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Short communication

Hesperornis escapes plesiosaur attack

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ABSTRACT

Evidence from the Pierre Shale (Late Cretaceous) of South Dakota is presented for an attack on a juvenile *Hesperornis* by a polycotylid plesiosaur. The wound healed and the *Hesperornis* grew to maturity. Evidence of survival provides our best information about predator prey interactions in the fossil record but are rare for birds where survival is an unlikely outcome.

1. Introduction

The large, flightless, foot-propelled diving bird, *Hesperornis* must have occupied a similar position in the ecology of the Late Cretaceous seas as do penguins today and shows a very similar size distribution for the different species (Martin and Lim, 2002). Although penguins are superb high-speed underwater swimmers, sharks, seals or killer whales occasionally do prey on them and it seems likely that the main predators on *Hesperornis* in the late Mesozoic were the reptilian equivalents of the toothed whales, the mosasaurs and plesiosaurs. Mosasaurs were giant sea-going lizards that propelled themselves through the Late Cretaceous seas by powerful thrusts of their tail.

Usually predator-prey relationships can only be inferred in the fossil record, but occasionally direct evidence can be observed consisting of unhealed bite marks, stomach contents and healed bite marks. The first two cannot be certainly separated from scavenging and the last may be evidence of predation, but not diagnostic of the predator. Evidence of predation on birds is rare in the fossil record, as their fragile skeletons usually do not survive intact enough to give much evidence about the cause of their death. Recently there have been findings of enantiornithine bird bones in the abdominal cavities of an ichthyosaur (Kear et al., 2003) and of a *Microraptor* (O'Connor et al., 2011). It seems likely that the ichthyosaur example results from scavenging (Kear et al., 2003) of a carcass of a bird removed some distance from its normal habitat. *Hesperornis*, because of its diving adaptations, has an unusually robust and heavy skeleton that provides some opportunity for preservation of a record of injury.

Evidence for mosasaur predation on *Hesperornis* consists of a *Tylosaurus* from the Late Cretaceous Pierre Shale of South Dakota with hesperorniform bones among other stomach contents (Martin and Bjork, 1987). They found portions of a shark (?*Cretolamna*), a teleost fish (*Bananogmius*), and a small mosasaur (*Clidastes*), as well as the bird. The bones of all these individuals appear highly disarticulated and may represent remnants of several days (weeks?) hunting. It also shows that they were opportunistic predators and/or scavengers who utilized a broad spectrum of prey species.

Until now there has been no evidence for plesiosaur predation on birds. Toothmarks were found on the tibiotarsus of a *Hesperornis* as described below. The pertinent specimens are from the Yale Peabody Museum Princeton University Collection, YPMPU and University of Kansas KUVP.

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2. Methods

Portions of a left leg (tibiotarsus, tarsometatarsus, phalanges) of a *Hesperornis* (YPMPU 17208) discovered in the Late Cretaceous Pierre Shale of South Dakota (Fig. 1) were macroscopically examined and subjected to standard X-ray examination. Mosasaur (*Clidastes*, KUVP 1028) and plesiosaur (*Dolichorhynchops osborni*, KUVP 1300; *Trinacromerum bentonianum*, KUVP 5070) skulls from the collections of the University of Kansas were assessed for tooth character and spacing as compared to the putative tooth marks on the *Hesperornis* tibiotarsus.

3. Results

Macroscopic examination of the *Hesperornis* tibiotarsus (YPMPU 17208) revealed foreshortening on the calcaneal (lateral) side with deviation (Fig. 1). The lateral condyle is pathologically eroded on the lateral side and shifted inwards so that the intercondylar space is narrowed (Fig. 2). The lateral-distal margin shows a smoothed worn surface. The lateral (intercondylar) side of the medial condyle is undercut by a groove that extends over its distal edge. There are three rounded depressions showing evidence of inwardly pressed bone fragments (Fig. 3). The depressions are round with a diameter of about 4.4–9.55 mm and arranged in straight lines on the anteriolateral and posteriomedial surfaces of the distal tibiotarsus, separated from each other by about 11.9 mm. We interpret them as tooth marks left by the jaw of a predator. A ridge is present on the lateral aspect of the lateral condyle suggesting slight osteoarthritis (Altman et al., 1986) (Fig. 4). Radiologic evaluation revealed a large radiolucent area with irregular margins, irregular internal density and intracortical resorption superior to the metaphysis on the foreshortened side, extending 5.4 cm (corrected for parallax) (Fig. 5). Skeletal radiologists refer to this as a moth-eaten appearance (Rothschild and Martin, 2006).

