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First gut contents in a Cretaceous sea turtle

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Modern sea turtles utilize a variety of feeding strategies ranging from herbivory to omnivory. In contrast, the diets of fossil sea turtles are poorly known. This study reports the first direct evidence: inoceramid bivalve shell pieces (encased in phosphatic material) preserved within the body cavities of several small protostegid turtles (cf. *Notochelone*) from the Lower Cretaceous of Australia. The shell fragments are densely packed and approximately 5–20 mm across. Identical shell accumulations have been found within coprolite masses from the same deposits; these are of a correct size to have originated from *Notochelone*, and indicate that benthic molluscs were regular food items. The thin, flexible inoceramid shells (composed of organic material integrated into a prismatic calcite framework) appear to have been bitten into segments and ingested, presumably in conjunction with visceral/mantle tissues and encrusting organisms. Although protostegids have been elsewhere interpreted as potential molluscivores, their primitive limb morphology is thought to have limited them to surface feeding. However, the evidence here that at least some forms were able to utilize benthic invertebrate prey indicates that, like modern sea turtles, protostegids probably exhibited a much broader range of feeding habits.

Keywords: protostegid turtles; gut contents; inoceramid bivalves; Cretaceous; Australia

1. INTRODUCTION

The earliest sea turtles (Chelonioidea) are known from the late Early Cretaceous (late Aptian/early Albian; see Hirayama 1998), and were common elements in many late Mesozoic marine reptile faunas. Cheloniids (green turtles, etc.) and dermochelyids (leatherback turtles) have survived until today, while the Cretaceous protostegids underwent a gradual decline in the Turonian (~89 mya) and became extinct at the end of the Maastrichtian (~65 mya), possibly in response to the marine faunal crisis at the Cretaceous–Tertiary boundary (Bardet 1994; Hirayama 1997). The dietary habits of extinct chelonioids are usually inferred from living relatives: cheloniids are considered mostly herbivorous, feeding on sea grasses or algae (e.g. *Chelonia*), or omnivorous, additionally ingesting invertebrates such as crustaceans and molluscs (e.g. *Caretta*); dermochelyids (represented solely by *Dermochelys coriacea*) are specialized jellyfish predators (Hendrickson 1980). Diets of extinct Cretaceous protostegids remain speculative. Hirayama (1994) suggested that they might have been molluscivores, adapted to feeding on hard-shelled planktonic prey such as ammonites. This was based on their robust cranial morphology (e.g. extensive buttressing of the quadrate by the pterygoid) and characteristic forelimb structure (e.g. lateral process of the humerus being restricted to the anterior portion of the humeral shaft, indicating a predominantly horizontal propulsive stroke and thus limited diving ability: see Hirayama 1997). Unfortunately, no direct evidence (i.e. stomach contents) has yet been found to support this pelagic feeding model.

The partial chelonioid skeletons (AM F87832, Australian Museum, Sydney; QM F49190, Queensland Museum, Brisbane; SAM P41107, South Australian Museum, Adelaide) discussed here are assignable to cf. *Notochelone* sp., a small (>1 m total length) protostegid turtle known from the Upper Albian (Lower Cretaceous) Toolebuc Formation of Queensland, Australia (Kear 2003). To date only two chelonioids, both protostegids, are known from the Cretaceous of Australia (Kear 2003). Of these, the small-bodied *Notochelone* is by far the most common (Molnar 1991), and more consistent in size with the current remains. The gastric masses present with the specimens comprise pieces of inoceramid bivalve shell encased within phosphatized coprolitic material. Evidence of predatory attack on inoceramids has been recorded elsewhere (e.g. Speeden 1971; Kauffman 1972; Crampton 1996; Harries & Ozanne 1998), although as yet these injuries have not been associated with turtles.

