey and the predator.

ACKNOWLEDGEMENTS

M.-C.B. gratefully thanks J.-M. Mazin (Poitiers) who gave her access to the unpublished manuscript, and for discussion. E."D." Frey (Karlsruhe) read this manuscript and greatly improved it by asking the right questions. He also brought essential logistical support to M.-C.B. Special thanks go to J.J. Liston (Glasgow) for English corrections _ once more. M.W. Maisch and A.T. Matzke (both Tübingen) brought valuable information about Triassic ichthyosaurs, and gave us access to literature in press and to their excellent drawings of the unpublished Paris material. Additionally M.W. Maisch, together with N. Bardet (Paris), made excellent suggestions as reviewers.

Note added in proof

It lately came to our knowledge that Motani (2000) already discussed the identification of the specimen SVT 203, suggesting it to be either a helvetiosaur or a placodont. We do not follow this hypothesis, the specimen being clearly ichthyosaurian (Maisch pers. comm.). Our interpretation of the remains is not modified.

REFERENCES

- AMARATUNGA T. 1983. The role of cephalopods in the marine ecosystem. *FAO fish. Tech. Pap.*, **231**: 379-415.
- BARNES R.D. 1986. Invertebrate zoology. *5th édition, Saunders College Publishing*, 893 pp.
- BOCHERENS H. 1992. Biogéochimie isotopique (¹³C, ¹⁵N, ¹⁸O) et paléontologie des Vertébrés: applications à l'étude des réseaux trophiques révolus et des paléoenvironnements. *Thèse de Doctorat de l'Université Paris VI, Mem. Sci. Terre*, **92**(6), 317 pp.
- BÖTTCHER R. 1989. Über die Nahrung eines *Leptopterygius* (Ichthyosauria, Reptilia) aus dem süddeutschen Posidonienschiefer (Unterer Jura) mit Bemerkungen über den Magen der Ichthyosaurier. *Stutt. Beitr. Naturk.*, B **155**: 1-19.
- EFIMOV V.M. 1997. A new genus of ichthyosaurs from the Late Cretaceous of the Ulyanovsk Volga Region. *Paleont. J.*, **31**(4): 422-426.
- ENGESER T.S. & CLARKE M.R. 1988. Cephalopod hooks, both recent and fossil. *The Mollusca*, **12**: 133-151.
- FAUCHALD K. 1977. The Polychaete worms. Definitions and keys to the Orders, Families and Genera. *Nat. Hist. Mus. Los Angeles County, Sci. Ser.*, **28**: 1-190.
- KELLER T. 1976. Magen- und Darminhalte von Ichthyosauriern des süddeutschen Posidonienschiefers. *N. Jb. Geol. Paläont., Mh.*, **5**: 266-283.
- KOZUR H. 1972. Die Bedeutung der triassischen Scolecodonten insbesondere für die Taxonomie und Phylogenie der fossilen Eunidica. *Mitt. Ges. Geol. Bergbaustud.*, **21**: 745-776.
- KULICKI C. & SZANIAWSKI H. 1972. Cephalopod arm hooks from the Jurassic of Poland. *Acta Pal. Pol.*, **17**(3): 379-419.
- MAISCH M.W. & MATZKE A.T. 1997. *Mikadocephalus gracilirostris* n.gen., n.sp., a new ichthyosaur from the Grenzbitumenzone (Anisian-Ladinian) of Monte san Giorgio (Switzerland). *Paläont. Z.*, **71**(3/4): 267-289.
- _____. 2000. The Ichthyosauria. *Stutt. Beitr. Naturk., Serie B*, **298**: 1-159.
- _____. 2002. Observations on Triassic ichthyosaurs. Part IX. The first associated skeletal remains of *Merriamosaurus* n.g. (Ichthyosauria, Lower Triassic) and their bearing on the systematic position of the Omphalosauria. *N. Jb. Geol. Paläont. Abh.*, **226**(1): 59-94.
- _____. 2003. Observations on Triassic ichthyosaurs. Part X: The Lower Triassic *Merriamosaurus* from Spitzbergen - additional data on its anatomy and phylogenetic position. *N. Jb. Geol. Paläont. Abh.*, **227** (1): 93-137.
- MARTILL D.M. 1986. The diet of *Metriorhynchus*, a Mesozoic marine crocodile. *N. Jb. Geol. Paläont., Mh.*, **10**: 621-625.
- MASSARE J.A. 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. *J. Vert. Pal.*, **7**(2): 121-137.
- MAZIN J.-M. 1981. *Grippia longirostris* Wiman, 1929, un Ichthyopterygia primitif du Trias inférieur du Spitzberg. *Bull. Mus. Natl. Hist. nat., Paris*, 4è ser., **3**(4), C: 317-340.
- MOORE C. 1856. On the skin and food of Ichthyosauri and Teleosauri. *Rep. 36th meeting Brit. Ass. Adv. Sci.*, 69-70.
- MOORE R.C. 1962-75. Treatise on invertebrate paleontology. *University of Kansas Press*, 24 vol.
- MOTANI R. 2000. Skull of *Grippia longirostris* : no contradiction with a diapsid affinity for the Ichthyopterygia. *Palaeontology*, **43** (1):1-14 .
- POLLARD J.E. 1968. The gastric contents of an Ichthyosaur from

- the lower Lias of Lyme Regis, Dorset. *Palaeontology*, **11**(3): 376-388.
- RIEGRAF W. & HAUFF R. 1983. Belemnitenfunde mit Weichkörper, Fangarmen und Gladius aus dem Untertoarcium (Posidonienschiffer) und Unteraalenium (Opalinuston) Südwestdeutschland. *N. Jb. Geol. Paläont., Abh.*, **165**: 466-483.
- TAUGOURDEAU P. 1968. Les scolécodontes du Siluro-Devonien et du Carbonifère de sondages sahariens. *Rev. I.F.P.*, **23**: 1219-1270.
- WIMAN C. 1929. Eine neue Reptilien-Ordnung aus der Trias Spitzbergens. *Bull. Geol. Inst. Univ. Upsala*, **22**: 183-196.
- WIMAN C. 1933. Über *Grippia longirostris*. *Nova Acta Reg. Soc. Sci. Upsaliensis*, **9**(4): 1-19.
- ZAWIDZKA K. 1971. A polychaete jaw apparatus and some scolecodonts from the middle Triassic. *Acta Geol. Pal.*, **21**(3): 361-377.