



PREY BONE UTILIZATION BY PREDATORY DINOSAURS IN THE LATE JURASSIC OF NORTH AMERICA, WITH COMMENTS ON PREY BONE USE BY DINOSAURS THROUGHOUT THE MESOZOIC

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ABSTRACT: The frequency of tooth-marked bone in the Mesozoic is decidedly lower than the frequency found in the Cenozoic, although most of the previous work has focused on Cretaceous dinosaur faunas. This report describes two new examples of tooth-marked bone from the Jurassic Morrison Formation of western North America. The pubic foot of a specimen of *Allosaurus* from the Morrison Formation is missing a large section of its right side as the result of a single bite of a large theropod. Based on the size of the bite and known tooth size in large Morrison theropods, either *Ceratosaurus* or *Torvosaurus* can be responsible for the bite. Because of the large size of the *Allosaurus* and the location of the bite, it is suggested that the bite occurred during scavenging rather than during an attack by a predator. The pattern of tooth marks on this specimen are supportive of the hypothesis that predatory dinosaurs did not routinely chew the bones of their prey. Similarly, the tooth marks on a *Camarasaurus* ilium can be attributed to accidental contact with the teeth of a large predatory dinosaur as it removed the flesh of its prey, rather than the result of intentional chewing of the bone. As with mammalian predators, patterns of tooth-marked bone provide insight into the behavior of predatory dinosaurs.

RESUMEN: La ocurrencia de huesos marcados por dientes en el Mesozoico es decididamente poca comparada con la del Cenozoico. La mayoría del estudio anterior ha enfocado en la fauna de dinosaurios del Cretácico. Este reporte describe dos ejemplos nuevos de huesos que provienen de la Formacion Morrison, Periodo Jurásico, en el occidente de Norte America. En el pie púbico de un *Allosaurus* de la Formacion Morrison le falta la mayor parte de los huesos del costado derecho, el resultado de una sola mordida de un gran terópodo. Usando el tamaño de la mordida y el tamaño conocido de los dientes de terópodos grandes de Morrison, puede que un *Ceratosaurus* o un *Torvosaurus*, fué quien dio la mordida. Dado el tamaño de *Allosaurus* y la localidad de la mordida, se sugiere que esta mordida ocurrió después de muerto en vez de por el ataque de un predador. El modelo de marcas de dientes de este espécimen soportan la hipótesis que los dinosaurios predadores usualmente no trituraban los huesos de sus presas. Igualmente las marcas de dientes en el ilium de un *Camarasaurus* se pueden atribuir a el contacto accidental de un gran dinosaurio predador según se comía la carne de la presa, en vez de mascar los huesos intencionalmente. Igual que con los predadores mamíferos, los huesos marcados por dientes nos dan un conocimiento más profundo de los hábitos de dinosaurios predadores.

INTRODUCTION

It is well established that some modern mammals in terrestrial ecosystems utilize bone from a carcass. For a variety of mammals, both carnivores (e.g. hyenas [*Hyaena*]; KRUUK, 1972) and herbivores (e.g. camels [*Camelus*]; GAUTHIER-PILTERS & DAGG, 1981), the bones of a carcass represent a nutritional resource for some elements such as calcium and phosphorus. Quite often, mammalian carnivores consume portions of prey bones, such as the proximal ends of humeri or femora, which contain an abundance of grease and fat as well as other nutrients (HAYNES, 1980). Alternatively, because they have incisors that are continuously growing throughout the life of the animal, rodents (e.g. BRAIN, 1981) use bone as a means to wear down their incisors.

With respect to dinosaurs, reports of tooth-marked bone are decidedly less common than what can be observed in mammal bone assemblages (FIORILLO, 1991a), and until recently the few reports made were in passing (BEASLEY, 1907; MATTHEW, 1908; DODSON, 1971; FIORILLO, 1991b; VARRICCHIO, 1995). However, detailed analysis and description of tooth marks has now begun (JACOBSEN, 1995; ERICKSON & OLSON, 1996). JACOBSEN (1995) found the frequency of tooth marks in Cretaceous dinosaur bones to be somewhat higher than previously considered. Many of the marks she found are small and delicate, and preserve detail sufficient to provide some taxonomic resolution as to the family, or even genus and species of the creator of the tooth marks. Such resolution remains unavailable for tooth-marked bone from earlier in the Mesozoic.

