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Reliability: Category 2B, functional morphology.

6AIIi Vertebrate predation on cephalopods (Figs. 184, 185)

EXAMPLES OF VERTEBRATE PREDATION ON CEPHALOPODS IN THE LATE CRETACEOUS OF THE WESTERN INTERIOR*

J.D. Stewart and Kenneth Carpenter

Predator-prey relationships are an integral part of modern communities, and there is abundant fossil evidence, seen as punctures, borings, abrasions, etc. (summarized in Bishop, 1975), to demonstrate these relationships in the geologic past. Study of predation evidence in the fossil record forms the basis for reconstructing these relationships. Evidence for predation of ammonites has received considerable attention. For example, Kauffman and Kesling (1960) documented mosasaur predation on an ammonite. Saul (1979) implicated a mosasaur as the source for punctures in another ammonite. Over fifty additional specimens of damaged ammonites, some with their living chambers bitten off, show the importance of ammonites in the diet of mosasaurs (Kauffman, this volume). Ammonites may also have been important in the diet of some plesiosaurs (Brown, 1904). Kennedy and Cobban (1976) have reviewed the literature on predated ammonites, but these authors incorrectly maintained that Frentzen (1936) described *Amaltheus* from saurian stomach contents. Frentzen believed that the animal which produced the mass may have been a fish, but he specifically discounted a reptilian origin for the concretion.

Ammonites may also have contributed to the diet of some Late Cretaceous fish, as suggested by a small

* Acronyms used to represent the following collections: KUVP = University of Kansas Vertebrate Paleontology collection; FFM = Fick Fossil Museum, Oakley, Kansas; UCM = University of Colorado Museum.

coprolite collected in the zone of *Clioscaphites choteauensis* in the Smoky Hill Chalk Member of the Niobrara Formation in sec. 13, T6S, R19W, Rooks County, Kansas. The specimen, KUVP 25870, is 1.8 cm × 1.44 cm and contains, in addition to elements of unidentified small bony fishes, a juvenile ammonite which has a maximum preserved width of 0.83 cm (Fig. 184A). W.A. Cobban (personal communication to Stewart) identified the ammonite as an undeterminable scaphitid of the *Scaphites–Clioscaphites* group. It possibly represents *C. choteauensis*, as this is the only abundant scaphitid in this horizon. The outer whorl of the ammonite is filled with coprolitic matrix, in contrast to the inner whorl's calcite filling. Like most ammonites from the Smoky Hill Chalk, none of the original aragonitic shell is preserved due to diagenetic dissolution. The sutural surface at the anterior terminus of the preserved portion of the

