



EVIDENCE OF PREDATORY BEHAVIOR BY CARNIVOROUS DINOSAURS

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ABSTRACT: Evidence for predatory behavior in the fossil record is rare, especially for dinosaurs. Two unambiguous examples document instances of predator-prey relationships among the dinosaurs. The first example is of the small predator *Velociraptor* OSBORN, 1924 buried with its prey, *Protoceratops* GRANGER & GREGORY, 1923. As interpreted, the right forearm of the *Velociraptor* is between the clenched beak of the *Protoceratops*, the left hand of the *Velociraptor* is grasping the face of the *Protoceratops*, and the sickle claw of the right foot of the *Velociraptor* is extended into what was the throat of the prey. The second example is a section of mutilated caudal neural spines in an adult specimen of the hadrosaur *Edmontosaurus* LAMBE, 1920. The damage suggests an attack by a very large theropod believed to have been *Tyrannosaurus* OSBORN, 1905. Bone regrowth indicates that the hadrosaur survived the attack, and that the damage could not have been caused by scavenging. These two examples suggest that both small and large theropods, *Velociraptor* and *Tyrannosaurus* in particular, could actively hunt and attack prey species.

INTRODUCTION

Fossil evidence of predator activity in the vertebrate fossil record has been summarized by BISHOP (1975) and in BOUCOT (1990). Among dinosaurs, evidence of active predation is less clear. Possible evidence of a theropod stalking its prey was given by BIRD (1953) from the Lower Cretaceous of Texas. He described a pair of trackways, which he thought, suggested that a large theropod stalked a sauropod. Whether the predator ever caught up with the prey is unknown, because only a short portion of the trackway was excavated. As FARLOW (1987) noted, it is just as possible that the passage of the two animals was separated by a considerable amount of time. THOMAS (1995), however, disputes this interpretation and concludes that the sauropod was indeed stalked and attacked by the theropod.

MATTHEW (1908) reported that a specimen of *Apatosaurus* MARSH, 1877 from the Upper Jurassic Morrison Formation of Wyoming bore theropod tooth marks. He suggested the marks were left by an *Allosaurus* MARSH, 1877, but admitted that it was unknown if the allosaur had stalked and killed this *Apatosaurus* or had scavenged on a carcass.

FARLOW (1976) reported that Barnum Brown had found a hadrosaur and several *Albertosaurus libratus* specimens in a single quarry in the Judith River Formation of Alberta. Although it is possible that the *Albertosaurus* OSBORN, 1905 traveled and died together, their association with a hadrosaur is not

proof that they perished while feeding on the hadrosaur. In fact, the fluvial nature of the sandstone encasing the specimens makes it more probable that the specimens were transported separately to the site. ERICKSON & OLSON (1996) have identified bite marks, possibly made by *Tyrannosaurus*, on the ventral surface of a ceratopsian ilium and sacral vertebrae. Approximately 653 N is estimated to have been applied to cause the damage (STAEDTER, 1997).

OSTROM (1969) and MAXWELL & OSTROM (1995) reported several specimens of *Deinonychus antirrhopus* OSTROM, 1969 associated with a possible prey specimen of *Tenontosaurus tilletti* OSTROM, 1970 at the YPM *Deinonychus* Quarry. However, the evidence is equivocal, because the *Tenontosaurus* specimen consisted of the distal most part of the tail, not the majority of the skeleton. The fact that the long bones and segments of bones on the MAXWELL & OSTROM (1995) quarry map are aligned within a northwest to northeast arc does not rule out a taphonomic artifact. This is not to say that *Deinonychus* did not feed on *Tenontosaurus*, because broken *Deinonychus* teeth are frequently found with *Tenontosaurus* remains. But it is equally likely that *Deinonychus* scavenged on *Tenontosaurus* carcasses as acknowledged by MAXWELL & OSTROM (1995). An occurrence of shed theropod teeth with sauropod bones was reported by BUFFETAUT & SUTEETHORN (1989). They argue that such an occurrence indicates no post-mortem transport of the

material, but were not able to determine if the sauro-pod was scavenged or preyed upon.

Unambiguous examples of predation by theropods include a juvenile *Coelophysis bauri* COPE, 1889 within the abdomen of an adult *Coelophysis* (COLBERT, 1989), and the lacertilian *Bavarisaurus* cf. *macrodactylus* (WAGNER, 1852) within the abdomen of *Compsognathus longipes* WAGNER, 1861 (OSTROM, 1978).

