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## Healed bite marks on a Cretaceous ichthyosaur

MARIA ZAMMIT and BENJAMIN P. KEAR

**Reports of pathological ichthyosaur fossils are very rare. The identification of a series of healed cuts and an associated gouge on the lower jaw of an adult (ca. 5 metres body length) *Platypterygius* specimen from the Lower Cretaceous of Australia is therefore significant, because it constitutes direct evidence of bite force trauma sustained during the life of the animal. Based on the close spacing and non-lethal facial positioning of the wounds, they were probably not inflicted by a predator. Alternative explanations might include an accidental aggressive encounter with another large vertebrate, or perhaps an intraspecific interaction such as during courtship or combat over food, mates, or territory.**

### Introduction

Tooth marks on fossilized bones and other organic remnants constitute direct evidence of interaction between extinct animals, and have been well documented in Mesozoic marine vertebrates, including fish (Shimada and Everhart 2004; Everhart 2005), turtles (Lingham-Soliar 1995; Schwimmer 2002; Shimada and Hooks 2004), ichthyosaurs (Martill 1996), crocodiles (Frey et al. 2002), plesiosaurs (Barnes and Hillier 2010; Einarsson et al. 2010; Shimada et al. 2010), and mosasaurs (Shimada 1997; Everhart 2004, 2008; Lingham-Soliar 2004; Rothschild et al. 2005). In some cases, these pathologies can be attributed to specific taxa and allow for palaeoecological inferences, including predator-prey contacts (Thulborn and Turner 1993), scavenging (Schwimmer et al. 1997), or intraspecific behaviours (Bell and Martin 1995; Everhart 2008). Unfortunately, traces of an aggressive encounter often cannot be distinguished from damage inflicted on a carcass after death, thus definitive interpretations are not always possible (Schwimmer et al. 1997). Nevertheless, evidence of healing processes provide a clear indication of non-fatal trauma and have been used to reconstruct the palaeobiology of some extinct vertebrates (see summaries in Rothschild and Martin 1993, 2006; Tanke and Currie 1998).

Documented examples of bite pathologies in ichthyosaurs are particularly rare, with the only published occurrence being an isolated vertebral centrum from the Upper Jurassic Kimmeridge Clay of England that exhibited puncture marks thought to have been made by a pliosaur (Martill 1996). Other reports have noted lesions around the teeth (dental caries: Kear 2002), and gastric residues, which provide direct evidence of feeding strategies (Pollard 1968; Kear et al. 2003) and predation (McGowan 1974; O'Keefe et al. 2009). This paper describes a novel addi-

tion to the ichthyosaurian palaeopathology record—a partial skeleton from the Lower Cretaceous of Australia that exhibits healed gouges along its lower jaw. The close spacing and non-lethal facial positioning of these wounds leads us to interpret them as bite marks, perhaps inflicted by another ichthyosaur during courtship or combat over mates/food.

*Institutional abbreviation.*—SAM, South Australian Museum, Adelaide, Australia.

### Identification and geological context

The specimen reported here (SAM P14508) is a fragmentary skull and postcranium recovered from the Lower Cretaceous (lower Aptian–lower Albian) Bulldog Shale at Bopeechee Siding, near Marree in northeastern South Australia (see Kear 2006: 838, fig. 1 for a locality map). The skeleton was collected in several sections, with part of the snout and lower jaw initially found in 1970 (Pledge 1980; Pledge and Tedford 1990), and the remainder discovered by Reg Dodd (Arabunna People's Community Centre and Museum, Marree, Australia) who excavated the specimen with the South Australian Museum in 2002. Kear (2006) assessed the assembled remains and assigned them to the cosmopolitan ophthalmosaurid genus *Platypterygius* (based on the possession of a robust dentition with quadrangular tooth roots; angular with extensive external exposure reaching as far anteriorly as the surangular; and the presence of three distal facets on the femur for the tibia, fibula and an anterior zeugopodial element; see Kear 2006: 850). This taxon is the only Cretaceous ichthyosaur currently identified from Australia and is represented by a single, regionally endemic species—*P. australis* (see Zammit 2010 for a recent review).