2. DESCRIPTION AND REMARKS

The turtle gastric residues (figure 1*a–c*) typically comprise irregular, light grey phosphatic masses (between 20 and 30 mm thick) positioned in the posterior section of the body cavity between the carapace and plastron (maximum carapace lengths ~50–60 mm). Natural breaks show that these contain numerous regularly shaped bivalve shell fragments, approximately 5–20 mm across and up to 4 mm thick. These are usually stacked, and aligned sub-parallel to the transverse axis of the turtle's carapace. The characteristic columnar arrangement of calcite prisms in the bivalve shell microstructure identifies them as belonging to inoceramids. These ubiquitous Cretaceous bivalves are widespread in the Toolebuc Formation, where they form a dominant component of the benthic invertebrate assemblage (Day 1969). The fragmentary nature of the bivalve material described here precludes assignment to genus or species; however, attribution to either *Inoceramus* and/or *Anopaea* is most probable (as these are the only recognized inoceramid genera from the Toolebuc Formation; see Stillwell & Crampton 2002).

Isolated phosphatic coprolites (figure 1*d*,*e*) containing identical inoceramid shell fragment accumulations occur throughout the Toolebuc Formation. The coprolites are typically cylindrical and of regular size (around 50–100 mm total length). The encased shell pieces lack distinct surface

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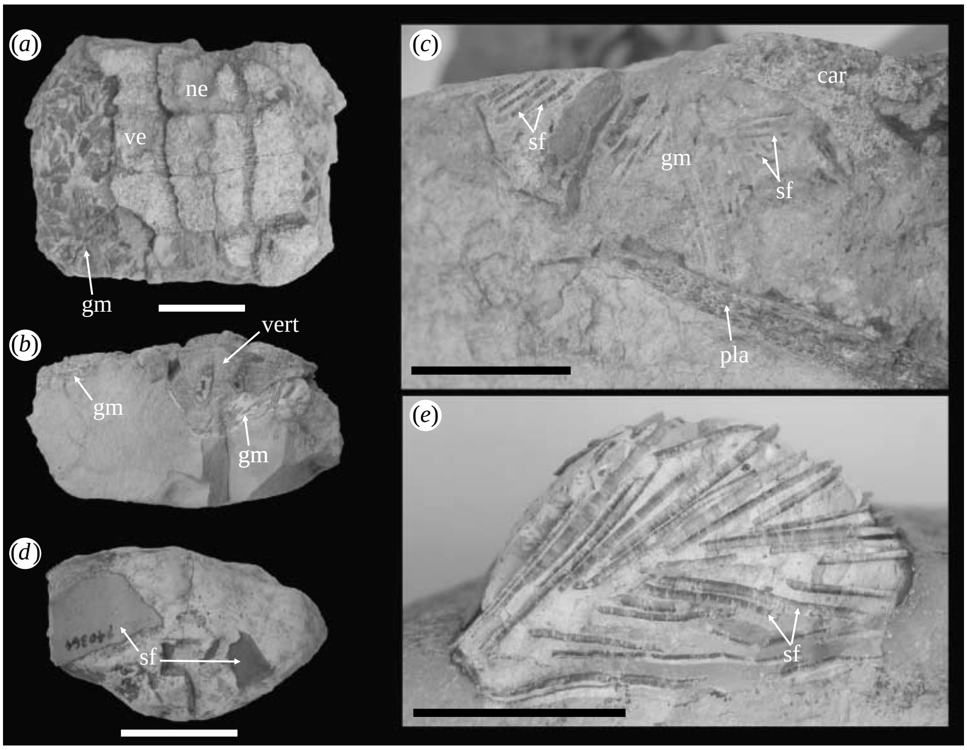

Figure 1. Gut contents and coprolites of protostegid sea turtles. SAM P41107, (*a*) dorsal and (*b*) anterior views of turtle body section (posterior) with carapace elements removed to show gastric mass. AMF87832, (*c*) cross-section through turtle body showing gastric mass *in situ* between carapace and plastron. Coprolite masses, (*d*) whole specimen (SAM P40364) and (*e*) cross-section (SAM P40534) showing 'stacked' inoceramid shell fragments. Scale bars, 20 mm. Abbreviations: car, carapace; gm, gastric mass; ne, neural; pla, plastron; sf, shell fragment; ve, vertebral; vert, vertebra.

ornamentation (e.g. fine commarginal growth lines), are polygonal, and have straight vertical edges (giving the appearance of being 'clipped'). There is some evidence of corrosive damage from gut acid (e.g. pitting, thinning and edge rounding along breaks) on several of the specimens.

