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Unusual gut contents in a Cretaceous ichthyosaur

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Despite ichthyosaurs being one of the most extensively studied Mesozoic marine reptile groups, there is little documented direct evidence of dietary habits in most taxa. Here, we report the discovery of hatchling-sized marine protostegid turtle remains and an enantiornithine bird (in association with actinopterygian fish and phosphatic nodules) within the body cavity of a gravid female ichthyosaur (*Platypterygius longmani*) from the Lower Cretaceous of Australia; this is the first evidence, to our knowledge, of feeding by ichthyosaurs upon both turtles and birds. The exceptionally preserved gut contents show little evidence of digestion, suggesting consumption shortly before the ichthyosaur's death. Poor swimming ability may have made hatchling turtles easy prey that could have been either swallowed whole or processed by shake feeding. Ingestion of bird remains probably occurred through scavenging. Opportunistic feeding on vertebrates is at odds with existing interpretations of dietary habits in Cretaceous ichthyosaurs, which favour predation primarily upon cephalopods. Such specialization is considered a contributing factor in the group's ultimate extinction. However, the evidence here that at least some forms were able to use a wide range of available food types suggests that the decline of ichthyosaurs in the mid-Cretaceous may be linked to other factors such as competition with ecologically analogous pursuit predators.

Keywords: ichthyosaurs; gut contents; hatchling turtles; enantiornithine bird; Cretaceous; Australia

1. INTRODUCTION

Ichthyosaurs, a highly successful group of Mesozoic marine amniotes, have been considered the dominant high-speed pursuit predators of the Mesozoic seas. The group is traditionally characterized by a superficially 'fish-like' body shape with a triangular stabilizing dorsal fin and vertically oriented lunate caudal fin. These features are best illustrated in taxa of Jurassic and Cretaceous age (Sander 2000). Current knowledge of ichthyosaur dietary habits is derived from preserved gastric residues (Pollard 1968), coprolites (Buckland 1829) and dental morphology (Massare 1987). Surprisingly, however, most documented direct evidence (i.e. gastric contents) is based on a handful of specimens from the famous Liassic (Lower Jurassic) deposits of Lyme Regis and Whitby in England and Holtzmaden in Germany. One of the earliest accounts (Buckland 1836) described coprolitic masses containing fish scales, within the body cavities of several ichthyosaurs from Lyme Regis. Later re-examination showed that the fish remains to belong to the Liassic holostean *Pholidophorus*, and identified numerous dibranchiate cephalopod hooklets (Pollard 1968). Large vertebrate remains including fish and small ichthyosaurs have been recorded as gut contents in some Jurassic ichthyosaur specimens (McGowan 1974). Cephalopods, however, represent the dominant component of most ichthyosaur gastric residues from Lyme Regis and Holtzmaden (see Pollard 1968; Keller 1976; Massare 1987; Böttcher 1989).

The partial ichthyosaur skeleton (QM F16811, Queensland Museum, Brisbane, Queensland, Australia) discussed here is assigned to *Platypterygius longmani*, a large (*ca*. 7 m in total length) ichthyosaur known primarily from the Upper Albian (Lower Cretaceous) of Queensland, Australia (Wade 1990). An exceptionally preserved foetal skull and fragmentary skeleton are preserved within the body cavity. Foetal remains are rare in Cretaceous ichthyosaurs and are best known in taxa of Triassic and Jurassic age (Deeming *et al.* 1993; Brinkman 1996). Gut contents were extracted during preparation with acetic acid and included actinopterygian fish remains, phosphatic nodules, disarticulated small turtle bones and the proximal tibiotarsus of a bird (figure 1). The turtle fossils represent one or several hatchling-sized protostegids, an extinct family of marine turtles classified with the Chelonioidea (Gaffney & Meylan 1988; Hirayama 1998). The bird bone is assigned to Enantiornithes, a basal subclass of Cretaceous birds with a widespread Gondwanan distribution (Chiappe 2002).