Reports of tooth marks from elsewhere in the Mesozoic remain rare (MATTHEW, 1908; FIORILLO, 1991a; FIORILLO & PADIAN, 1993). However, this paucity might be more apparent than real. Incomplete preparation, the use of plaster to fill "imperfections", and the dark shellac put on specimens collected in the early part of this century could make tooth marks, especially subtle ones, difficult to detect.

We report here on two striking tooth-marked specimens from the Upper Jurassic Morrison Formation, a pubis of *Allosaurus* (American Museum of Natural History [AMNH] 813) and an ilium of a *Camarasaurus* (University of Utah [UUV] 5309; on long-term loan to the Royal Tyrrell Museum of Palaeontology and renumbered RTMP 83.35.3). There are more individual tooth marks on these two specimens than can be seen on the thousands of bones that have been collected from the best-studied source of Morrison Formation dinosaurs, Dinosaur National Monument. Though heavily tooth-marked, we conclude that the primary purpose of chewing at these

bones was to scrape flesh from the bone rather than to chew the bone itself. This report, though brief, represents the most thorough study of tooth-marked bone from the Morrison Formation.

DESCRIPTION OF *ALLOSAURUS* SPECIMEN

American Museum (AMNH) 813 is an incomplete skeleton of a large *Allosaurus* from the Morrison Formation of Wyoming. It was collected by Reed in 1902 from Reed's Quarry R and includes a sacrum, a left ilium, both pubes, right and left ischia, two anterior dorsal, five dorsals, two anterior caudals and a number of dorsal rib heads.

Tooth marks are seen only on the massive foot of the pubes. The foot is 475 mm in length and 237 mm wide at its cranial end. The caudal two-thirds of the right side of the foot is missing and its lateral surface is vertical and covered by a series of grooves which run cranioventrally at a 45° angle to the ventral surface of the foot (Fig. 1A, 2). These grooves are subparallel and do not cross one another. The grooves are still matrix filled and the cross-section can not be determined. In ventral view the margin of the missing piece of the foot is a smooth, gentle curve (Fig. 1B). This curvature is reminiscent of the curve (in ventral view) of the maxilla and premaxilla in many large theropods in the Morrison Formation.

DESCRIPTION OF *CAMARASAURUS* SPECIMEN

University of Utah (UUV) 5309 is a partial skeleton of *Camarasaurus supremus* from the Morrison Formation. The specimen which consists of a partial pelvis and some limb bones is from the Cleveland-Lloyd Quarry in eastern Utah. Three areas on the ilium have multiple grooves identified as theropod tooth marks because of their distribution and morphology.

The largest area (Fig. 3) is located at the edge of the ilium and is 28 cm x 18 cm. The area has twelve parallel grooves, each about 0.5 cm deep, and with a maximum length of 16.5 cm, and a minimum length of 6 cm. The grooves are separated from each other by 2-3 cm. The grooves do not intersect with adjacent grooves. Neither redirection of bone fibres nor serration marks from denticles can be seen. The grooves in the left part of the area has matching grooves on the opposite edge of the bone, and these run together at the edge of the bone. The morphology and position of the grooves suggests a row of biting premaxilla teeth biting in apposition to the anterior dentary teeth.

