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# Bite marks on an ichthyodectiform fish from Australia: possible evidence of trophic interaction in an Early Cretaceous marine ecosystem

LOVISA WRETMAN and BENJAMIN P. KEAR

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A well-preserved fish skull from late Albian deposits of the Allaru Mudstone near Richmond in Queensland displays a conspicuous V-shaped pattern of indentations, punctures and depression fractures consistent with a vertebrate bite trace. This is the first direct evidence of trophic interaction between vertebrates within an Early Cretaceous marine ecosystem from Australia. The specimen is taxonomically referable to the large-bodied (ca 1 m snout–tail length) ichthyodectiform *Cooyoo australis*, but the size and spacing of the tooth marks is incompatible with attack by a conspecific individual. The lack of osseous growths concordant with healing also suggests that the bite occurred shortly before or after the animal's death. Comparison with the dentitions of other coeval vertebrates indicates compatible tooth arrangements in longirostrine amniote predators such as polycotylid plesiosaurs, ornithocheiroid pterosaurs and especially the ichthyosaurian *Platypterygius*. The implications of this as a potential predator–prey association are that Early Cretaceous actinopterygians occupied middle-level trophic niches and were in turn consumed by higher-level amniote carnivores, similar to many extant marine vertebrate communities of today.

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TROPHIC INTERACTIONS between Mesozoic marine vertebrates have been reconstructed from preserved gut contents (e.g., Pollard 1968, Wilby & Martill 1992, Maisey 1994, Shimada 1997, Sato & Tanabe 1998, Cicimurri & Everhart 2001, Kear *et al.* 2003, Everhart 2004a, McHenry *et al.* 2005, Kear 2006, Martin & Fox 2007, O'Keefe *et al.* 2009), coprolites (e.g., Martin & Kennedy 1988, Maisey 1994, Kear 2006, Everhart 2007, Everhart *et al.* 2010, Harrell & Schwimmer 2010, Eriksson *et al.* 2011), regurgitates (e.g., Hattin 1996, Oji *et al.* 2003, Salamon *et al.* 2012), broken shells/bones/teeth (e.g., Lingham-Soliar 2004, Zátón & Salamon 2008, Vullo 2011) and, most evocatively, bite marks (e.g., Kauffman & Kesling 1960, Kauffman 1972, 2004, Martill 1990, 1996, Ward & Hollingworth 1990, Neumann 2000, Kear & Godthelp 2008, Klomp-maker *et al.* 2009, Kellner *et al.* 2010, Kauffman & Swado 2013). Because bite traces directly reflect the actions of living animals, they can also provide information on behaviours such as feeding strategies and social activities. Documented examples include predation and/or scavenging by selachians (Schwimmer *et al.* 1997, Shimada 1997, Everhart 2004b, 2005, Shimada &

Hooks 2004, Everhart & Hamm 2005, Rothschild *et al.* 2005, Kaddumi 2006, Barnes & Hiller 2010, Shimada *et al.* 2010), mosasauroids (Barnes & Hiller 2010, Einarsson *et al.* 2010) and marine crocodylians (Forrest 2003), intraspecific combat in ichthyosaurs (Zammit & Kear 2011) and thallosuchians (Frey *et al.* 2002) and dramatically violent encounters between plesiosaurs (Thulborn & Turner 1993) and mosasauroids (Lingham-Soliar 1995, 2004, Everhart 2008). In contrast, incidences of bite marks on Mesozoic fishes are rare, which is surprising given their abundance in many deposits. Nevertheless, accounts exist of healed punctures on hybodontiform shark fin spines (Maisey 1978) and embedded large lamniform teeth/cut marks on actinopterygian skull elements and vertebrae (Shimada & Everhart 2004, Shimada & Fielitz 2006). This paper provides a novel addition to this currently scant bite trace record: an ichthyodectiform teleost skull from the Early Cretaceous of Australia that exhibits bone modifications consistent with attack by a large vertebrate predator.