The Bulldog Shale is an epicontinental shallow marine unit comprising carbonaceous mudstone and shale beds (Krieg and Rogers 1995). It is highly fossiliferous, yielding a rich assemblage of marine invertebrates (Ludbrook 1966), osteichthyan fish and chimaerids (Alley and Pledge 2000), marine reptiles (plesiosaurs and ichthyosaurs: Kear 2003, 2006), and occasional dinosaurs (Barrett et al. 2010). Significantly, the Bulldog Shale also preserves sedimentary (ice-rafted boulders, glendonites) and fossil (dense growth banding in coniferous driftwood) indicators of highly seasonal, near freezing climates and is associated with an Early Cretaceous high latitude zone (~70° S; Frakes et al. 1995). Kear (2006) speculated that this extreme palaeoenvironment was probably only intermittently occupied

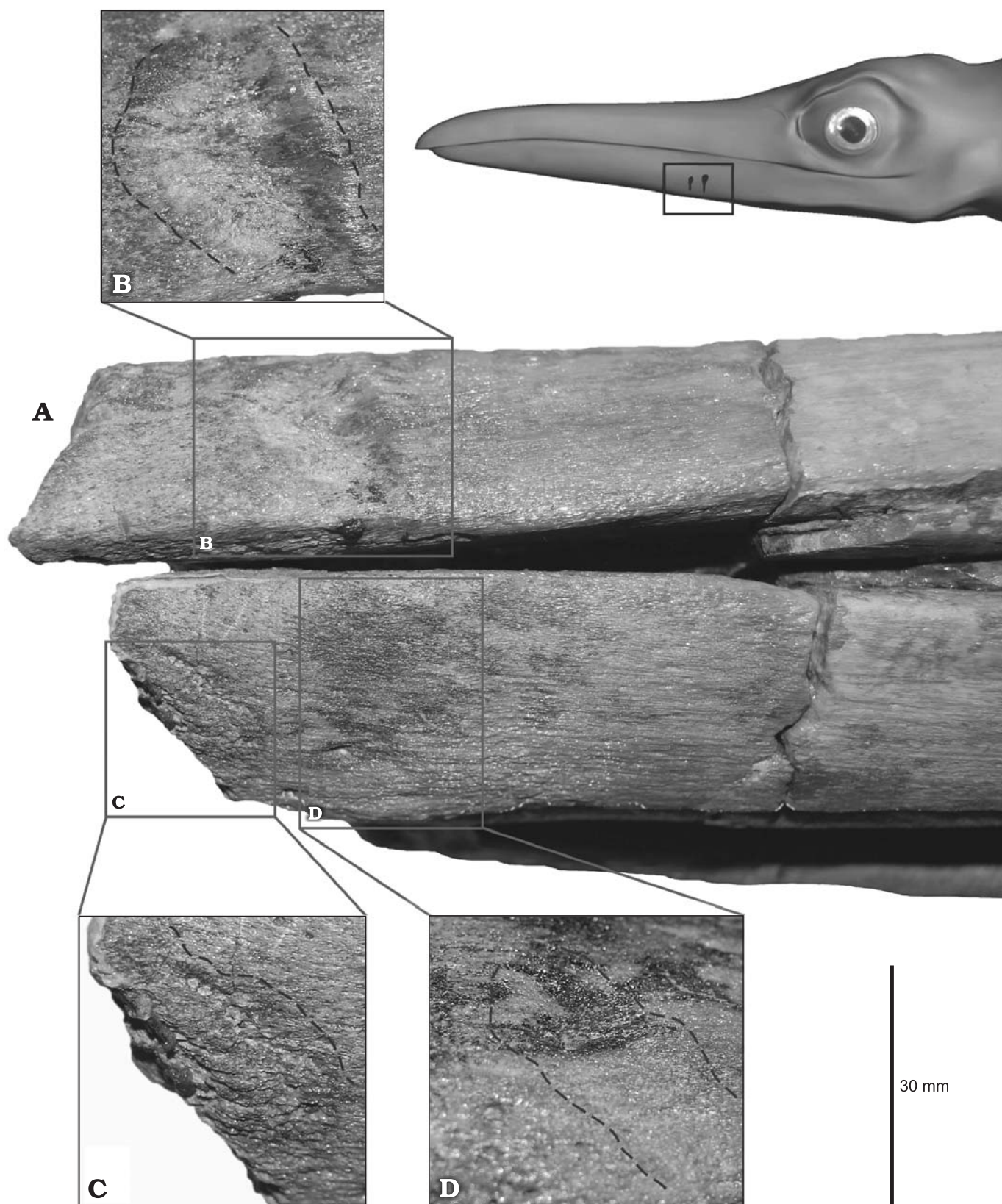


Fig. 1. Pathological specimen (SAM P14508) of the Cretaceous ichthyosaur *Platypterygius* sp., near Marree, South Australia, with reconstruction of the head in lateral view (top right) indicating position of the bite injuries (enclosed). **A.** Articulated mandible in ventral view showing healed lesions on both the left and right dentary (enlarged in B–D). **B.** Prominent gouge with raised margins formed during osseous callus deposition. **C.** Callus-like surface texturing associated with a furrow. **D.** Ragged furrow extending transversely across dentary. Computer generated reconstruction produced by Ben Hill (Adelaide, Australia).

by pelagic marine reptiles, whose fossils predominantly include small-bodied, osteologically immature individuals that might have used cold water, near-shore habitats as nutrient-rich summer refugia.

## Description of the pathologies

The injuries on SAM P14508 are restricted to the lower jaw. The rest of the skeleton had broken up during weathering on the surface and was strewn down a shallow erosion gully cutting into an exposed outcrop of laminated shale. Nevertheless, the tip of the lower jaw was still preserved in situ and declined at an angle of around 10° relative