A second area has four grooves about 0.3 cm deep, and separated by 1.5 cm (Fig. 4). The grooves are between 10 cm and 3.5 cm long, parallel to each

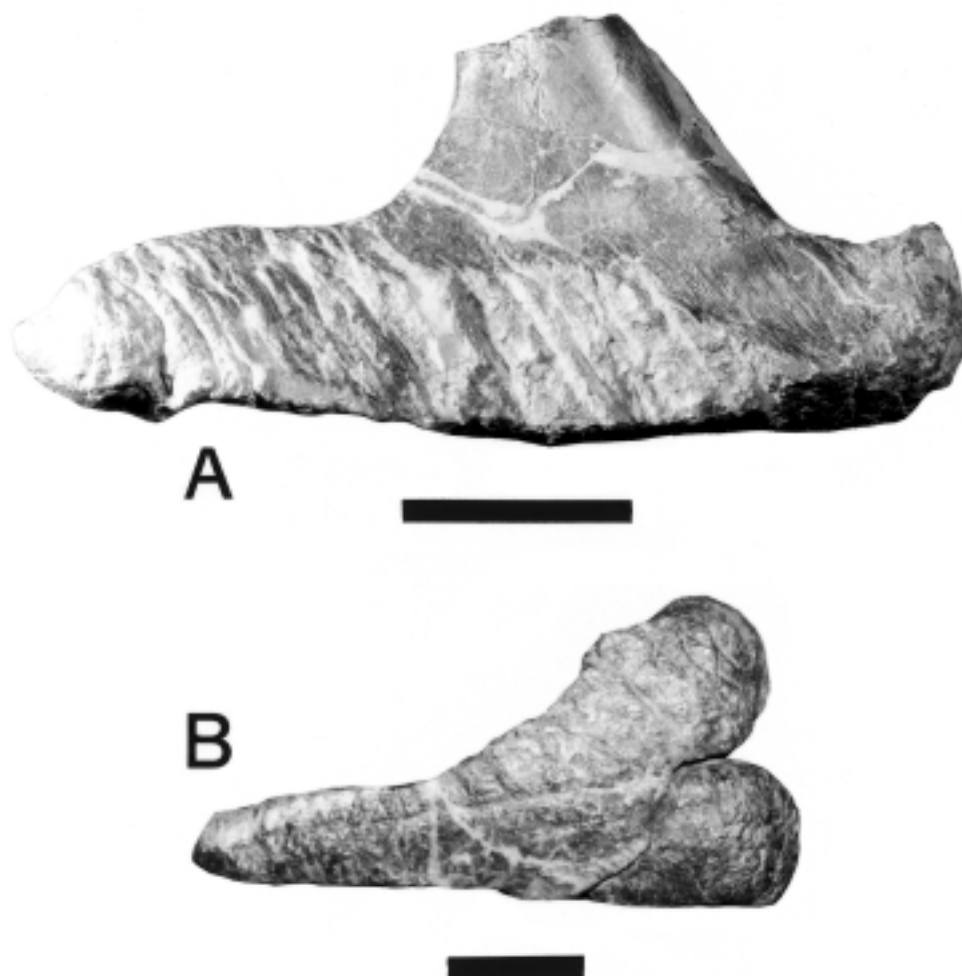


Fig. 1 - **A** - Right lateral view of pubic foot of *Allosaurus* AMNH 813. **B** - Ventral view of pubic foot of *Allosaurus* AMNH 813. Scale bar equals 10 cm.

other, and do not intersect. No serration marks or re-direction of bone fibres can be seen.

The third and final area, which is much smaller than the other two areas, contains four grooves. These grooves are only approximately 0.1 cm deep, spaced 1 cm apart, and are between 1 cm and 3 cm long.

DISCUSSION

The tooth marks on the pubic foot of AMNH 813 are probably the result of a single bite of the lateral and anterolateral part of the tooth row of a large theropod. This interpretation is supported by the curvature of the bite, as seen in ventral view, and that the tooth marks do not cross. Most non-avian theropods have four premaxillary teeth. Exceptions to this among Morrison theropods are *Ceratosaurus* and

Torvosaurus, with three, and *Allosaurus*, with five. The large number of tooth marks on AMNH 813 would require multiple bites if only the snout was being used to bite and that would almost certainly result in tooth marks cross-cutting, rather than being sub-parallel, and would not leave the smooth crescent outline seen in ventral view.