3. DISCUSSION

The position of the bivalve shell pieces and phosphatic material in AM F87832, QM F49190, and SAM P41107 suggests that they were the contents of these turtles' guts. All are concentrated in the narrow space between the carapace and plastron, and situated in the posterior (intestinal) region of the body cavity. The presence of light-coloured phosphatic material itself is characteristic of both marine reptile gastric residues and coprolites. For example, Kear *et al.* (2003) recorded phosphatic nodules associated with the gut contents of an ichthyosaur from the Toolebuc Formation. Similarly, Pollard (1968) reported 'buff coprolitic clay' inclusions within the body cavities of Lower Jurassic ichthyosaurs from Lyme Regis, England. Buckland (1835) identified this (and other coprolitic remains) as the preserved remnants of digested organic material.

Interestingly, none of the inoceramid shell fragments from either gastric masses or coprolites shows signs of extensive corrosion or disaggregation of individual calcite prisms by the digestive process. This suggests that the organic framework sheathing the prismatic shell structure (see Stilwell & Crampton 2002) was not broken down by the turtle's gut acids; rather, it may have been resistant and rapidly transported through the digestive tract as nutrient-poor waste material.

Crampton (1996) speculated that inoceramid shells might have been flexible, imparting a degree of protection during predatory attack by allowing maintenance of a seal during breakage of the shell margin. This conclusion may be supported by the material at hand, which shows that the inoceramid shell pieces remained intact (as regular-sized, straight-sided chunks) after being bitten off and ingested by the turtle. This probably resulted from plastic deformation and 'splitting' in response to force, unlike a more rigid, brittle shell structure, which would tend to shatter into irregular shards.

The variable thickness of the bivalve fragments (around 2–4 mm) in the turtle gastric masses and isolated coprolites indicates that they derive from both the main body and growth margin of inoceramid shells (see Stilwell & Crampton 2002). The turtles could have attacked both these areas in an effort to expose the fleshy viscera. However, ingestion of mantle tissues along the shell periphery, together with any encrusting/boring organisms (e.g. cirripeds or sponges; see Bromley 1970; Hattin 1982; Dhont & Dieni 1990), could have provided additional nutrition.

The robust skull and jaw apparatus of protostegids is consistent with a diet of benthic molluscs. The extensive quadrate-pterygoid contact (a feature linked to reinforcing the jaw joint) suggests an ability to cope with hard-shelled prey (Hirayama 1997). Their limb morphology is poorly adapted for diving (Hirayama 1997); however, the shallow water setting

(<100 m depth; Cook & McKenzie 1997) of the Toolebuc Formation indicates that these turtles did not have to travel to great depths in order to feed on benthic organisms.

The direct evidence of dietary habits presented here provides insight into the feeding strategies of extinct protostegids. However, the inferred preference for benthic bivalves is inconsistent with previous interpretations of diet for the group (e.g. Hirayama 1994). These suggest that protostegids were primarily pelagic hunters, particularly of ammonites, a specialization that may have led to their ultimate extinction during the marine faunal collapse at the Cretaceous–Tertiary boundary (an event that affected pelagic systems the hardest; Bardet 1994). Nevertheless, the present evidence shows that obligatory pelagic feeding habits are untenable for all members of the group, with at least some primitive ancestral forms (e.g. *Notochelone*) having been active predators on bottom-oriented prey. This feeding strategy is comparable with that of some modern cheloniids, whose early ancestors notably replaced protostegids (perhaps via competition) as the dominant chelonioid lineage in many marine assemblages during the Late Cretaceous (Hirayama 1997).