to the horizontal bedding plane of the sediments. The skull of SAM P14508 was extremely fragmented and required reassembly in the laboratory. The restored specimen is 509 mm long, and consists of the snout and lower jaw extending from near the bony nasal aperture to the anterior extremity of the mandibular symphysis around the mid-section of the rostrum. Apart from the mandibular apex, all other cranial elements had been destroyed. Many of the teeth in SAM P14508 were still intermeshed in the dental groove, indicating that the jaws remained in articulation and tightly closed after death (see Kear 2006: 849, text-fig. 6A). Nineteen functional (non-replacement) teeth remained in place on the premaxillae (ten on the left side and nine on the right) and 12 were present on the left-hand side of the dentary. Further preparation also exposed a prominent gouge (22.58 mm long by 15.56 mm wide; Fig. 1A, B) just anterior to the tooth row on the ventrolateral surface of the left dentary. In direct opposition were two parallel jagged furrows (20.74/11.62 mm long and 14.72 mm apart; the anterior-most probably associated with another gouge) running obliquely across the ventral edge of the right dentary and ascending towards its tooth-bearing surface (Fig. 1A, C, D). The bone surrounding all these marks was raised and abnormally rugose, consistent with formation of a callus (osseous tissue deposited at a site of trauma) and secondary zonal lamellar remodelling incurred during healing. Similar texturing was also detected along the broken anterior edge of the left dentary (20.02 mm from the prominent gouge), perhaps indicating that another injury might have been present there (Fig. 1A). There was no evidence of exostosis (bony outgrowth associated with infectious abnormality), suggesting an absence of subsidiary infections such as osteomyelitis which is propagated by spread of microorganisms to the bone through haematogenous dissemination, open wounds, or adjacent soft tissue contagion (Revell 1986; Aufderheide and Rodriguez-Martin 1988).