Although the theropod fauna of the Morrison Formation is fairly diverse, the size of the bite on AMNH 813 precludes a number of taxa from being the bite maker (*Koparion* CHURE 1994, *Marshosaurus* MADSEN 1976a, *Coelurus*, *Ornitholestes* OSBORN 1903, *Stokesosaurus* MADSEN 1974). Although the type skeleton of *Ceratosaurus nasicornis* is probably too small to have made the marks on AMNH 813, a new species of this genus (MADSEN & WELLES, in press) is twice the size of the type and in the appropriate size range. Other potential bite makers are *Allosau-*

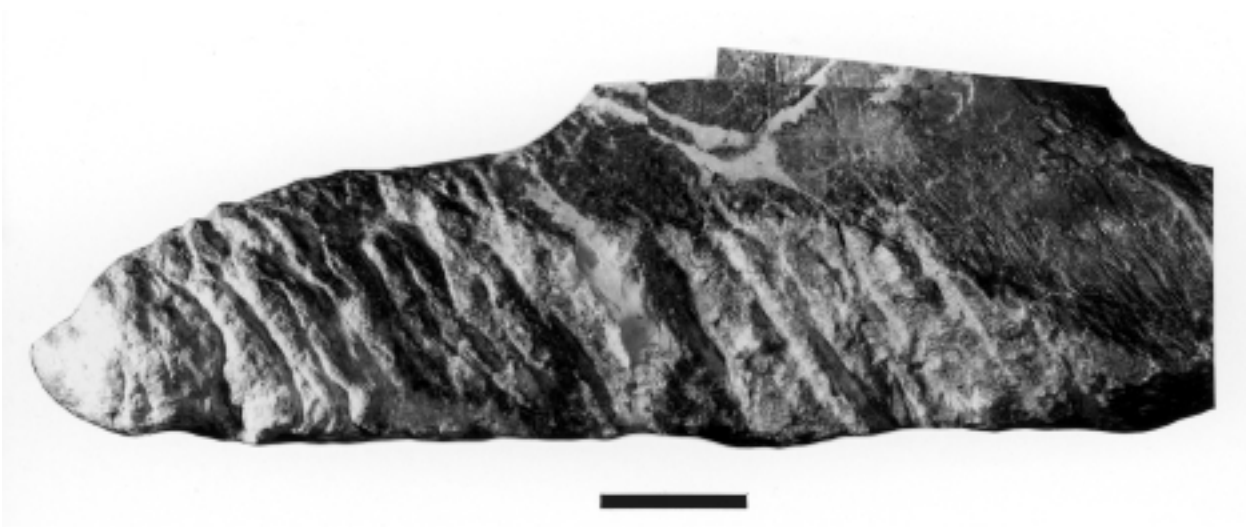


Fig. 2 - AMNH 813, pubic foot of *Allosaurus* in right lateral view showing details of tooth marks. Scale bar equals 5 cm.