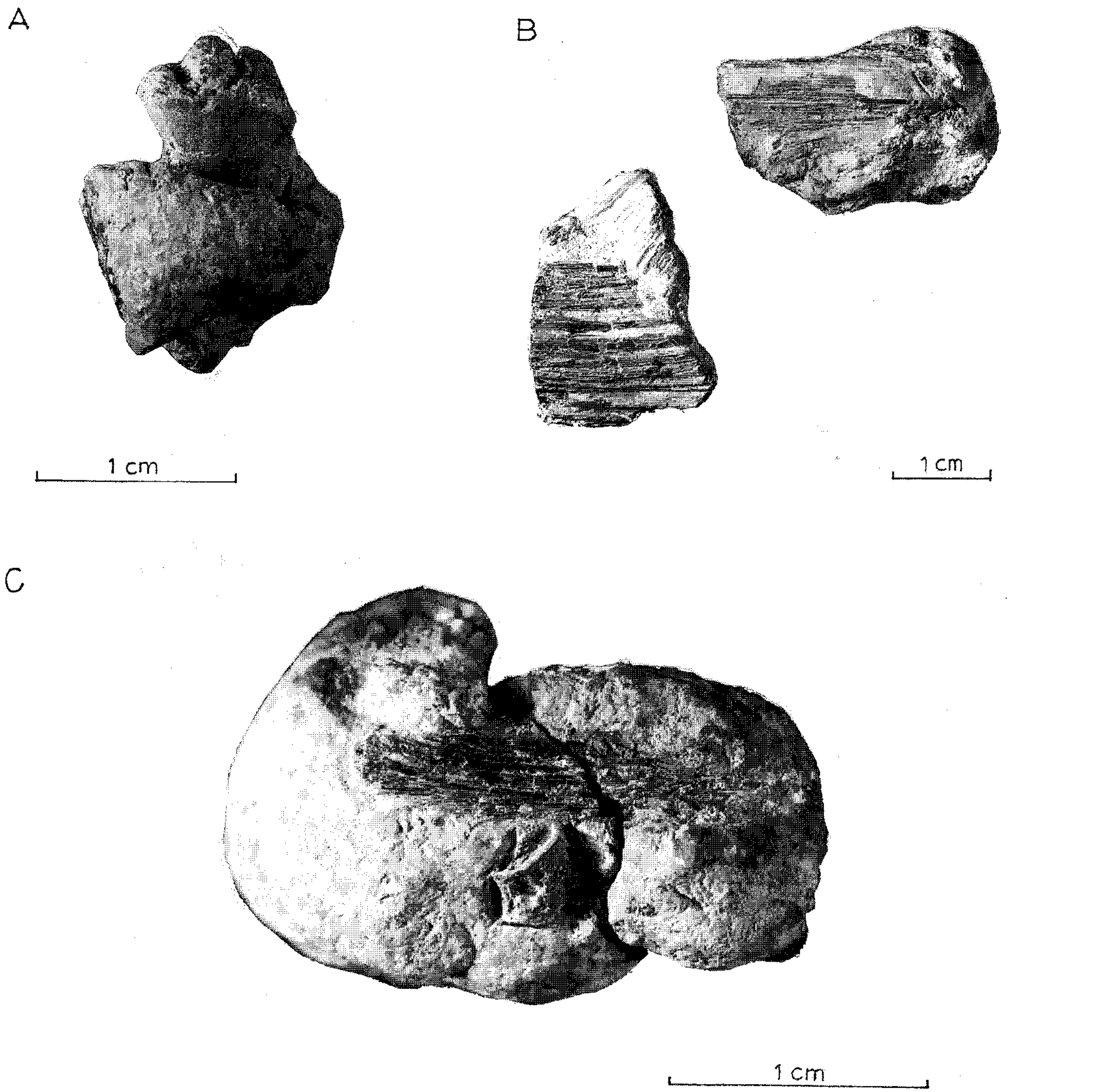

Fig. 184. Coprolites from the Niobrara Formation of Kansas. A. Coprolite with scaphitid inclusions; KUVP 25870. B. Associated coprolites containing rachis fragments of *Tusoteuthis longa*; KUVP 65095. C. Coprolite containing small rachis fragments of *Tusoteuthis longa* and teleostean vertebrae; KUVP 65730.

shell indicates that at least the living chamber has been broken away, presumably as a result of its ingestion or through digestion. An adjacent impression of a scaphitid ribbed whorl fragment may belong to this or another individual.

Squid may have been another cephalopod important in the diet of some Late Cretaceous marine vertebrates. Predation on squids was a common occurrence in the Pierre and Niobrara seaways as indicated by numerous fragmented and distorted gladii (Carpenter, unpublished notes; Stewart, unpublished notes). Several coprolites with squid inclusions further substantiate this idea. Two associated coprolites, KUVP 65095, were collected from the Smoky Hill Chalk in the same section as KUVP 25870, the coprolite with the scaphitid. The two coprolites (Fig. 184B) measure 3.34 cm × 2.0 cm and 2.79 cm × 2.06 cm and contain three fragments of a kelaenid teuthid rachis. Although four genera and five species of teuthids have been described from the Niobrara Formation of Kansas, all are assignable to the taxon *Tusoteuthis longa* (J.D. Stewart, 1977; Nicholls and Isaak, 1987; Waage and Stewart, in preparation). The ventral median cleft of the rachis is visible in the rachis fragments in KUVP 25870, confirming the identification as *Tusoteuthis*. An exposure of the Smoky Hill Chalk near its contact with the Pierre Shale in E1/2 sec. 15, T14S, R31W, Gove County, Kansas, has produced two additional coprolites containing small *Tusoteuthis* inclusions. KUVP 65729 is a relatively large coprolite (4.78 cm × 3.82 cm) containing two slivers of a *Tusoteuthis* rachis, as well as a tooth and numerous bones of an actinopterygian fish. A second, KUVP 65730 (Fig. 184C), likewise contains at least three fragments of *Tusoteuthis* rachis plus three teleostean vertebrae and measures 2.78 cm × 2.0 cm. Also recovered at this locality was a 1.95 cm × 1.13 cm compact bolus of badly distorted and fragmented *Tusoteuthis* rachis. While this specimen, KUVP 65728, appears to be of fecal origin, no phosphatic groundmass can be seen in the specimen. These five specimens were collected by Stewart.