## Geological setting

The fish skull, Kronosaurus Korner (KK) regional museum (an accredited Queensland State Government repository for significant natural history and cultural

artifacts) R0457, was found preserved within a limestone concretion probably derived from bedrock exposures of the Allaru Mudstone along the Flinders River in central-northern Queensland, Australia (see Henderson & Kennedy 2002, p. 234, fig. 1 for a geological map of the area). KK R0457 was collected by local property owners David Goodman and Wayne Rhodes from a weathering residuum of unconsolidated alluvial sands at 'Wayne Rhodes rapids' (20°45'40.37" S, 143°10'58.00" E), about 6 km east of the town of Richmond. The Allaru Mudstone constitutes a subdivision of the Rolling Downs Group (Eromanga Basin) and has a conformable lower boundary with the Toolebuc Formation and an upper conformity with the Mackunda Formation using the northern Eromanga Basin

nomenclatural scheme (see Cook 2012 for summary). Senior *et al.* (1978) and Krieg & Rogers (1995) detailed the lithology, stratigraphical relationships and outcrop distribution (including geological and locality maps) for the Allaru Mudstone together with its southern Eromanga Basin equivalent, the Oodnadatta Formation. Collectively, these successions comprise *ca* 50–120 m of laminated claystone and siltstone, with fine-grained sandstone beds and abundant calcareous and ferruginous concretions (Krieg & Rogers 1995). Age determinations for the Allaru Mudstone based on macroinvertebrates (Henderson *et al.* 2000, Henderson & Kennedy 2002) and dinoflagellates/sporomorphs (Krieg & Rogers 1995) place it within the late Albian *Pseudoceratium ludbrookiae* dinoflagellate zone/upper *Phimopollenites pannosus*