EXAMPLE 1, THE "FIGHTING" PAIR

There is no question that the Mongolian dromaeosaur *Velociraptor mongoliensis* was an active predator based on a specimen (Fig. 1) found locked in combat with a *Protoceratops andrewsi* (KIELAN-JAWOROWSKA & BARSBOLD, 1972; KIELAN-JAWOROWSKA, 1975; UNWIN, PERLE & TRUEMAN, 1995; however, see OSMÓLSKA, 1993 and HAMLEY, 1993 for opposing views). Both specimens were briefly described by BARSBOLD (1974), with additional notes on the *Velociraptor* presented later (BARSBOLD, 1983). The "fighting" specimens were found in 1971 in the middle Campanian (?) Djadokhta Formation about 30 km west of Bayn Dzak at Toogreek (= Tugrikiin-Uz = Tugruk = Toogreegeen Shireh = Toogreeg), southern Mongolia. The sediments have been interpreted as freshwater deltaic by Soviet geologists, e.g. TVERDOKHLEBOV & TSYBIN (1974), as paludal by BARSBOLD (1974), but as eolian by Polish and Canadian geologists (LEFELD, 1972; GRADZINSKI, KIELAN-JAWOROWSKA & MARYA SKA, 1977; JERZYKIEWICZ *et al.*, 1993). The sedimentological studies by LEFELD (1972) and JERZYKIEWICZ *et al.* (1993) are thorough and leave little doubt about the eolian nature of the Djadokhta sands.

The *Velociraptor* (GI SPS 100/25; 170 cm long; BARSBOLD, 1974) is lying on its right side (Fig. 1A) almost parallel to the *Protoceratops* (GI SPS 100/512; 120-130 cm long; BARSBOLD, 1974). The *Protoceratops* is crouched, with body and skull turned sharply towards the right, and the tail curved towards the left (Fig. 1B). Erosion has destroyed much of the face and upper portion of the frill (Fig. 1C). Inexplicably, both scapula-coracoids are present (although displaced), but both forelimbs, the left hind limb and distal end of the tail are missing.

It was *Protoceratops* skull fragments on the ground surface that led to the discovery of the specimens. The pelvic region of the *Protoceratops* is steeply angled so that the posterior ends of the ischia almost touch the ground. The metatarsals of the right foot are horizontal, with the limb folded in a manner suggesting the *Protoceratops* was crouching at the time of death. The ribcage is partially collapsed due to the decay of the soft tissue and settling of the body. This activity has also displaced the

shoulder girdle. Tissue decay or shrinkage has also allowed some of the upper cheek teeth to fall partially out of their alveoli as can be seen below the orbit in Figure 1B.

The skeleton of the *Velociraptor* is not horizontal, but slopes posteriorly a few degrees. This angle probably represents the original angle of the sand surface upon which the animals fought. The neck of the *Velociraptor* is in a tight S-curve and the skull is pulled down so the chin almost touches the base of the neck. A similar position seen in mummified moas (e.g., HOLDWAY & WORTHY, 1991: 55). The tail (100 cm long, BARSBOLD, 1974) curves dorsally, especially at the base of the tail. The ribcage of the *Velociraptor* collapsed as a result of decay, so that the right coracoid overlaps the front edge of the left coracoid and the ventral surface of the sternal plates are visible (Fig. 1A). Compaction of the sand encasing the specimens was minimal so that the skull was not crushed as is the case with the holotype (AMNH 6515, OSBORN, 1924).

The upper portion of the right forearm (just distal to the elbow) of the *Velociraptor* is clenched in the beak of the *Protoceratops* (Fig. 1C), whereas the left hand rests on the *Protoceratops* face just anterior to the jugal horn (Fig. 1A-B). The right leg of *Velociraptor* appears to have been trapped beneath the body of the *Protoceratops* (Fig. 1A, C), and the left foot is positioned with the toes flexed down and back, exposing the large sickle-like claw (Fig. 1A). This claw is located in what appears to have originally been the throat of *Protoceratops* (Fig. 1A). From the position of the skeletons, the *Velociraptor* was apparently unable to escape from the grip the *Protoceratops* had of its forearm, and from the weight of the *Protoceratops* body on its right leg.