The circular nature of the indentations rules out shark predation. Attempts to fit small mosasaur jaws to the bite marks were unsuccessful. The teeth in mosasaurs and dinosaurs (even those with conical teeth) are usually unequally spaced, related to replacement pattern and impact at larger intervals, quite distinguishable from the very evenly spaced bite marks on the *Hesperornis* tibiotarsus. Attempt to fit *Xiphactinus* teeth was also unsuccessful. This contrasted with the jaws of a small polycotylid plesiosaur KUVP 1300, whose long narrow snout and equal tooth spacing worked perfectly. The associated tarsometatarsus shows polishing (eburnation) on the lateral cotyle while the medial cotyle is cut out by pressure erosion in the posterior groove and the posterior lateral ridge enlarged.

4. Discussion

We report here a healed injury in the leg of a *Hesperornis*, where tooth marks clearly implicate a small reptile in the attack. The specimen is smaller than the common *Hesperornis regalis* of the Niobrara Chalk, but it differs from the slender limbed, contemporary *H. chowi* (Martin and Lim, 2002) by having a broader tarsometatarsus with a more enlarged outer trochlea. *H. chowi* appears to be a member of a more northern radiation of *Hesperornis* that was brought south by global cooling in the Late Cretaceous (Martin and Lim, 2002). *Hesperornis*, like other foot-propelled diving birds, has the tibiotarsus tied by muscles to the elongated pelvis nearly to the ankle. This results in separation of the leg from the pelvis distally by only a few centimeters. The leg could not be swung under the center of gravity. Because of this, *Hesperornis* could not have walked on land and probably pushed itself along with its hind feet like a seal. The femora are laterally spread and fixed in that position by a tight articulation to the antitrochanter, and the acetabulum is mostly closed (Martin and Tate, 1976). The feet are immense and are longer than the elongated tibiotarsus. The toes were lobed and show the same rotational modifications found in the lobed toes of modern grebes. The body is slender with the wing bones reduced to a pencil-sized humerus, apparently lacking the radius, ulna and manus. Stomach contents in a related form, *Baptornis*, show that the diet of hesperornithiform birds consisted of small fish (Martin and Tate, 1976).

The position of the bite marks reveals a very awkward location for the injury, as the attacking animal would have had to have its head at ninety degrees to the axis of the bird's body, with the snout inserted between the body and the foot so that a single row of teeth could come into contact with the tibiotarsus. In this position, the foot would probably have been engulfed by the predator's mouth.

As the calcaneal (lateral) side of the distal tibiotarsus is shorter than the medial, we propose that the injury occurred while the

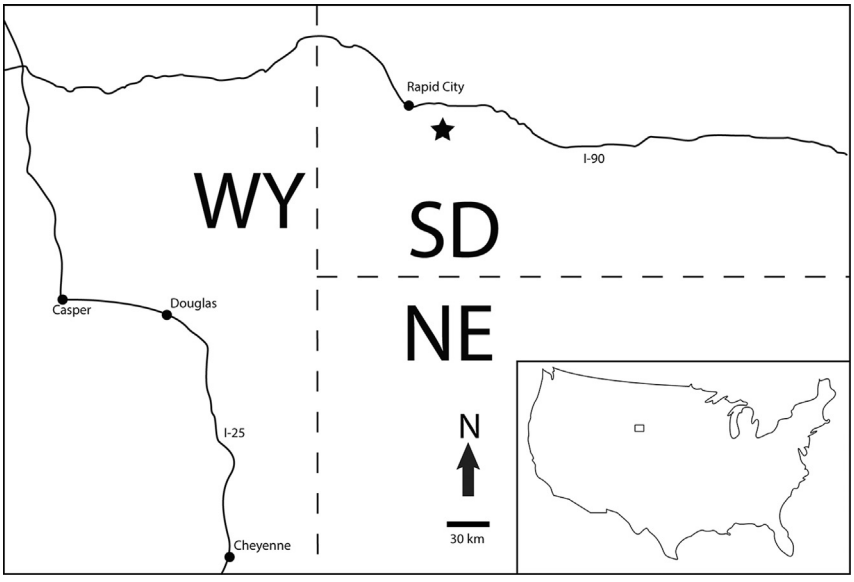

Fig. 1. Location of YPMPU 17208 in South Dakota, USA.