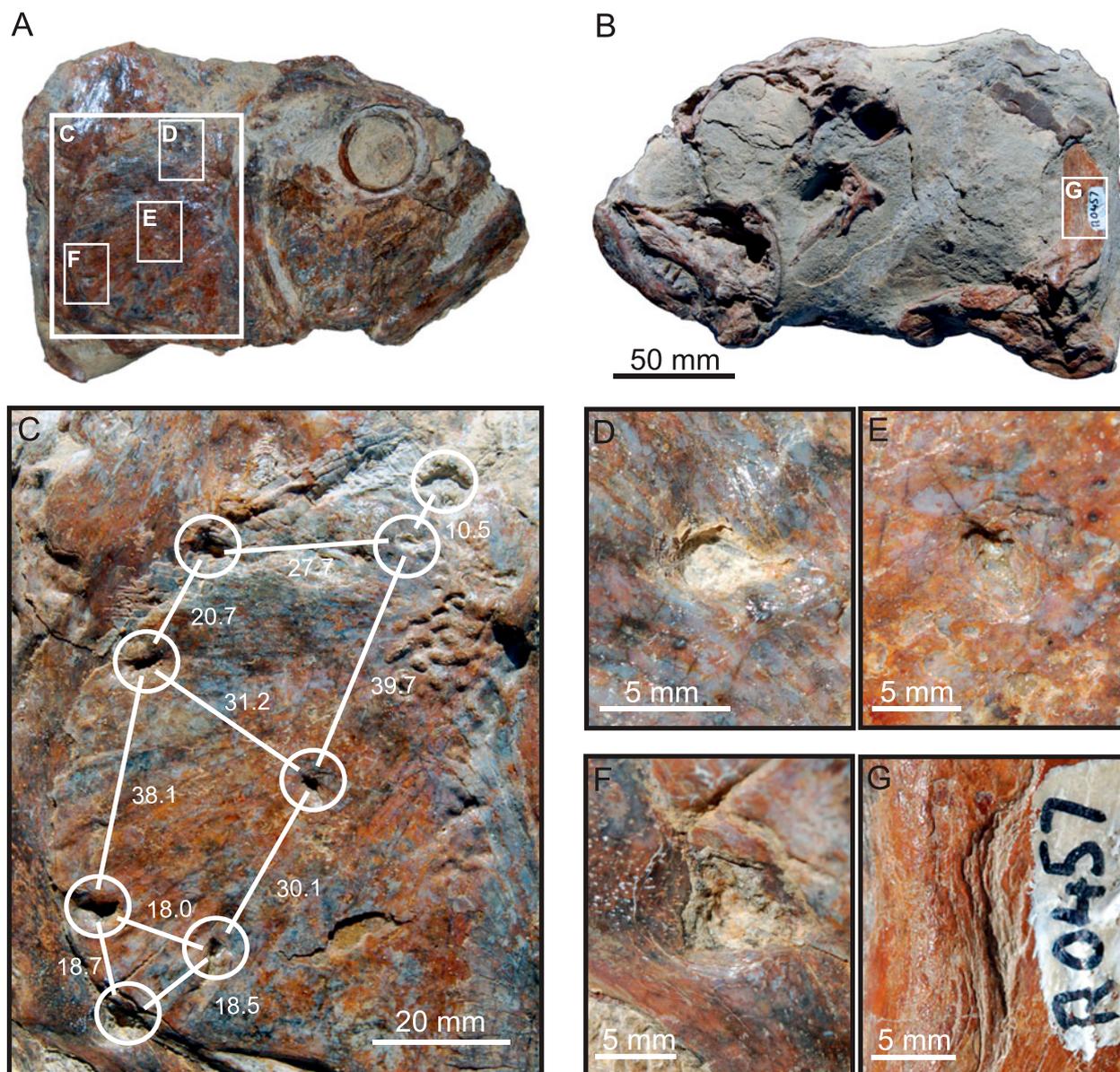


Fig 1. *Cooyoo australis* specimen KK R0457 displaying vertebrate bite marks. A, Right, and B, left-hand sides of the skull with areas of damage indicated by enlargements. C, Right opercular region with distribution of indentations and puncture marks indicated in millimetres. Exemplary enlargements of D, a puncture, E, indentation and F, depression fracturing found on the right operculum and cleithrum. G, Enlargement of left cleithrum showing longitudinal gouge and crack.

spore-pollen zone. This has been corroborated by Sr-isotope ratios, which likewise advocate a late Albian range (Williamson *et al.* 2012).

The Allaru Mudstone exposures at Richmond frequently yield fossils contained within limestone concretions that are disaggregated during exfoliation of the laminated parent rock. Invertebrate (ammonites, bivalves: Day 1969, Henderson *et al.* 2000, Henderson & Kennedy 2002) and vertebrate remains (a possible dicynodont, dinosaurs, marine amniotes, fishes: Lees & Bartholomai 1987, Molnar 1996, 2011, Kear 2003, Thulborn & Turner 2003, Bartholomai 2004, 2008, 2010a, 2012, Molnar & Salisbury 2005, Kear & Hamilton-Bruce 2011) are typically articulated, suggesting accumulation in offshore environments with well-oxygenated surface waters but quiet bottom conditions. Palaeogeographical interpretations also reconstruct a regressive marine seaway that was contiguous with the southern Tethys Ocean via an open shelf connection through the Carpenteria Basin and Money Shoals Platform (Henderson 1998, Cook 2012).