BARSBOLD (1974) thought that the two animals fell fighting into water and that the last moments of the "duel" occurred underwater. He suggested that they may have been sucked into a swamp or that the viscous bottom of a lake kept them together. Considering the eolian nature of the sediments such a scenario is unlikely. OSMÓLSKA (1993) suggested that a bank of sand collapsed burying the struggling animals, or that the *Velociraptor* was scavenging when it died of unknown cause. UNWIN, PERLE & TRUEMAN. (1995), however, concluded that the two were buried alive by a sandstorm. These three scenarios are not satisfactory because they fail to explain the missing limbs of the *Protoceratops*. An alternative scenario, has the *Protoceratops* bleeding to death from the slashes of the *Velociraptor's* sickle-like claws about the throat. Dying, the *Protoceratops* trapped the *Velociraptor* beneath it by the weight of the body on the right leg, as well as by a grip on the right forearm by the beak. Eventually, the *Velociraptor* died and the body desiccated. The two bodies

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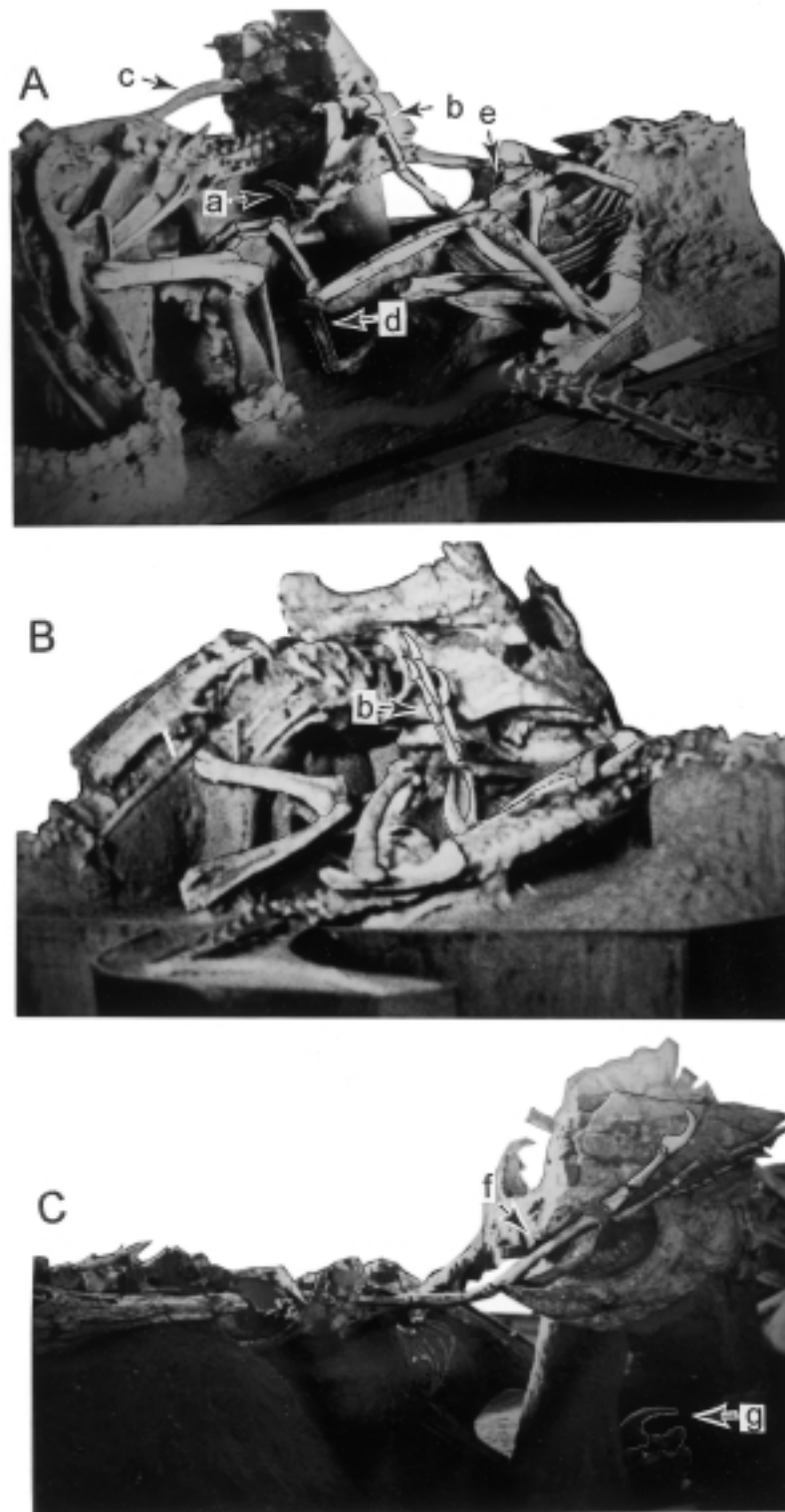