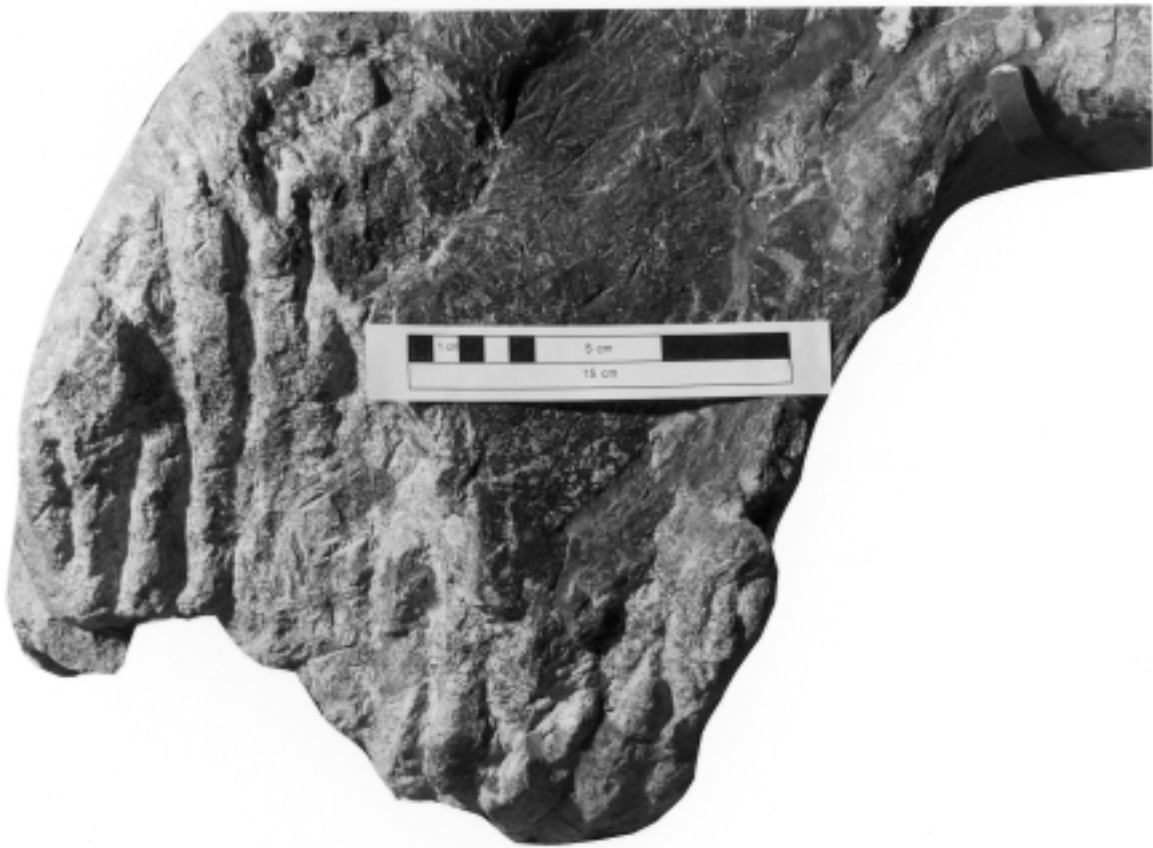


Fig. 3 - The largest tooth-marked area of the *Camarasaurus* ilium (University of Utah [UVP] 5309). Note that the grooves do not intersect with each other. Neither redirection of bone fibres nor serration marks from denticles can be seen. The grooves in the left part of the area have matching grooves on the opposite edge of the bone. Scale bar equals 15 cm.



Fig. 4 - The second most tooth-marked area on the *Camarasaurus* ilium (University of Utah [UUV] 5309). No serration marks or redirection of bone fibres can be seen. Scale bar equals 15 cm.

rus (MADSEN, 1976b), *Epanterias amplexus* (COPE, 1878; OSBORN & MOOK, 1921), *Saurophaganax maximus* (CHURE, 1995), and *Torvosaurus tanneri* (BRITT, 1990). Of these taxa the maxilla is known only in *Torvosaurus*, where it is approximately 500 mm long, and *Allosaurus* where it can reach lengths of 400 mm. The lateral teeth crowns of *Allosaurus* are relatively small, compared to the large, blade like lateral teeth of *Ceratosaurus* and *Torvosaurus*. Three incomplete tooth crowns are known for *Saurophaganax*, and they appear to be more similar to *Allosaurus* than other taxa. In light of all this evidence we infer that *Torvosaurus* or *Ceratosaurus* are the most likely candidates for making the tooth marks seen on AMNH 813.

The pubic foot in large theropods is the most massive bone in the skeleton, with the possible exception of the sacrum. This, plus the location of the foot in the skeleton (i.e. positioned such that it would be improbable as the point of attack by a predator), leads us to believe that the bite on AMNH 813 was made after the animal was dead, and not during an attack. The large size of AMNH 813 (length of left ilium is 811 mm) makes it unlikely that this individual was the object of an attack by another theropod and leads us to infer that the bite was made during scav-

enging of an already dead *Allosaurus*, although we recognize the difficulty of testing this hypothesis.