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Bardet, N. 1994 Extinction events among Mesozoic marine reptiles. *Hist. Biol.* **7**, 131–324.

Bromley, R. G. 1970 Predation and symbiosis in some Upper Cretaceous clinoid sponges. *Bull. Geol. Soc. Den.* **19**, 398–405.

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.* **3**, 223–238.

Cook, A. & McKenzie, D. 1997 *The Great Artesian Basin.* Ilfracombe, Queensland: M'Choinneach Publishers.

Crampton, J. S. 1996 Inoceramid bivalves from the Late Cretaceous of New Zealand. *Inst. Geol. Nucl. Sci. Monogr.* **14**, 1–188.

Day, R. W. 1969 The Lower Cretaceous of the Great Artesian Basin. In *Stratigraphy and palaeontology: essays in honour of Dorothy Hill* (ed. K. S. W. Campbell), pp. 140–173. Canberra: ANU Press.

Dhont, A. V. & Dieni, I. 1990 Unusual inoceramid-spondylid association from the Cretaceous Scaglia Rossa of Passo del Brocon (Trento N. Italy) and its palaeoecological significance. *Mem. Sci. Geol.* **42**, 155–187.

Harries, P. J. & Ozanne, C. R. 1998 General trends in predation and parasitism on inoceramids. *Acta Geol. Pol.* **48**, 377–386.

Hattin, D. E. 1982 Stratigraphy and depositional environment of Smoky Hill Chalk Member, Niobrara Chalk (Upper Cretaceous) of the type area, Western Kansas. *Kansas Geol. Surv. Bull.* **225**, 1–108.

Hendrickson, J. R. 1980 The ecological strategies of sea turtles. *Am. Zool.* **20**, 597–609.

Hirayama, R. 1994 Phylogenetic systematics of chelonioid sea turtles. *The Island Arc* **3**, 270–284.

Hirayama, R. 1997 Distribution and diversity of Cretaceous chelonioids. In *Ancient marine reptiles* (ed. J. M. Callaway & E. L. Nicholls), pp. 225–241. San Diego, CA: Academic Press.

Hirayama, R. 1998 Oldest known sea turtle. *Nature* **392**, 705–708. (doi:10.1038/33669)

Kauffman, E. G. 1972 *Ptychodus* predation upon a Cretaceous *Inoceramus*. *Palaeontology* **15**, 439–444.

Kear, B. P. 2003 Cretaceous marine reptiles of Australia: a review of taxonomy and distribution. *Cretaceous Res.* **24**, 277–303. (doi:10.1016/S0195-6671(03)00046-6)

Kear, B. P., Boles, W. E. & Smith, E. T. 2003 Unusual gut contents in a Cretaceous ichthyosaur. *Proc. R. Soc. B* **270**(Suppl. 2), S206–S208. (doi:10.1098/rsbl.2003.0050)

Molnar, R. E. 1991 Fossil reptiles in Australia. In *Vertebrate palaeontology of Australasia* (ed. P. Vickers-Rich, J. M. Monaghan, R. F. Baird & T. H. Rich), pp. 605–702. Melbourne: Pioneer Design Studio, Monash University.

Pollard, J. E. 1968 The gastric contents of an ichthyosaur from the Lower Lias of Lyme Regis, Dorset. *Palaeontology* **11**, 376–388.

Speeden, I. G. 1971 Notes on New Zealand fossil Mollusca—2. Predation on New Zealand Cretaceous species of *Inoceramus* (Bivalvia). *NZ J. Geol. Geophys.* **14**, 56–60.

Stilwell, J. D. & Crampton, J. S. 2002 Unusual belemnite–inoceramid bivalve association from the Albian (late Early Cretaceous) of Queensland, Australia. *Alcheringa* **25**, 391–394.