Fig. 1 - The "fighting pair" as found. **A** - Rear view with *Protoceratops andrewsi* (GI SPS 100/512) on left, *Velociraptor mongoliensis* (GI SPS 100/25) on right. **B** - Side view, note that the hands of *Velociraptor* were clutching the head of *Protoceratops* during life. **C** - Front view of fighting pair; missing part of *Protoceratops* face reconstructed by dashed lines. Key: a - Extended sickle-claw of the left foot in the vicinity of the *Protoceratops* neck; b - Left manus on right side of *Protoceratops* skull; c - Left scapula of *Protoceratops*; d - Right leg trapped beneath skeleton of *Protoceratops*; e - Sternal plates of *Velociraptor*; f - Right forearm of *Velociraptor* in beak of *Protoceratops*; g - Sickle claw of the right leg of *Velociraptor* beneath the skeleton of *Protoceratops*.

were ultimately buried by drifting sand, but not before scavengers removed the forelimbs and left hind limb of the *Protoceratops*. Why the *Velociraptor* was not scavenged is puzzling but it may have been partially or completely buried by drifting sand.

The fighting pair provides the best evidence for the function of the sickle claw in dromaeosaurid theropods. This function is not the same as that suggested by OSTROM, (1969) for another dromaeosaurid, *Deinonychus*. Ostrom proposed that *Deinonychus* "caught and held its prey in its fore hands and disemboweled it with the large pedal talon" (OSTROM 1969: 143). However, in the *Velociraptor*, the sickle claw is extended in the vicinity of the throat (Fig. 1A). This evidence suggests that the claw was not used to disembowel the prey, but that it may have been used to pierce the jugular vein, carotid artery, or trachea. These are areas that many extant mammalian carnivores attack in prey.

In support for this alternative hypothesis I would note: 1) morphologically, the long, slender, tapering shape of the sickle claw seems best adapted for piercing. The ventral edge (plantar side) of the ungual is rounded in cross-section (Fig. 2A,B) and does not have a razor sharp edge. It is not certain how much the keratin sheath reflected the morphology of the ungual because the correlation between bony core and keratin claw in extant birds and mammalian predators varies from little to a lot (personal observation of museum specimens). Nevertheless, in predators that use claws in hunting (e.g., raptors and cats), the claws are used to pierce and holding prey, not for disemboweling; 2) the muscles through which the *Velociraptor* pedal claw would have to cut to disembowel its prey extend antero-posteriorly (*M. rectus abdominis*), and obliquely anteriorly (*M. obliquus externus abdominis* and *M. obliquus internus abdominis*); only the deep *M. transversus abdominis* has fibers that extend parallel to the cut. Cutting muscle requires a sawing action, especially when cutting across the grain of the muscle fibers as would be the case for attacking the abdomen of the prey; 3) skin is thickest on the sides and abdomen of animals partly to protect these regions. Skin also contains a considerable amount of elastin, a tissue that resists tearing, but allows the skin mobility. A claw embedded in the skin would find it difficult to cut the thick hide; 4) although we do not know how sharp the keratin sheath of a dromaeosaurid claw was, it was probably less sharp than a dull knife because there was no way for the dromaeosaur to hone an edge (cats hone the tips of their claws on objects, such as furniture). Considering how difficult it is to cut skin and raw meat with a dull knife (e.g., table knife), it is highly unlikely that the less sharp dromaeosaurid sickle claw could have cut through the thick hide and abdominal muscles of the prey; 5) the reports of dis-