## Interpretations

Close spacing of the injuries (10–20 mm apart), their proximal orientation on the left and right sides of the mandible, and localized positioning on the facial region of SAM P14508 is closely comparable to tooth-strike lesions described from other fossil vertebrates (see Tanke and Rothschild 2002). The lack of any obvious impacted bone coupled with extensive healing suggests that the osseous surface was probably not punctured but rather

scored (producing redirection of bone grain; see Fig. 1B), causing a series of painful yet not debilitating wounds. Restriction of the marks to the dentary symphysis also implies that the bite was directed against the vulnerable underside of the animal, but in an area that would have had minimal fleshy tissue (Kear 2005).

The identity of the aggressor is unknown, although the injuries suggest a predator attack, accidental encounter, or intraspecific interaction involving mates, territory, and/or food. Damage sustained from prey is less likely because *Platypterygius* and many other post-Triassic ichthyosaurs appear to have preferred easily subduable food items such as small fish and cephalopods (indicated by preserved gut contents; see Kear et al. 2003 and references therein). However, more hazardous prey may have occasionally formed part of the diet. For example, Kear et al. (2003) reported the teeth (up to 7 mm tall) of larger-bodied fish (around 500 mm long) in gastric residues of *Platypterygius australis*, and McGowan (1974) also noted ichthyosaur remains in the body cavity of a *Temnodontosaurus* skeleton from the Lower Jurassic of England.

Based on its size, SAM P14508 was probably a mature individual of about 5–6 m long (estimated from comparisons with more complete specimens; see Wade 1984). Nevertheless, its massive bulk would not have precluded attack by predators. Indeed, the Bulldog Shale marine reptile assemblage includes at least one sympatric plesiosaur taxon, the gigantic pliosaurid *Kronosaurus* (see Kear 2006), which might have exceeded 10 m and is known to have actively hunted very large marine vertebrates (e.g., elasmosaurs and sharks; Thulborn and Turner 1993; Turner and Thulborn 2003). The teeth of *Kronosaurus* are widely spaced and enormous (up to 250 mm long with a crown height of 100 mm and apical separation of around 80 mm; Longman 1924; White 1935; Thulborn and Turner 1993), and would have inflicted horrific injuries (see examples in Thulborn and Turner 1993) quite unlike those on SAM P14508. In addition, bite marks on SAM P14508 were not targeted at a vital part of the body and so would not have immobilized or killed the ichthyosaur outright (cf. a wound to the cranium, viscera, or tail), although a failed attack perhaps involving a glancing bite or ramming impact cannot be ruled out. Other potential predators could include very large lamniform sharks, which are known from the Aptian of Australia (Darwin Formation; Turner and Rozefelds 1992), but have not yet been recovered from the Bulldog Shale (Kear 2006). Lamniform feeding traces tend to comprise steep-sided punctures (Shimada 1997) or parallel sets of cuts (Einarsson et al. 2010); these are not unlike the furrows evident on the jaw of SAM P14508 but bear little similarity to the circular gouge on the left dentary.

An accidental, non-predatory encounter with another carnivorous marine vertebrate might alternatively explain the pathologies on SAM P14508, and certainly, a variety of smaller-bodied plesiosaurs manifesting closely spaced, conical teeth have been documented from the Bulldog Shale (e.g., elasmosaurs, aristonectids, pliosauroids; Kear 2006; Kear et al. 2006). However, given the complex social behaviours exhibited by modern aquatic reptiles, it is not implausible that another ichthyosaur might have been involved. Aggressive intraspecific contact has been inferred for a

variety of extinct crocodylomorphs (Buffetaut 1983; Mackness and Sutton 2000; Avilla et al. 2004; Katsura 2004), phytosaurs (Abel 1922; Tanke and Currie 1998), and mosasaurs (Lingham-Soliar 1998, 2004). Interestingly, all of these groups also appear to have focussed attacks on the cranium and jaws presumably during courtship and mating or combat over territory, food, or social dominance (see Tanke and Currie 1998 for discussion). Whether such behaviours were exhibited in *Platypterygius* is of course unknown, but the shallow, closely spaced bite traces on SAM P14508 are not inconsistent with the densely packed teeth and narrow premaxillary/mandibular rostra characteristic of this taxon (Romer 1968; Kear 2005; Kolb and Sander 2009). Indeed, it is tempting to reconstruct the positioning of the marks on the ventral side of the mandible as the result of a restraining bite, delivered when another ichthyosaur approached SAM P14508 from below and attempted to neutralize the threat of a counter attack by clamping onto and forcing aside its elongate jaws.

