

GUT CONTENTS FROM A CRETACEOUS TYRANNOSAURID: IMPLICATIONS FOR THEROPOD DINOSAUR DIGESTIVE TRACTS

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ABSTRACT—A partial skeleton of *Daspletosaurus* sp. from the Late Cretaceous (Campanian) Two Medicine Formation of western Montana preserves the first gut contents reported for a tyrannosaurid. Associated remains found with this skeleton consist of acid-etched vertebrae and a fragmentary dentary from juvenile hadrosaur dinosaurs. Hadrosaur bonebed data and comparisons of hadrosaur and tyrannosaurid limb proportions suggest that juvenile hadrosaurs represented both an abundant and accessible food source. The surface corrosion exhibited by the hadrosaur elements matches that produced by stomach acids and digestive enzymes in a wide variety of living vertebrates. Based upon these and other gut contents, and also upon tooth-marked bone studies, it appears that *Daspletosaurus* and most theropods ingested and digested prey in a manner similar to that of extant archosaurs (crocodilians and birds), employing a two-part stomach with an enzyme-producing proventriculus followed by a thick-walled muscular gizzard. This two-part stomach appears to be an archosaur synapomorphy.

INTRODUCTION

THE TYRANNOSAURIDAE includes large (8 to 12 m long), bipedal dinosaurs such as *Tyrannosaurus rex*, *Gorgosaurus*, and *Daspletosaurus* (Carpenter, 1997a). Debate continues over whether tyrannosaurids were primarily active predators or scavengers (Horner and Lessem, 1993; Farlow, 1994; Erickson et al., 1996), but abundant and identifiable tooth marks occurring on Cretaceous dinosaur bones clearly indicate a carnivorous habit. These tooth marks suggest a diet of largely hadrosaurs and ceratopsians (Jacobsen, 1998; Erickson and Olson, 1996) and typically occur more commonly on limb bones than on vertebrae (Jacobsen, 1998). Although tooth-marked juvenile bones are unreported, a recently described *Tyrannosaurus rex* coprolite consists largely of subadult dinosaur bone fragments (Chin et al., 1998).

For extant taxa the analysis of stomach contents provides information on feeding methods, habitat preferences, and digestion rates, in addition to definitive dietary data (Delany and Abercrombie, 1986). Unfortunately for paleontologists, gut contents are only rarely preserved in the fossil record. Reported remains among the Theropoda, the carnivorous dinosaur clade, include partial lizards in the small Jurassic *Compsognathus* (Ostrom, 1978) and *Sinosauropteryx* (Chen et al., 1998); a juvenile *Coelophysis* within an apparently cannibalistic adult (Colbert, 1989); and miscellaneous acid-etched juvenile *Iguanodon* bones and fish scales associated with the unusual Cretaceous theropod *Baryonyx* (Charig and Milner, 1997). This paper reports the first gut contents for a tyrannosaurid from a Late Cretaceous deposit of western Montana and briefly discusses the implications of these and of those from other theropods.

DESCRIPTION

The material described herein comes from the lower Two Medicine Formation (Campanian) at the Old Trail Museum's Locality L-6 (Bob's Tuesday Site), Teton County, Montana. This site is located within the Seven Mile Hill badlands, an area with sediments largely consisting of fluvial channel sandstones, green to gray overbank mudstones with common paleosol development, and ephemeral floodplain pond deposits. The specimen consists of a partial skeleton of a tyrannosaurid associated with remains of juvenile hadrosaur dinosaurs (Fig. 1). Specimens are housed at the Old Trail Museum in Choteau, Montana (OTM catalogue numbers: OTM 200 and 201).

All tyrannosaurid and hadrosaur bones lie horizontally within a 20 cm thick blocky, green claystone with occasional calcitic nodules and vertical to subvertical burrows. Other associated fossils include two teeth from the small theropod *Saurornitholestes*,

and aquatic gastropods and small (<1 cm) bivalves. The pulmonate gastropod, *Physa*, is the most abundant invertebrate suggesting that deposition took place in quiet ephemeral waters (Brown, 1991) such as in a floodplain pond. Below the bone-bearing unit lies a green claystone distinguished only by an increased number of molluscs and shell debris. Overlying the bone-bearing unit, sediments gradually coarsen over a 10–15 cm interval to a very fine sandstone with more common calcitic nodules. The locality's stratigraphic position relative to dated volcanic ash beds (Rogers et al., 1993) suggests an age of roughly 79 m.y.a.