2. DESCRIPTION AND REMARKS

The presence of an advanced foetus within the body cavity of QM F16811 indicates that this individual was a gravid female close to parturition at the time of death. The large size (skull length of *ca*. 400 mm) and the articulated state of the foetus suggest that it was not ingested as prey. Its anterior (craniad) placement and positioning with the head towards the anterior end of the adult ichthyosaur's body cavity is also consistent with the condition observed in other gravid ichthyosaur specimens (Böttcher 1990).

The remains interpreted as gut contents are entirely disarticulated and occur as a disaggregated mass throughout the anterior portion of the rib cage of the adult ichthyosaur. There is no evidence of gastroliths. The most common bony fossils are the teeth, cranial and postcranial elements of fish. These include mainly vertebrae (*ca*. 2–8 mm in total length), although numerous well-preserved skull bones (neurocranials, operculars and a small ceratohyal) are present. Several fragmentary spine-like elements might represent ribs and fin rays. The small size and morphology (including a prominent central foramen in the ceratohyal) of the fish remains suggest that they belong to teleosts. This group is common in the Toolebuc Formation of Queensland and includes some smaller-bodied taxa (e.g. *Dugaldia*) to which the material might be attributed. Three teeth (of 5–7 mm in height) and a jaw fragment also suggest the presence of larger fish in the gastric mass, possibly the clupeomorphs *Cooyoo* or *Pachyrhizodus*.

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Numerous light grey irregular phosphatic nodules occur in conjunction with the fossil remains in the adult ichthyosaur's rib cage. These are uniform and almost featureless in internal structure but do occasionally contain small inclusions, possibly representing digested bone fragments. Pollard (1968) reported 'buff coprolotic clay' masses within the body cavities of Lower Jurassic ichthyosaurs from Lyme Regis. Buckland (1835) identified similar material as phosphatic in composition and showed it to be derived from the digestion of fish and reptile bones.

The turtle remains recovered from the gastric residue are disarticulated but were found within the same area of the body cavity: anteriorly in the vicinity of the pectoral girdle. All of the remains are poorly ossified, being composed of cancellous endochondral bone, and appear to derive from one or more hatchling-sized (*ca*. 100–120 mm in total length) individuals. The cranial elements are well-preserved and include a complete left frontal, left opisthotic, right prootic, supraoccipital and left quadrate. Postcranial remains include a thoracic vertebral centrum, two anterior costals, a well-preserved left femur, two proximal carpal or tarsal elements and a damaged ilium. The thoracic centrum shows no evidence of fusion with the neural arch, although paired elongate dorsal facets suggest the presence of cartilage. Similarly, the limb bones lack ossified articular ends and the ilium does not appear to have a fully formed acetabular extremity. This morphology is consistent with the early developmental stage of the individual(s).

The turtle remains are identified as protostegid owing to the well-developed pterygoid suture that extends to the mandibular articular surface on the quadrate. To date, only two sea turtle (chelonioid) taxa are known from the Cretaceous of Australia and both have been placed within Protostegidae (Kear 2003). Out of these, the small-bodied (less than 1 m total adult length) *Notochelone costata* is by far the more common (Molnar 1991) and probably represents the taxon to which the hatchling remains can be attributed.

The bird tibiotarsus is small (19.45 mm in length) and lacks its distal articular end. The apparently complete fusion of the proximal tarsals to the tibia suggests that it represents an adult individual. The proximal end of the tibiotarsus shows several features supporting assignment to Enantiornithes (e.g. thin, laterally convex shaft; well-expressed fibular crest bordered cranially and caudally by elongate depressions), and the specimen's small size and morphology make it a good match for the type specimen of the enantiornithine *Nanantius eos* Molnar, 1986. This, and several other bones assigned to the genus, also come from the Toolebuc Formation (Molnar 1986; Kurochkin & Molnar 1997).