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## References

- Abel, O. 1922. Die Schnauzenverletzungen der Parasuchier und ihre biologische Bedeutung. *Paläontologische Zeitschrift* 5: 26–57.
- Alley, N.F. and Pledge, N.S. 2000. The plants, animals and environments of the last 280 (290) millions years. In: W.J.H. Slaytor (ed.), *Lake Eyre South Monograph Series Volume 5*, 35–82. Royal Geographical Society of Australia, Adelaide.
- Aufderheide, A.C. and Rodriguez-Martin, C. 1988. *The Cambridge Encyclopedia of Human Palaeopathology*. 496 pp. Cambridge University Press, New York.
- Avilla, L.S.A., Fernandes, R., and Ramos, D.F.B. 2004. Bite marks on a crocodylomorph from the Upper Cretaceous of Brazil: evidence of social behaviour? *Journal of Vertebrate Paleontology* 24: 971–973.
- Barnes, K.M. and Hillier, N. 2010. The taphonomic attributes of a Late Cretaceous plesiosaur skeleton from New Zealand. *Alcheringa* 34: 333–344.
- Barrett, P.M., Kear, B.P., and Benson, R.B.J. 2010. Opalised archosaur remains from the Lower Cretaceous of South Australia. *Alcheringa* 34: 293–301.
- Bell, G.L. Jr., and Martin, J.E. 1995. Direct evidence of aggressive intraspecific competition in *Mosasaurus conodon* (Mosasauridae: Squamata). *Journal of Vertebrate Paleontology* 15: 18A.
- Buffetaut, E. 1983. Wounds on the jaw of an Eocene mesosuchian crocodilian as possible evidence for the antiquity of crocodilian intraspecific fighting behaviour. *Paläontologische Zeitschrift* 57: 143–145.
- Einarsson, E., Lindgren, J., Kear, B.P., and Siverson, M. 2010. Mosasaur bite marks on a plesiosaur propodials from the Campanian (Late Cretaceous) of southern Sweden. *FGG* 132: 123–128.
- Everhart, M.J. 2004. Late Cretaceous interaction between predators and prey. Evidence of feeding by two species of shark on a mosasaur. *PalArch, Vertebrate Palaeontology Series* 1: 1–7.
- Everhart, M.J. 2005. *Oceans of Kansas. A Natural History of the Western Interior Sea*. 322 pp. Indiana University Press, Bloomington.
- Everhart, M.J. 2008. A bitten skull of *Tylosaurus kansasensis* (Squamata: Mosasauridae) and a review of mosasaur-on-mosasaur pathology in the fossil record. *Transactions of the Kansas Academy of Science* 111: 251–262.
- Frakes, L.A., Alley, N.F., and Deynoux, M. 1995. Early Cretaceous ice rafting and climate zonation in Australia. *International Geology Review* 37: 567–583.
- Frey, E., Buchy, M., Stinnesbeck, W., and Lopez-Oliva, J.G. 2002. *Geosaurus vignaudi* n. sp. (Crocodyliformes: Thalattosuchia), first evidence of metriorhynchid crocodilians in the Late Jurassic (Tithonian) of central-east Mexico (State of Puebla). *Canadian Journal of Earth Sciences* 39: 1467–1483.