With respect to the *Camarasaurus* specimen (UUV 5309), the similarity in morphology of the two most substantially tooth-marked areas is suggestive of bite marks left by theropod premaxilla teeth. The grooves are parallel, similar in size and shape, and match what would be expected from row of premaxilla teeth nipping meat from bone. Because the largest area that is tooth-marked actually consists of two high-density, tooth-marked areas separated by 5 cm, this area probably represents at least two separate bites. Each groove in the second area is similar in size and shape, and most likely is a result of a single bite by premaxillary teeth. The tooth marks in the third area are only surficial.

The function of the premaxillary teeth was to nip meat off from bones, whereas that of the maxillary teeth was to "grab and rip" in Late Cretaceous tyrannosaurids (ERICKSON *et al.*, 1996; JACOBSEN, 1996). It is likely that large theropods from the Jurassic had similar biting strategies, although the absence of D-shaped premaxillary teeth suggest they were less adept at it. The superficial marks in the third area described, which are short in length but evenly spaced, have been attributed to tooth marks

made by maxillary teeth (JACOBSEN, 1995). Even though tyrannosaurids are believed to have been capable of powerful bites (ERICKSON *et al.*, 1996), no theropod is believed to have practiced bone gnawing behavior such as is known for mammalian carnivores (FIORILLO, 1991a; JACOBSEN, 1995, in press). Bite marks on bones generally would have been the result of accidental contact between teeth and bone. The morphology of the tooth marks found on this *Camarasaurus* pelvis support this biting strategy in that only three isolated areas are affected, probably as a result of four isolated bites.

In conclusion, the tooth marks on the *Allosaurus* pubis are attributed to only one bite of the lateral tooth row of a predatory dinosaur, and the tooth marks on the *Camarasaurus* ilium are attributed to several nipping bites by the premaxillary region of a similarly sized predatory dinosaur. Therefore, we conclude that these tooth-marked specimens support the contention that predatory dinosaurs, unlike many modern mammalian predators, did not routinely chew the bones of their prey (FIORILLO, 1991a; JACOBSEN, 1995, in press).