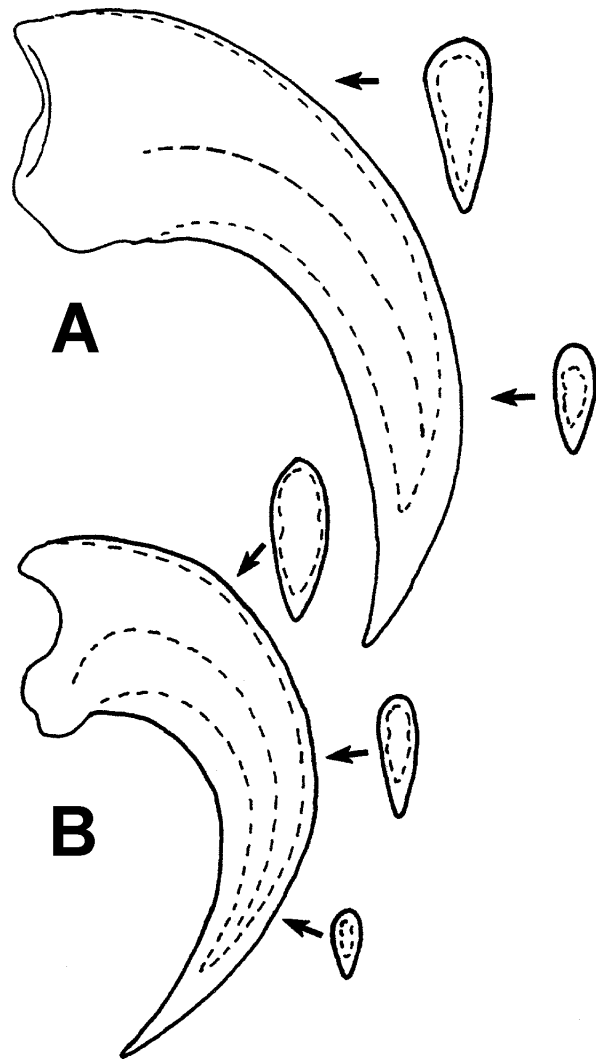


Fig. 2 - **A** - Sickle claws of *Utahraptor ostrommaysorum* KIRKLAND *et al.*, 1993 (CEU 184v.86). **B** - Sickle claws of *Deinonychus antirrhopus* (YPM 5205) in lateral profile. Cross-sections show the narrowness of the claw and the absence of a razor edge on the plantar edge. Extent of keratin sheath is best approximation. Modified from OSTROM (1969) and KIRKLAND *et al.* (1993).

emboweling of humans or lions by ratite birds cited by OSTROM (1969) seems to be rare and unusual events. The disemboweling is the result of the bird's great mass behind the kick rather than cutting by the claws because none of the pedal claws bear any resemblance with the laterally compressed sickle claw of the dromaeosaurid foot. The light weight of most dromaeosaurids (30-80 kg, OSTROM, 1990) makes it doubtful that they had enough mass to effectively disembowel their prey with their sickle claw. Furthermore, it seems doubtful that the dromaeosaurid could hop one legged along side of a fleeing prey while sawing through the tough hide and muscle with the claw of its other foot.

EXAMPLE 2, PREDATOR ATTACK ON AN ADULT HADROSAUR

The hadrosaur specimen is *Edmontosaurus annectens* (MARSH, 1892) on display at the Denver Museum of Natural History (DMNH 1493, formerly AMNH 5058). It was collected by Darwin Harbicht and Barnum Brown of the American Museum of Natural History in 1933 from the Hell Creek Formation (Upper Maastrichtian) along Dry Creek, Dawson County, Montana. The specimen has been illustrated during its excavation by COLBERT (1965: pl. XIX). The skeleton was preserved articulated and lying on its right side, and was missing only the manus and pes, distal end of the tail and some ribs (letter from B. Brown to J. Figgins, 1934, DMNH archives). The specimen was acquired through exchange in 1934. The missing parts were reconstructed of plaster of Paris or are actual bone from other hadrosaur specimens. Because so few hadrosaur measurements have been published, these are presented in TABLE I.

As may be seen in Figures 3-5, the neural spines of caudal vertebrae 13-17 have suffered trauma. This trauma is especially evident on neural spine 15 where approximately the upper one-third is missing (Fig. 4A-B). The spine is 19.1 cm tall along its anterior edge compared to 27.3 cm for neural spine 14, and 28 cm for neural spine 16. What remains of neu-

ral spine 15 has an oblique, saddle-shaped groove that shows exostotic regrowth of bone at its terminus (Figs. 4B, 5B). This regrowth area is not smooth, but very rough possibly do to mild case of osteomyelitis as would be expected from an open bone wound. Infection was probably the result of pathogens introduced from the saliva of the attacker (AUFENBERG, 1981; ABLER, 1992).

The other neural spines (numbers 13, 14, 16, and 17) have sigmoidal kinks in them making them appear mangled in dorso-posterior view (Fig. 5A). The kinks occur progressively higher in each preceding or succeeding neural spines from neural spine 15, resulting in an arc-like pattern of damage. In addition, there is a pit at the level of the traumatized area in neural spines 13, 14 and 16 (Fig. 4A, B). The center of the pit in neural spine 16 is 8.8 cm from the top and 8.3 cm from the center of the groove of neural spine 15. The traumatized regions of all neural spines do not retain the normal flat bladed appearance, but show exostosis similar to that of healed bone.