The tyrannosaurid remains (OTM 200) include several teeth, dentary, splenial, 30 vertebrae representing all regions (cervical, dorsal, sacral, and caudal), several ribs and chevrons, and most of the pelvis (fused pubes, portions of both ilia, and an ischium). The typical tyrannosaurid teeth (Currie et al., 1990) and concave ventral margin of the dentary (Lehman and Carpenter, 1990) allow tentative assignment of this specimen to the genus *Daspletosaurus*.

Preserved *Daspletosaurus* elements range from approximately 1 m (rib and fused pubes) to less than 4 cm (distal caudals) in greatest length (Fig. 1). The large pelvic elements and sacral vertebrae are concentrated in the southern portion of the quarry; dorsal vertebrae and ribs in the central; and cervical vertebrae, ribs and skull parts in the north. The caudal vertebrae occur throughout but show a general decrease in size (i.e., proximal to distal) from the southern to northern portions. Notably absent are the cranium, shoulder girdle and all limb elements. Although disarticulated, the bones maintain some anatomical organization. Taphonomic studies indicate that appendicular skeletal elements disarticulate prior to the axial skeleton (Lyman, 1994) perhaps explaining this distribution of *Daspletosaurus* elements. None of the bones exhibit any surface modification such as weathering or abrasion-induced damage. Except for breakage resulting from recent exposure, elements appear complete.

The associated hadrosaur material (OTM 201) consists of four caudal vertebrae and a fragmentary dentary (Figs. 2, 3). All occur in the central or southern portions of the quarry in close proximity to dorsal and pelvic tyrannosaurid elements (Fig. 1). The vertebrae include proximal, mid and distal caudals. Their small but matching sizes (Table 1), unfused proximal and mid-caudal neural arches, and notochordal pits on the most distal centra indicate that they pertain to a single juvenile hadrosaur about 3 m in body length.

Each of the vertebrae has lost the thin periosteal bone that covers juvenile caudals (Fig. 2). The exposed vascular canals and intertrabecular spaces have been enlarged, giving the bone a



FIGURE 1—Quarry map showing the tyrannosaurid (OTM 200) and associated hadrosaur (OTM 201) elements at the Old Trail Museum Locality L-6, Bob’s Tuesday Site, from the lower Two Medicine Formation (Late Cretaceous), Seven Mile Hill area, Teton County, Montana. The western edge is the original edge of the site where recent erosion had exposed many elements. Shading is as follows: black, cranial and cervical elements; diagonal striping, dorsal and sacral elements; dots, caudal vertebrae and chevrons; cross-hatched, unidentified or unprepared elements; white, hadrosaur bones. Note that the hadrosaur elements, marked by circles, all lie in close association to the tyrannosaurid bones and the absence of other bones away from the tyrannosaurid carcass. Scale bar equals 1 m.

spongy appearance clearly distinct from fresh bone. Some of these vertebrae show greater damage with the loss of deeper bone tissues. The loss of the periosteal bone and the overall pitted appearance become increasingly apparent with magnification; scanning electron microscope photographs reveal a cratered network of trabeculae over the entire surface (Fig. 3). Comparison of these vertebrae with better preserved juvenile remains from other Two Medicine localities clearly shows that these surface features do not represent normal ontogenetic stages (Figs. 2, 3). None of the tyrannosaurid-associated vertebrae show significant rounding nor a concentration of external-bone loss to projecting surfaces as indicative of abrasion (Lyman, 1994). At least two exhibit pre-fossilization breakage, with one centrum cleaved lengthwise.

The hadrosaur dentary retains only the coronoid process and

an adjoining area of the tooth row. It is poorly preserved, toothless, with multiple broken edges. Its small size (maximum anterior-posterior breadth of the coronoid = 15.8 mm) indicates a very young animal roughly 1 to 1.2 m in length. Some surficial bone damage is present, but its extent is difficult to gauge given the immature, porous nature of the bone.