The diet of the predators which produced these coprolites was certainly not limited to cephalopods, as demonstrated by the numerous fish bone inclusions. It is also of some interest to note that only the rachis of the gladius is represented in these specimens. The more expanded posterior aspect of the gladius occupied a considerable portion of the *Tusoteuthis* body, and should be recognizable if preserved. It is not positively known which of the many carnivorous vertebrates known from the Smoky Hill Chalk could have been the predators in these cases, although the size of the coprolites suggests a piscine origin. It may be significant in this context that of all the marine organisms found in the Smoky Hill Chalk, only fish and hesperornithiform bird skeletons have produced obvious preserved gut contents or fecal material in direct association.

A larger Smoky Hill Chalk specimen which indicates predation of *Tusoteuthis* is FFM 1972.127.12aF. This specimen consists of a mass of bones measuring 26.7 cm × 16.5 cm × 4.4 cm. The bones are primarily those of teleosts; identifiable among them are the jaw, neurocranium, and vertebrae of *Gillicus arcuatus*, alepisauroid vertebrae (cf. *Stratodus*), an alepisauroid tooth (cf. *Cimolichthys*), jaws of *Enchodus dirus*, and vertebrae of *Pachyrhizodus* sp. In addition to these remains are several thorn-like dermal ossicles, probably of batoid origin, and many laminated conchiolinic fragments of a teuthidid gladius. Fragments of the rachis as well as the expanded posterior portion are represented. This mass is either the stomach contents or the gastric ejecta of a large carnivore. The compact, discrete nature of the specimen favors the former interpretation. This specimen was collected in Logan County by Vi and Ernest Fick.

For two specimens of *Tusoteuthis* from the Sharon Springs Member of the Pierre Shale at Red Bird, Wyoming, the predators are identifiable. One specimen, collected by James Mellinger, consists of a partial skeleton of the alepisauroid teleost *Cimolichthys nepaholica*, UCM 20056, with a nearly complete *Tusoteuthis longa* gladius, UCM 29667, in the gastric area (Fig. 185A). Nicholls and Isaak (1987) assigned large *Tusoteuthis* specimens from the Pembina Member of the Pierre Shale Formation of Manitoba to *T. longa*, and we follow that usage in referring the large *Tusoteuthis* material from the temporally equivalent Sharon Springs Member of the Pierre Shale to that species. The posterior parts of both the fish and squid are eroded. The preserved length of the gladius is 66 cm; that of the fish is 152 cm. Extrapolation based on the distance from the occiput to the 40th centrum of KUVP 49014 and KUVP 55062 indicates a standard length of 173 cm for the *Cimolichthys*. The squid is clearly located between the pleural ribs of the fish, with the anterior tip of the rachis just medial to the posterior edge of the operculum. Since the gladius of a squid does not extend beyond the anterior edge of the mantle, the tentacles and possibly part of the head of the squid projected beyond the mouth of the fish if they had not already been severed. This is similar to feeding by the sperm whale, *Physeter catodon*, which may swallow whole squids even as large as an *Architeuthis* with a standard length of nearly 5 m and a total length of over 10 m (Clarke, 1956). Furthermore, the widely spaced, conical teeth of *Cimolichthys* with modest carinae are more suitable for puncturing rather than shearing. Death of the *Cimolichthys* was probably due to choking, unless decompositional gas buildup forced the squid back out of the throat.

The other specimen of *Tusoteuthis longa* for which the predator is known is a complete gladius, UCM 29668, collected by Carpenter. The specimen is 128 cm long and bears three punctures on the anterior portion of the rachis (Fig. 185B, C). The punctures have caused the rachis rod bundles to splay apart and caused some twisting of the anterior part of the rachis. The site of the punctures indicates that the predator was a very large mosasaur, possibly *Tylosaurus proriger* which is known from the Sharon Springs Member of the Pierre Shale (Russell, 1967, 1970; Carpenter, unpublished notes). The extreme distance separating two of the punctures, 31 cm, is probably due to an oblique attack on the squid by the mosasaur (Fig. 185B, C). It is not known how many times the mosasaur bit the squid, but it apparently caused its death. Possibly the mosasaur released the struggling squid because of the groping tentacles, or the mosasaur severed and swallowed the head and tentacles, allowing the rest of the body to sink to the sea floor.