## Identification and description

KK R0457 can be confidently attributed to the ubiquitous Australian Early Cretaceous ichthyodectiform (Ichthyodectidae *sensu* Taverne & Chonet, 2000) *Cooyoo australis* Lees & Bartholomai, 1987 on the basis of its crested supraoccipital, anteriorly placed (within the orbital region) fused parietals, ridged frontals, maxillary dentition comprising small (*ca* 4 mm) tooth crowns, deep maxillary-premaxillary attachment and corresponding mandibular symphysis and massive opercular (see Taverne 2008 for a character state synopsis). The skull as preserved (Fig. 1A, B) is 224.5/139.9 mm in maximum length/height, yielding an estimated total body length of *ca* 1 m following the proportions reported by Lees & Bartholomai (1987). The cranial roof of KK R0457 has collapsed and been displaced obliquely into a slanted orientation relative to the orbits. There are few remnants of the postcranium, although parts of both the left and right cleithra are exposed. The concave articular face of a vertebral centrum (embedded in matrix) is also visible posteriorly, and remains in life position towards the caudal end of the neurocranium. The left-hand side of the skull has been severely damaged by weathering, and the entire left orbital region and suspensorium are now lost. The left operculum has also been shunted dorsally and eroded away, probably during exposure on the surface; however, the adjacent left cleithrum is still in place and partly covered by matrix (Fig. 1B). In contrast, the right-hand side of the skull is fully articulated and almost completely intact, having suffered only superficial weathering (perhaps from plant roots) on the maxillary-premaxillary and infraorbital series of bones (Fig. 1A). The visible bite marks are localized to the right operculum (Fig. 1C), but possibly related bone

modifications are also evident on the right and left cleithra (Fig. 1C, G). The right operculum bears eight irregular, crater-like indentations up to 3 mm deep and 5.5 mm in diameter (individual maximum diameter measurements taken clockwise from the dorsal-most are 2.8 mm; 3.3 mm; 2.9 mm; 3.2 mm; 2.9 mm; 2.3 mm; 2.6 mm; 5.5 mm: see Fig. 1C). These are arranged in a narrow V-shaped pattern that extends 56.1 mm obliquely from the anterodorsal to posteroventral edge of the operculum and onto the exposed dorsal margin of the right cleithrum. The indentations are also regularly spaced (10.5–39.7 mm apart) and aligned along tapering longitudinal axes 31.2–18 mm wide. Towards the thinner peripheral margins of the operculum, the bony tissue has been completely punctured and there is a surrounding area of depression cone fracturing associated with all of the marks; this presumably resulted from collapse of the bone surface under point loading (see enlargements in Fig. 1D–F). Compatible modifications have been attributed to the ichnotaxon *Nihilichnus nihilicus* Mikuláš, Kadlecová, Fejfar & Dvořák, 2006, which is characterized by triangular, circular or oval impact shapes surrounded by irregular fractures (Mikuláš *et al.* 2006).

It is unknown whether corresponding damage was evident on the left operculum, but two obvious marks (5.6/2.5 mm in maximum diameter) are present on the left cleithrum. The dorsal-most of these is a shallow gouge (11.2 mm long) with a longitudinal crack running ventrally away from the centre of damage (Fig. 1G). This could either be biogenic in origin, or the result of post-depositional compaction.

None of the identified bone modifications show traces of callus formation (deposition of osseous tissue at the site of trauma) or secondary zonal lamellar remodelling associated with healing. There are also no exostotic outgrowths or infectious abnormalities indicative of open wounds or adjacent soft tissue contagion (see Revell 1986, Aufderheide & Rodriguez-Martin 1988).

## Interpretation and discussion

Regularly spaced indentations/punctures with associated depression fractures and opposing placement on both the right and left opercular-pectoral regions of KK R0457 are compatible with vertebrate bite traces described in other fossil marine organisms (e.g., Shimada 1997, Tsujita & Westermann 2001, Mikuláš *et al.* 2006, Boessenecker & Perry 2011, Fahlke 2012). The absence of secondary osseous overgrowth or bone surface remodelling during healing also implies that the damage to KK R0457 occurred either peri- or postmortem. Despite this, the superficial nature of the modifications (puncture depth  $\leq$  3 mm) suggests that they were not immediately fatal, nor were they proximal to any areas of vital fleshy tissue. Moreover, their tapered sub-parallel arrangement and oblique orientation

across the anterodorsal to posteroventral sides of the skull indicate that the inflictor's jaws approached perpendicular to the longitudinal axis of the body with a slight 20° cranial slant relative to its dorsal surface, rather than against the more vulnerable underside. The lack of tooth drag marks or closely adjacent punctures additionally accords with a single bite and there is no other obvious evidence of subsequent readjustment of the fish's head within the mouth (compare with the observations of Fahlke 2012).