DISCUSSION

The claystone matrix and the aquatic invertebrates in the deposit indicate a low-energy, ponded environment. The great disparity between bone and sediment size precludes the bones being an accumulation of individual elements washed to this site. Either floodwaters floated in a limbless and buoyant carcass, or a tyrannosaurid died at this locality with subsequent bone loss occurring by scavenging or recent weathering. Regardless, a significant portion of a tyrannosaurid carcass was present at this site. It then disarticulated and eventually became buried. The anatomical organization, the wide range of element size (i.e., from distal caudals to fused pubes), and the lack of breakage and abrasion indicate minimal hydraulic transport and winnowing. However an insufficient number of elongate elements prohibited testing for hydraulic alignment using a stereonet. The overlying coarsening-upward unit and the calcite nodules suggest burial by overbank deposition such as a crevasse splay with some subsequent paleosol development.

The hadrosaur elements are considered to be gut contents and

TABLE 1—Dimensions of the partially digested hadrosaur caudal vertebrae associated with the tyrannosaurid skeleton. All are Old Trail Museum (OTM 201) specimens. Length refers to anteroposterior, width to lateral, and height to dorsoventral dimensions of the centrum. All measurements in mm. Position refers to relative placement within the tail. *Only one lateral half of OTM 201-18 is preserved; total width is estimated.

Specimen#	Length	Width	Height	Position
OTM 201-17	22.7	33.5	27.5	proximal
OTM 201-18	29.5	~34*	27.0	mid
OTM 201-46	~20	~21	~15	distal
OTM 201-61	20.3	22.5	14.7	distal