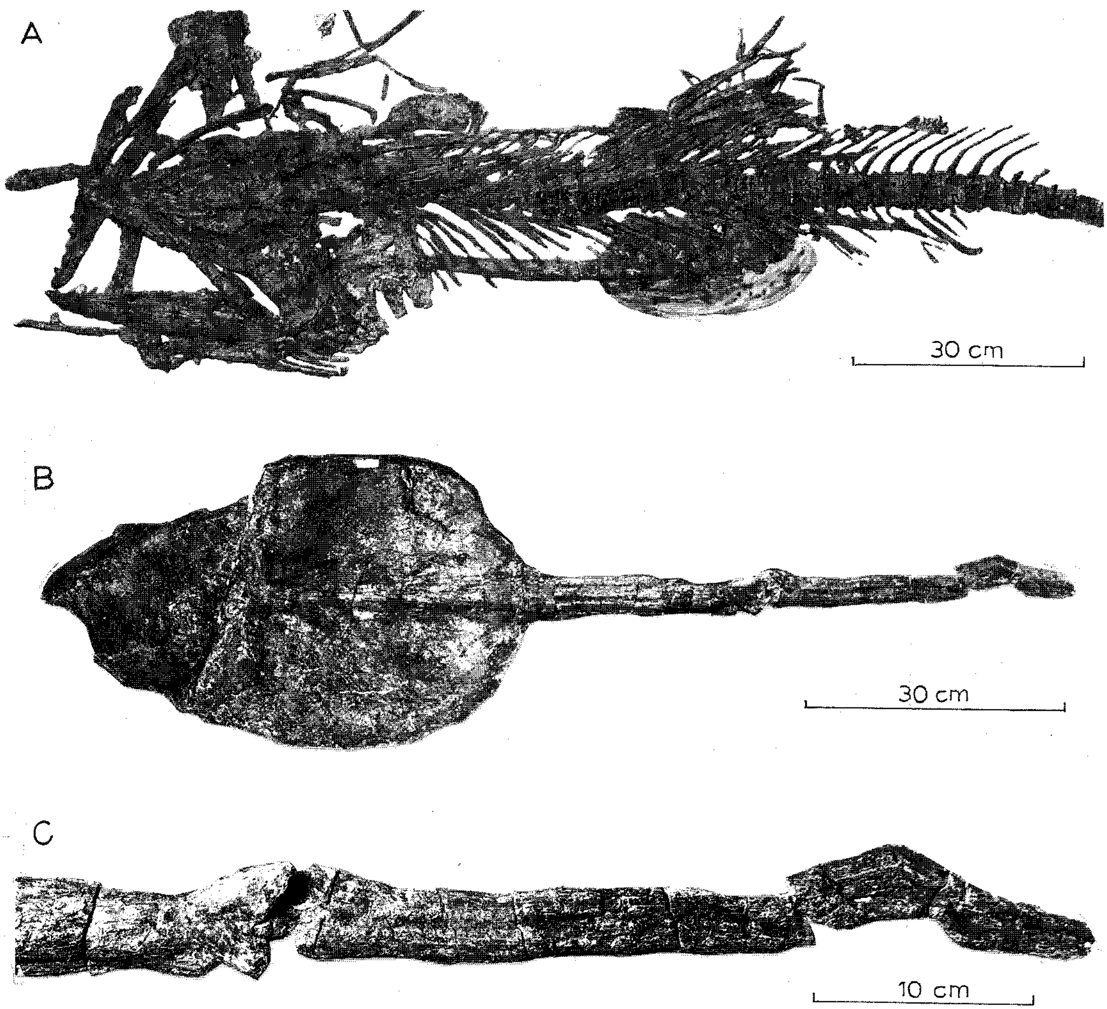

Fig. 185. Pierre Shale fossils documenting predation on squids. A. *Cimolichthys nepaholica* (UCM 20556), with *Tusoteuthis longa* (UCM 29667) in visceral region. B. *Tusoteuthis longa* with presumed mosasaur-induced punctures; UCM 29668. C. Closeup of rachis of UCM 29668.

Careful re-examination of fossil squids, ammonites, and other cephalopods in museum collections will undoubtedly reveal that cephalopod predation had a long geologic record.

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