3. DISCUSSION

The position of the fish, hatchling turtle and bird remains suggests that they were the contents of the adult ichthyosaur's gut. All are concentrated between the ribs in the anterior and mid-dorsal region of the adult ichthyosaur. Both protostegid turtles and actinopterygian fishes represent common vertebrate fossils in the Albian deposits of Queensland (Long 1991; Molnar 1991), but rarely occur in aggregations as they do here. Bird remains are rare. The limestone concretion encasing the specimens, as well as the surrounding clayey mudstone, also lacked any distinct sedimentary structures to suggest concentration through current action.

All of the turtle remains studied are poorly ossified (a feature consistent with their early developmental stage) and exhibit a fibrous surface texturing. This differs from the surface-pitting characteristic of bones modified by digestion, which commonly also possess corroded articular ends, thinning of long-bone shafts and edge rounding along breaks (Andrews 1990). The absence of such features from both the turtle and bird elements at hand may indicate that they were ingested shortly before the adult ichthyosaur's death.

Poor swimming ability may have made hatchling protostegid turtles easy prey for ichthyosaurs. Their small size would have enabled them to be swallowed whole, although, the characteristically robust teeth of *P. longmani* were certainly suitable for dismembering larger individuals, perhaps by shake feeding (Kear 2002).

Predation upon hatchling turtles is consistent with the elongate skull and mandible of *P. longmani*, which suggest a preference for small-bodied prey. Indeed, this may have prompted ingestion of the enantiornithine bird, whose floating carcass could have been scavenged from the water's surface. Direct capture of birds by ichthyosaurs is unlikely because most enantiornithines are thought to have been volant and non-aquatic, their remains occurring in marine deposits probably as a result of post-mortem fluviatile transport from nearby coastal woodland habitats (Molnar 1986).

The direct evidence of dietary habits presented here, together with corresponding studies of tooth morphology (Massare 1987), offers insight into the prey preferences and habits of Cretaceous ichthyosaurs and indicates that they may have been far more opportunistic feeders than previously suspected. This is at odds with some existing interpretations, which suggest that Cretaceous ichthyosaurs were primarily specialized cephalopod hunters and that this may have led to their extinction (via a break in the food chain) following a major marine invertebrate faunal collapse at the Cenomanian–Turonian boundary (Bardet 1994). However, evidence that at least some forms may have both scavenged and preyed extensively on small vertebrates, including sea turtles and fishes, is inconsistent with this explanation. The decline of these ichthyosaurs may therefore be linked to other factors such as competition with ecologically analogous pursuit predators. Some previous workers (see, for example, Russell 1967) have considered mosasaurs (Cretaceous marine lizards) to have been likely competitors with Cretaceous ichthyosaurs. However, this hypothesis cannot be accepted because mosasaurs only radiated after the extinction of the ichthyosaurs, and their adaptation to a pursuit predator role was far less advanced (Mazin 2001). Consequently, the rapid diversification of other groups such as teleost fish (see Massare 1988) and polycotylid plesiosaurs may have provoked the decline of ichthyosaurs. The earliest polycotylids occur often sympatrically with ichthyosaurs in deposits of Aptian–Albian age (Druckenmiller 2002; Kear 2003) and show morphological characteristics consistent with fast swimming pursuit-style hunting of small-bodied prey (Adams 1997). Such a lifestyle could have brought polycotylids into direct competition with ichthyosaurs and

Figure 1. Gut contents of the ichthyosaur QM F16811. Fish remains, (*a*) Ceratohyal (medial view). Scale bar, 8.55 mm. Turtle remains, (*b*) Quadrate (medial view) showing pterygoid suture (arrowed) extending to mandibular articular surface. Scale bar, 7.92 mm. (*c*) Frontal (dorsal view). Scale bar, 11.29 mm. (*d*) Femur (ventral view). Scale bar, 11.45 mm. (*e*) Thoracic centrum (ventral view). Scale bar, 6.53 mm. (*f*) Anterior costal (ventral view). Scale bar, 11.09 mm. Bird remains, proximal tibiotarsus in (*g*) caudal and (*h*) cranial views. Scale bar, 19.45 mm.

facilitated the final extinction of the latter by the end of the Cenomanian.

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