I interpret the traumatized tail section of this *Edmontosaurus* to be due to the bite of a large theropod because: 1) the trauma is localized to a small section of the tail, specifically the tops of several adjacent neural spines; 2) neural spine 15 was obliquely sheared off and adjacent ones mangled; 3) a pit in-

TABLE I
Measurements (cm) of *Edmontosaurus annectens*, DMNH 1493.

ELEMENT	LEFT	RIGHT
Skeleton length as mounted along neural spines		699.5(e)
Skull length (BO-PM)		90(e)
Cervical series length		115.6
Dorsal series length		175.3
Sacral series length		74
Caudal series length		incomplete
Scapula length	94.3(e)	92.8
Coracoid height		
Humerus length	59.9	61
Ulna length	61.5	59.9
Radius length	54.3	54
Manus		missing
Ilium length	117(e)	114.5
Prepubic blade from acetabulum	66.5	60.9
Ischium length from acetabulum	111	111(e)
Femur length	104.5	102.4
Femur circumference below 4th trochanter	49.5	42.4
Tibia length	87.5	88.3
Fibula length	86.1	85.5
Pes		missing
Leg length as mounted (from center of acetabulum)	227.2	230



Fig. 3 - *Edmontosaurus annectens* (DMNH 1943), showing position of damaged neural spines on tail.

terpreted as a tooth puncture is present on three of the neural spines in the mangled section; and 4) the arc formed by the mangled sections of the neural spines and the tooth punctures seem to delineate the size and shape of a large theropod mouth (Fig. 4A). The hadrosaur undoubtedly survived the attack as indicated by the regrowth of bone in the damaged areas. However, the animal died before regrowth obliterated the tooth punctures and masked the groove of the sheared off neural spine. Because the animal is an adult based on its large size (TABLE I) and degree of ossification, the attack did not occur when the animal was a smaller juvenile.

It is not known how much the attack may have contributed to the eventual death of the animal. The regrowth of bone indicates a passage of time. The regrowth on neural spine 15 shows some irregular and cancellous texture typical of diseased bone (Fig. 3B), but this irregularity is not very extensive. This suggests that the immediate cause of death was not due to bone infection (osteomyelitis). On the other hand, it is possible that disease organisms were introduced into the soft tissue during the attack. AUFFENBERG (1981) reports that death of large prey mammals from *Varanus komodoensis* OWENS, 1912 bites may occur up to two years later. Thus, death of the hadrosaur may have been due to

septic infection by the introduction of bacteria from the saliva of the attacker.

An alternative hypothesis about the time of death of the hadrosaur is based on the articulated condition of the skeleton when found. The apparent lack of scavenging is analogous to that seen in other, apparently drought killed dinosaurs (CARPENTER, 1987). It is possible that the individual was already weakened by infectious disease introduced by the attack and that death resulted as a result of drought induced stress.

Regarding the identity of the attacker, it would have had to have been a theropod as tall as, or taller, than the *Edmontosaurus*. Hadrosaurs are believed to have held their bodies and tails horizontally (GALTON, 1970), therefore the top of the tail of this specimen would have been at least 2.9 m above the ground. The only known theropod from the Hell Creek Formation tall enough to have caused the injury is *Tyrannosaurus rex*. For comparison, a skeleton of *T. rex* mounted at The Academy of Natural Sciences of Philadelphia with the body and tail horizontal and the knees flexed, stands 2.8 m at the hips.

In reconstructing the attack, the *Tyrannosaurus* apparently approached from the right rear, because neural spine 15 is sheared in that direction. The attack probably did not come from the left front, be-