- Katsura, Y. 2004. Paleopathology of *Toyotamaphimeia machikanensis* (Diapsida, Crocodylia) from the Middle Pleistocene of Central Japan. *Historical Biology* 16: 93–97.
- Kear, B.P. 2002. Dental caries in an Early Cretaceous ichthyosaur. *Alcheringa* 25: 387–390.
- Kear, B.P. 2003. Cretaceous marine reptiles of Australia: a review of taxonomy and distribution. *Cretaceous Research* 24: 277–303.
- Kear, B.P. 2005. Cranial morphology of *Platypterygius longmani* Wade, 1990 (Reptilia: Ichthyosauria) from the Lower Cretaceous of Australia. *Zoological Journal of the Linnean Society* 145: 583–622.
- Kear, B.P. 2006. Marine reptiles from the Lower Cretaceous of South Australia: elements of a high-latitude cold-water assemblage. *Palaeontology* 49: 837–856.
- Kear, B.P., Boles, W.E., and Smith E.T. 2003. Unusual gut contents in a Cretaceous ichthyosaur. *Proceedings of the Royal Society of London* 270: S206–S208.
- Kear, B.P., Schroeder, N.I., and Lee, M.S.Y. 2006. An archaic crested plesiosaur in opal from the Lower Cretaceous high latitude deposits of Australia. *Biology Letters* 2: 615–619.
- Kolb, C. and Sander, P.M. 2009. Redescription of the ichthyosaur *Platypterygius hercynicus* (Kuhn 1946) from the Lower Cretaceous of Salzgitter (Lower Saxony, Germany). *Palaeontographica Abteilung A* 288: 151–192.
- Krieg, G.W. and Rogers, P.W. 1995. Stratigraphy—marine succession. In: J.F. Drexel and W.V. Preiss (eds.), *The Geology of South Australia. Volume 2, The Phanerozoic*, 112–123. South Australia Geological Survey Bulletin, Adelaide.
- Lingham-Soliar, T. 1995. Anatomy and functional morphology of the largest marine reptile known, *Mosasaurus hoffmanni* (Mosasauridae, Reptilia) from the Upper Cretaceous, Upper Maastrichtian of The Netherlands. *Philosophical Transactions of the Royal Society of London B* 347: 155–180.
- Lingham-Soliar, T. 1998. Unusual death of a Cretaceous giant. *Lethaia* 31: 308–310.
- Lingham-Soliar, T. 2004. Palaeopathology and injury in the extinct mosasaurs (Lepidosauromorpha, Squamata) and implications for modern reptiles. *Lethaia* 37: 255–262.
- Longman, H.A. 1924. Some Queensland fossil vertebrates. *Memoirs of the Queensland Museum* 10: 16–28.
- Ludbrook, N.H. 1966. Cretaceous biostratigraphy of the Great Artesian Basin in South Australia. *Geological Survey of South Australia Bulletin* 40: 7–223.
- Mackness, B. and Sutton, R. 2000. Possible evidence for intraspecific aggression in a Pliocene crocodile from northern Australia. *Alcheringa* 24: 55–62.
- Martill, D.M. 1996. Fossils explained: ichthyosaurs. *Geology Today* 12: 194–196.
- McGowan, C. 1974. A revision of the longipinnate ichthyosaurs of the Lower Jurassic of England, with descriptions of two new species (Reptilia: Ichthyosauria). *Royal Ontario Museum Life Sciences Contributions* 97: 1–37.