The identity of the attacker is unknown. However, the characteristically diminutive dentition of *Cooyoo australis*, which comprises only a few slender dentary teeth (up to 10 mm high) followed by homodont rows of small conical crowns (*ca* 4 mm high) on the dentaries and premaxillae-maxillae (see Lees & Bartholomai 1987, p. 182, tables 1, 2; p. 186, fig. 10), would seem to preclude an intraspecific encounter. Likewise, although ichthyodectiforms are known to have been macrophagous piscivores (e.g., Everhart *et al.* 2010), none of the other sufficiently large coeval actinopterygians (jaw length  $\geq 55$  mm) have teeth that precisely match the tooth indentations on KK R0457, nor do they appear capable of puncturing and cracking fresh bone. For example, the edentulous aspidorhynchid *Richmondichthys* (Bartholomai 2004) and elopomorph *Flindersichthys*, which has a minute villiform dentition (Bartholomai 2010a), can obviously be discounted. The common pachyrhizodont *Pachyrhizodus* (Bartholomai 2012) and rare possible albuloid *Euroka* (Bartholomai 2010b) are both similar to *Cooyoo* in possessing small marginal crowns (up to around 5 mm high) and only a few larger teeth (*ca* 10 mm long) at the anterior-most tip of the dentary or palatal midline, respectively. Lastly, the pachycormid *Australopachycormus* exhibits a distinctive arrangement of procumbent and upright lanceolate fangs (20 mm high) that are thin and separated by wide diastemae, together with an isolated medial pair of rearward-pointing rostral blades and convex rows of closely spaced, triangular teeth on the laterally situated premaxillae (Kear 2007). In light of these inconsistencies, we propose that the bite marks on KK R0457 were more likely made by a non-actinopterygian predator.

KK R0457 is not among the largest-known specimens of *Cooyoo australis* (Lees & Bartholomai 1987 and Kear & Hamilton-Bruce 2011 have reported skulls up to 400 mm long), but was substantial enough (*ca* 1 m long in life: Lees & Bartholomai 1987) to have made an attractive prey item for various sympatric sharks and amniotes. Certainly, many macrocarnivorous selachian species, together with marine reptiles and pterosaurs, are present in the Allaru Mudstone and slightly older Toolebuc Formation assemblages (see Kear & Hamilton-Bruce 2011 for faunal summaries). Sharks, however, can be excluded because their feeding traces characteristically comprise parallel sets of cuts or steep-sided punctures usually arranged in a wide arc