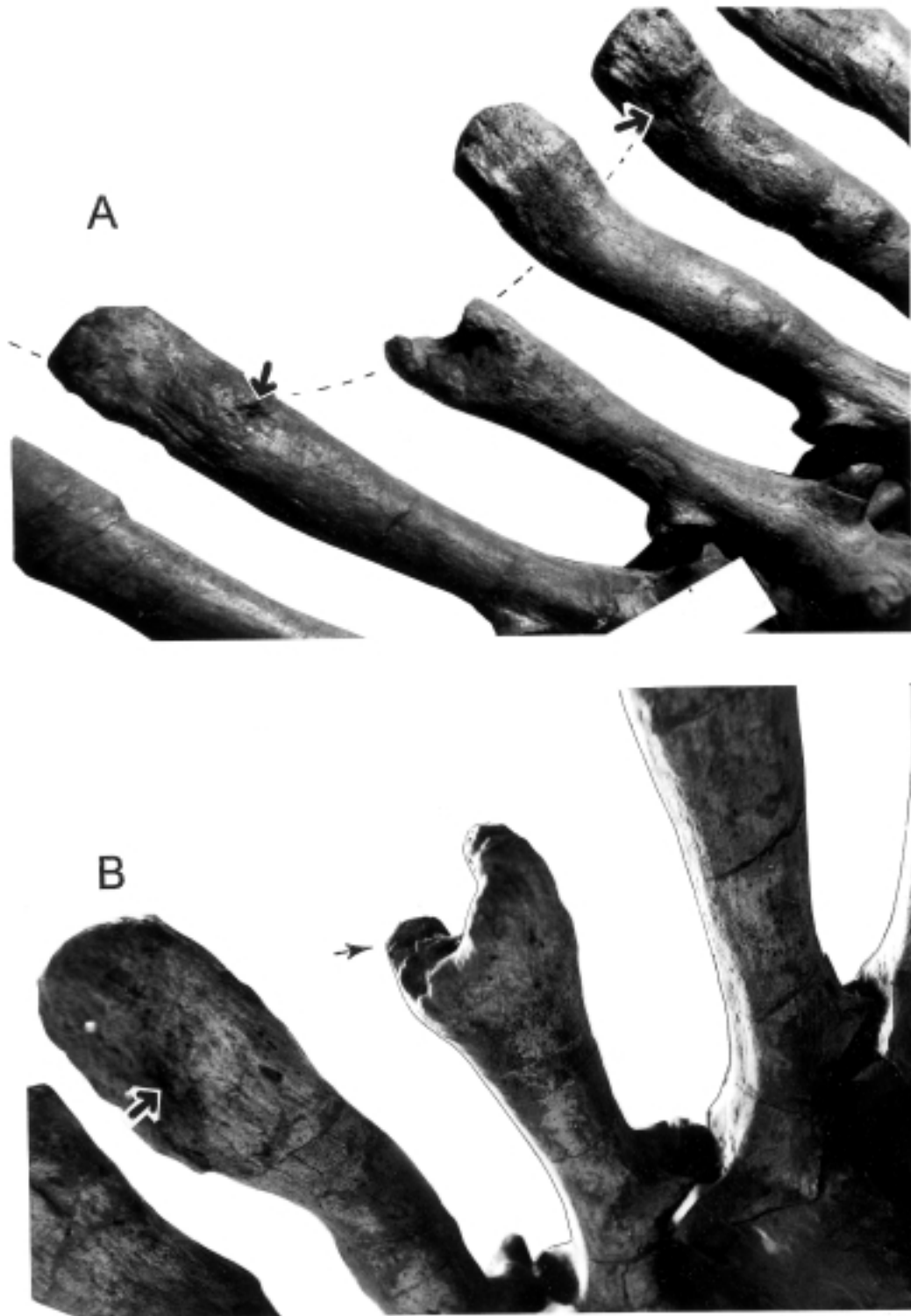


Fig. 4 - Details of the traumatized tail section of *Edmontosaurus annectens* (DMNH 1943). **A** - Right lateral view showing damage to neural spines 13-16, including sheared off neural spine 15. Anterior towards right. Puncture marks on neural spines 13 and 16 shown with arrows. Dashed line shows arc of tooth row and the large size of the mouth. **B** - Oblique view of the left side emphasizing the sheared off neural spine 15. Small arrow indicates the irregular and cancellous texture of the diseased bone (osteomyelitis) and exostosis of bone regrowth. Large arrow indicates a puncture mark on neural spine 14.