- O'Keefe, R.R., Street, H.P., Cavigelli, J.P., Socha, J.J., and O'Keefe, R.D. 2009. A plesiosaur containing an ichthyosaur embryo as stomach contents from the Sundance Formation of the Bighorn Basin, Wyoming. *Journal of Vertebrate Paleontology* 29: 1306–1310.
- Pledge, N.S. 1980. *Vertebrate Fossils of South Australia*. 11 pp. Government Printer, Adelaide.
- Pledge, N.S. and Tedford, R.H. 1990. Vertebrate Fossils. In: M.J. Tyler, C.R. Twidale, M. Davies, and C.B. Wells (eds.), *Natural History of the North East Deserts*, 199–209. Royal Society of South Australia, Incorporated, Adelaide.
- Pollard, J.E. 1968. The gastric contents of an ichthyosaur from the Lower Lias of Lyme Regis, Dorset. *Palaeontology* 11: 376–388.
- Revell, P.A. 1986. *Pathology of Bone*. 451 pp. Springer-Verlag, Berlin.
- Romer, A.S. 1968. An ichthyosaur skull from the Cretaceous of Wyoming. *Contributions to Geology, University of Wyoming* 7: 27–41.
- Rothschild, B.M. and Martin, L.D. 1993. *Paleopathology. Disease in the Fossil Record*. 386 pp. CRC Press, Boca Raton.
- Rothschild, B.M. and Martin, L.D. 2006. *Skeletal Impact of Disease*. 226 pp. New Mexico Museum of Natural History, Albuquerque, NM.
- Rothschild, B.M., Martin, L.D., and Schulp, A.S. 2005. Sharks eating mosasaurs, dead or alive? *Netherlands Journal of Geosciences* 84: 335–340.
- Schwimmer, D.R. 2002. *King of the Crocodylians. The Paleobiology of Deinosuchus*. 220 pp. Indiana University Press, Bloomington.
- Schwimmer, D.R., Steward, J.D., and Williams, G.D. 1997. Scavenging by sharks of the genus *Squalicorax* in the Late Cretaceous of North America. *Palaos* 12: 71–73.
- Shimada, K. 1997. Paleoecological relationships of the Late Cretaceous lamniform shark, *Cretoxyrhina mantelli* (Agassiz). *Journal of Paleontology* 71: 926–933.
- Shimada, K. and Everhart, M.J. 2004. Shark-bitten *Xiphactinus audax* (Teleostei: Ichthyodectiformes) from the Niobrara Chalk (Upper Cretaceous) of Kansas. *The Mosasaur* 7: 35–39.
- Shimada, K. and Hooks, G.E. III 2004. Shark-bitten protostegid turtles from the Upper Cretaceous Mooreville Chalk, Alabama. *Journal of Paleontology* 78: 205–210.
- Shimada, K., Tsuihiji, T., Sato, T., and Hasegawa, Y. 2010. A remarkable case of a shark-bitten elasmosaurid plesiosaur. *Journal of Vertebrate Paleontology* 30: 592–597.
- Tanke, D.H. and Currie, P.J. 1998. Head-biting behaviour in theropod dinosaurs: paleopathological evidence. *Gaia* 15: 167–184.
- Tanke, D.H. and Rothschild, B.M. 2002. Dinosaurs: An annotated bibliography of dinosaur paleopathology and related topics—1838–2001. *New Mexico Museum of Natural History and Science Bulletin* 20: 1–96.
- Thulborn, T. and Turner, S. 1993. An elasmosaur bitten by a plesiosaur. *Modern Geology* 18: 489–501.
- Turner, S. and Rozefelds, A. 1992. Tip of the pyramid? Cretaceous megasharks from Australia. *The Beagle. Records of the Northern Territory Museum and Art Gallery* 9: 262–263.
- Turner, S. and Thulborn, T. 2003. Second course for *Kronosaurus*? Further evidence of plesiosaur predation in the Cretaceous of Queensland. In: S. Hocknull and A. Cook (eds.), *9th Conference on Australasian Vertebrate Evolution, Palaeontology & Systematics—Heber A. Longman Symposium, Brisbane, Abstracts*, 29–30. Queensland Museum, Brisbane.
- Wade, M. 1984. *Platypterygius australis*, an Australian Cretaceous ichthyosaur. *Lethaia* 17: 99–113.
- White, T.E. 1935. On the skull of *Kronosaurus queenslandicus* Longman. *Occasional Papers of the Boston Society of Natural History* 8: 219–228.
- Zammit, M. 2010. A review of Australasian ichthyosaurs. *Alcheringa* 34: 381–292.

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