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REFERENCES

- BEASLEY, W.L. (1907) - A carnivorous dinosaur: a reconstructed skeleton of a huge saurian. *Sci. Am.*, **97**: 446-447.
- BRAIN, C.K. (1981) - *The Hunters or the Hunted? An Introduction to African Cave Taphonomy*. Univ. Chicago Press, Chicago, 365 pp.
- BRITT, B.B. (1991) - Theropods of Dry Mesa Quarry (Morrison Formation, Late Jurassic), Colorado, with emphasis on the osteology of *Torvosaurus tanneri*. *Brigham Young Univ. Geol. Studies*, **37**: 1-72.
- CHURE, D.J. (1994) - *Koparion douglassi*, a new dinosaur from the Morrison Formation (Upper Jurassic) of Dinosaur National Monument; the oldest troodontid (Theropoda: Maniraptora). *Brigham Young Univ. Geol. Studies*, **40**(1): 11-15.
- CHURE, D.J. (1995) - A reassessment of the gigantic theropod *Sauropagus maximus* from the Morrison Formation (Upper Jurassic) of Oklahoma, USA, in SUN, A.L. & WANG, Y.Q. (Eds.), *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota*, Short Papers, China Ocean Press, Beijing, pp. 103-106.
- COPE, E.D. (1878) - A new opisthocoelian dinosaur. *Am. Naturalist*, **12**: 406.
- DODSON, P. (1971) - Sedimentology and taphonomy of the Oldman Formation (Campanian), Dinosaur Provincial Park, Alberta (Canada). *Palaeogeog., Palaeoclimatol., Palaeoecol.*, **10**: 21-74.
- ERICKSON, G.M. & OLSON, K.H. (1996) - Bite marks attributable to *Tyrannosaurus rex*: preliminary description and implications. *J. Vertebr. Paleontol.*, **16**(1): 175-178.
- ERICKSON, G.M.; VAN KIRK, S.D.; SU, J.; LEVENSTON, M.E.; CALAR, W.E. & CARTER, D.R. (1996) - Bite-force estimation for *Tyrannosaurus rex* from tooth-marked bones. *Nature*, **382**: 706-708.
- FIORILLO, A.R. (1991a) - Prey bone utilization by predatory dinosaurs. *Palaeogeog., Palaeoclimatol., Palaeoecol.*, **88**: 157-166.
- FIORILLO, A.R. (1991b) - Taphonomy and depositional setting of Careless Creek Quarry (Judith River Formation), south-central Montana. *Palaeogeog., Palaeoclimatol., Palaeoecol.*, **81**: 281-311.
- FIORILLO, A.R., & PADIAN, K. (1993) - Taphonomy of the Late Triassic Placerias Quarry (Petrified Forest Member, Chinle Formation) of eastern Arizona, in LUCAS, S. & MORALES, M. (Eds.), *The Nonmarine Triassic, New Mexico Museum Nat. Hist. & Sci., Bull.*, **3**: 133-134.
- GAUTHIER-PILTERS, H. & DAGG, A.I. (1981) - *The Camel, its Evolution, Ecology, Behavior, and its Relationship to Man*. Univ. Chicago Press, Chicago, 208 pp.
- HAYNES, G. (1980) - Evidence of carnivore gnawing on Pleistocene and Recent mammalian bones. *Paleobiol.*, **6**: 341-351.
- JACOBSEN, A. (1995) - Ecological interpretations based on theropod tooth marks feeding behavior of carnivorous dinosaurs. *J. Vertebr. Paleontol.*, **15** (suppl. to n° 3): 37A.
- JACOBSEN, A. (1996) - Wear patterns on tyrannosaurid teeth: an indication of biting strategy. *J. Vertebr. Paleontol.*, **16** (suppl. to n° 3): 43A.
- JACOBSEN, A. (in press) - Feeding behaviour of carnivorous dinosaurs as determined by tooth marks on dinosaur bones. *Hist. Biol.*
- KRUUK, H. (1972) - *The Spotted Hyena, A Study of Predation and Social Behavior*. Univ. Chicago Press, Chicago, 335 pp.
- MADSEN, J.H. (1974) - A new theropod dinosaur from the Upper Jurassic of Utah. *J. Paleontol.*, **48**(1): 27-31.
- MADSEN, J.H. (1976a) - A second new theropod dinosaur from the Late Jurassic of east central Utah. *Utah Geol.*, **3**(1): 51-60.
- MADSEN, J.H. (1976b) - *Allosaurus fragilis*: a Revised Osteology. *Utah Geol. Mineral Survey Bull.*, **109**: 1-161.
- MADSEN, J.H. & WELLES, S.P. (in press) - *Ceratosaurus* (Dinosaur, Theropoda). A Revised Osteology. *Utah Geol. Surv. Miscellaneous Publ.*
- MATTHEW, W.D. (1908) - *Allosaurus*, a carnivorous dinosaur, and its prey. *Am. Museum J.*, **8**: 2-5.
- OSBORN, H.F. (1903) - *Ornitholestes hermanni*, a new compsognathoid dinosaur from the Upper Jurassic. *Bull. Am. Museum Nat. Hist.*, **19**: 459-464.
- OSBORN, H.F. & MOOK, C.C. (1921) - *Camarasaurus, Amphicoelias*, and other sauropods of Cope. *Mem. Am. Museum Nat. Hist.*, (N.S.) **3**: 247-287.
- VARRICCHIO, D.J. (1995) - Taphonomy of Jack's Birthday Site, a diverse dinosaur bonebed from the Upper Cretaceous Two Medicine Formation of Montana. *Palaeogeog., Palaeoclimatol., Palaeoecol.*, **114**: 297-323.