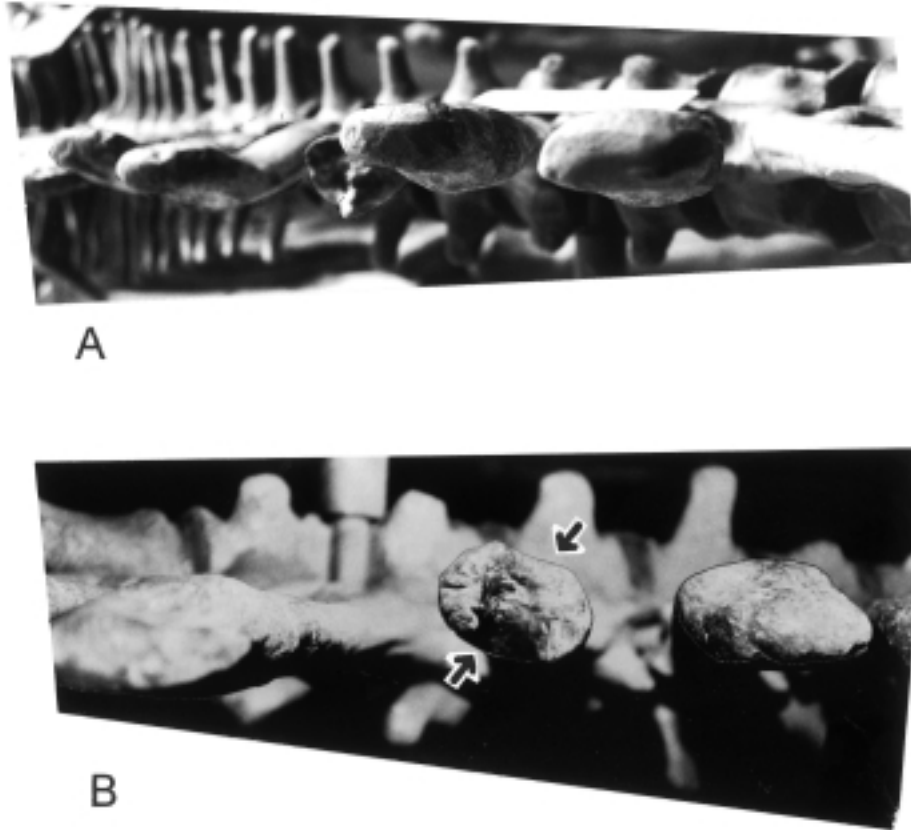


Fig. 5 - **A** - posterior view of neural spines showing kink in neural spines 13-16. **B** - Dorsal view of neural spines 13-16 showing the swollen neural spines from bone regrowth (exostosis) possibly accompanied by mild osteomyelitis, and the oblique shear on neural spine 15 (axis of arrows).

cause an attack from that direction would most likely be directed against a more vital region, such as the throat or stomach. The bite was quick and apparently fractured the neural spines. Later bone regrowth "froze" the neural spines in their mangled positions. At least two of the neural spines were punctured, whereas a third was severed. These two spines might have been punctured by teeth not fully erupted. Regrowth of bone around the injuries indicates the animal survived the attack.

A possible contributing factor as to why this particular individual was attacked may be the massive callus at the base of the preacetabular process of the left ilium. This bone growth is indicative of a healed fracture. Considering how extensive the callus is compared with that around the damaged neural spine, the fracture must have occurred prior to the attack. The function of the *M. ilio-femoralis* was compromised and the hadrosaur probably walked with a limp. Because extant carnivores often attack the weak (VAN LAWICK-GOODALL & VAN LAWICK-GOOD-

ALL, 1970), a limping hadrosaur made an ideal prey for a hunting *T. rex*. There remains, however, the question why the attacker did not complete the kill, and this may shed some light on the defensive behavior of solitary hadrosaurs. Either the hadrosaur was bitten while being chased by the *T. rex* and it managed to outrun or outmaneuver the predator, or it was bitten while lashing the tail from side to side to keep the predator at bay. Considering how deep, well muscled and massive hadrosaur tails are, a defensive role for the tail is a reasonable hypothesis. Exactly how the hadrosaur managed to survive the attack in order for bone regrowth of the damaged neural spine to occur is a mystery that we may never know.

CONCLUSION

The discovery of the *Protoceratops* being attacked by a *Velociraptor* and of a hadrosaur skeleton showing evidence of an attack by a large theropod, provides conclusive evidence that theropods ac-

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tively hunted and were not strictly scavengers as has been suggested, especially for *Tyrannosaurus* (e.g. HOTTON, 1963; HORNER & LESSEM, 1993). Furthermore, the prey in both instances were not young animals, but adults, and in the case of the "fighting" pair, the prey was more massive than the predator. It still is not known how either *Velociraptor* or *Tyrannosaurus* hunted, whether by ambush with a short running chase, or slashing and stalking the bleeding prey as suggested by PAUL (1987), or whether they employed a mixture of tactics depending on vegetation cover, prey and opportunity. Finally, like many modern mammalian carnivores (VAN LAWICK-GOODALL & VAN LAWICK-GOODALL, 1970), theropods were probably opportunistic feeders, scavenging when possible and hunting when necessary, a conclusion also reached by FARLOW (1994).

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ABBREVIATIONS

CEU - College of Eastern Utah Prehistoric Museum, Price, Utah, U.S.A; DMNH - Denver Museum of Natural History, Denver, Colorado, U.S.A.; YPM - Yale Peabody Museum, New Haven, Connecticut, U.S.A.; GISP - Geological Institute, Section of Paleontology and Stratigraphy, Mongolian Academy of Sciences, Ulan Bator, Mongolia.

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