(e.g., Shimada 1997). Similarly, the colossal pliosaurid *Kronosaurus*, which is known to have fed upon large vertebrates (e.g., elasmosaurids and lamniforms: Thulborn & Turner 1993, 2003), has massive, widely spaced teeth (up to 250 mm long from the base of the root, with a crown height of 100 mm and apical separation of around 80 mm: Longman 1924, White 1935, Thulborn & Turner 1993) that would have inflicted severe crushing and breakage (see example illustrated by Thulborn & Turner 1993). The short, triangular snout of the elasmosaurid *Eromangasaurus* (Kear 2005a) is likewise too broad (73 mm wide based on the holotype skull QM F11050) and, incongruously, bears procumbent fangs with widely divergent distal apices (around 34 mm apart measured from QM F11050). Polycotyloid plesiosaurs (see Kear & Hamilton-Bruce 2011, p. 102), the ornithocheiroid pterosaur *Mythunga* (Molnar & Thulborn 2007, Fletcher & Salisbury 2010) and the endemic ichthyosaurian *Platypterygius australis* (Kear 2005b), on the other hand, all possessed suitably narrow maxillary and mandibular rostra together with stout conical teeth that could have indented and punctured bone. The Allaru Mudstone polycotyloid taxon has yet to be described but exhibits anteriorly inclined, massive teeth (up to 25 mm in diameter in QM F18041: BPK pers. obs.) at the front of both the premaxillae and dentaries. Dentigerous fragments from *Mythunga* (Molnar & Thulborn 2007) and other ornithocheiroids (*Aussiedraco* and indeterminate remains: Fletcher & Salisbury 2010, Kellner *et al.* 2011) are also commonly delicate (QM F44423, the distal part of the mandible described by Fletcher & Salisbury 2010, measures only 18.5 mm at its broadest point). Given our interpretation, the ichthyosaurian *P. australis*, therefore, displays the most compatible tooth arrangement with compact tooth rows *ca* 40 mm apart and vertically oriented crowns separated by gaps of *ca* 20 mm (based on the articulated individual QM F2453). Kear (2005b) suggested that *P. australis* probably fed on small-bodied cephalopods and vertebrates; however, vigorous dismemberment of large, bony prey items appears feasible based on tooth wear patterns and dental pathology (see Kear 2001). Indeed, this conclusion is strengthened by the discovery of isolated *Cooyoo*-like remains within the gut contents of at least one *P. australis* individual (Kear *et al.* 2003).

## Conclusions and implications

The recognition of preserved vertebrate bite traces on the *Cooyoo australis* specimen KK R0457 not only provides the first documented example of a bite-modified actinopterygian fossil from Australia (previous examples include digested remnants in coprolites: Beattie & Avery 2012), but also elucidates potential interspecific interactions within the Early Cretaceous marine lagerstätten assemblages of the Eromanga Basin. Interestingly, the distribution and spacing of the individual tooth impact depressions/punctures does

not match the dentition of conspecific individuals, nor does it comply with any other described actinopterygian or selachian that occurs sympatrically. Rather, the conspicuously narrow bite mark arrangement and associated fracturing indicates an encounter with a longirostrine amniote that bore small, robust teeth, perhaps a polycotylid plesiosaurian (see Kear & Hamilton-Bruce 2011, p. 102 for comparative image), ornithocheiroid pterosaur (e.g., *Mythunga*: Molnar & Thulborn 2007, Fletcher & Salisbury 2010) or the coeval ichthyosaurian *Platypterygius australis* (e.g., Kear 2005b). Whether this event was accidental (non-feeding), predatory or scavenging is unknown but, tellingly, only *P. australis* has been directly identified as having fed upon large fish such as *Cooyoo* (Kear *et al.* 2003). In addition, the unusual orientation of the bite, which was directed against the dorsal side of the skull, could imply that the body was floating and either inverted or prone at the surface; this accords with the absence of healing and indicates that the animal was already dead or dying when attacked. The non-lethal condition of the damage also suggests that fatal injuries (if any) must have been located on the postcranium. Note however that there are no obvious traces of violent disarticulation on the cleithra or exposed vertebral centrum. Irrespectively, this scenario infers that KK R0457 was a potential prey item and could have been either actively hunted or opportunistically scavenged. Subsequent trophic implications infer a hierarchical relationship, in which intermediate-level predators such as *Cooyoo* appear to have constituted prey for high-level consumers, feasibly represented in this case by an ichthyosaurian (see also Kear *et al.* 2003). This is consistent with other Early Cretaceous epeiric communities (e.g., the Santana Formation of Brazil: see Maisey 1994), in which actinopterygians constitute a prominent component of the lower- to middle-level trophic niches. Uniquely, however, the Toolebuc Formation and Allaru Mudstone lagerstätten have also yielded direct evidence of marine amniotes as intermediate-level benthic ‘grazers’ (protostegid turtles, elasmosaurs: McHenry *et al.* 2005, Kear 2006) and apex carnivores (*Kronosaurus*: Thulborn & Turner 1993, Turner & Thulborn 2003), thus occupying ecological niches not unlike their marine mammal equivalents of today.

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