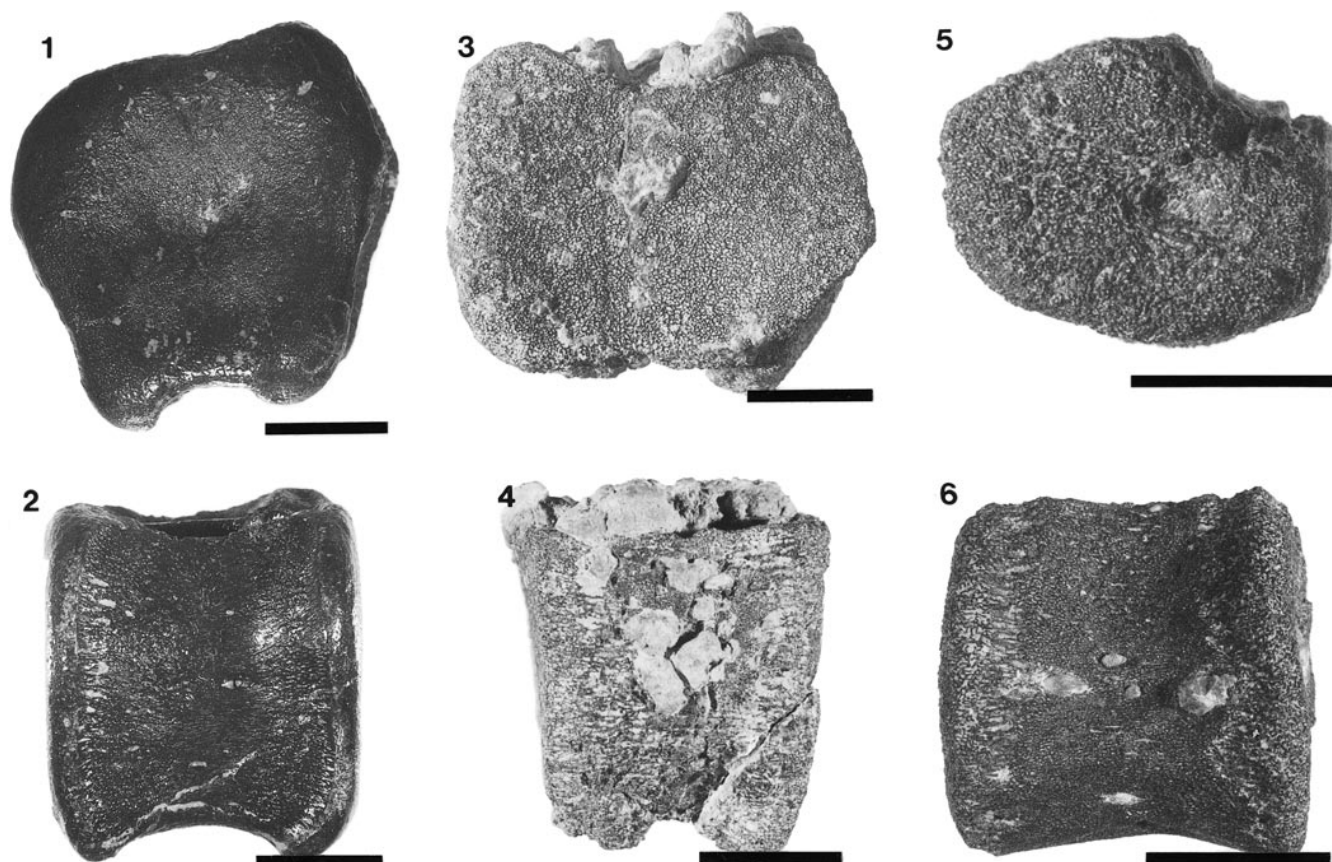


FIGURE 2—Uncorroded and partially digested hadrosaur caudal vertebrae. 1–2, anterior and lateral views of a well-preserved mid caudal from MOR 547, a *Maiasaura* bonebed. 3–4 and 5–6, anterior and lateral views of a proximal caudal (OTM 201–17) and a distal caudal (OTM 201–61), respectively, associated with the tyrannosaurid. Note the loss of the periosteal bone leaving a spongy and irregular surface texture. All three vertebrae represent individuals about 3 m in total body length. All scale bars equal 1 cm.

not the products of random depositional processes for the following reasons: 1) the specimens occur in a fine-grained, low energy deposit (Shimada, 1997); 2) they appear only in close association with the tyrannosaurid trunk elements (Fig. 1); 3) all exhibit a preservation (surface modification and breakage) distinct from that of the adjacent *Daspletosaurus* bones; and 4) the external bone loss matches digestive corrosion observed in a wide variety of extant vertebrate scat, regurgitate, and stomach contents (Richardson et al., 1986; Rensberger and Krentz, 1988; Kusmer, 1990; Lyman, 1994). Such damage results from the low pH (2.0) of stomach acids working in conjunction with the digestive enzyme pepsin (Skoczylas, 1978; Rensberger and Krentz, 1988; Kusmer, 1990; Lyman, 1994; Kardong, 1998). Although bone corrosion can result from acidic (pH less than 6.0) environmental conditions (Lyman, 1994; Fernandez-Jalvo and Andrews, 1992), the unaffected tyrannosaurid elements and the presence of thin calcite-shelled molluscs at this site preclude this interpretation.

The finding of hadrosaurs as gut contents in a tyrannosaurid concurs with previous studies in North America. Along the western margin of the Western Interior Cretaceous seaway, hadrosaurs were the most common Campanian herbivore (Beland and Russell, 1978) with the highest incidence of tooth-marked bones (Jacobsen, 1998). In a random sample of 1,000 dinosaur bones from the Campanian Dinosaur Park Formation of Alberta, Canada, theropod tooth marks occurred on 14 percent of hadrosaur elements but only on five and two percent of ceratopsian and tyrannosaurid bones respectively (Jacobsen, 1998). These percentages roughly

hold for strictly tyrannosaurid-marked bones as well (Jacobsen, personal commun.).

The two records of tyrannosaurid-ingested bones (this study and an analysis of a coprolite; Chin et al., 1998), consist solely of juveniles. Given the combination of oviparity, large clutch size, and large adult size, juveniles likely predominated in standing hadrosaur populations: bonebed data confirm this (Varricchio and Horner, 1993; Fig. 4.1). Limb-segment proportions, often used to assess relative speed in extinct taxa like dinosaurs (Coombs, 1978), likely gave tyrannosaurids an advantage over hadrosaurs, even young ones. Three-meter-long juvenile hadrosaurs from a *Maiasaura* bonebed, Museum of the Rockies (MOR) 547, have tibia/femur and metatarsal III/femur ratios of 0.89 and 0.38 respectively. An adult *Daspletosaurus* also from the Two Medicine Formation (MOR 590) has ratios of 0.93 and 0.58. Immature tyrannosaurids possessed even more gracile proportions (Russell, 1970). Although definitive dietary interpretations can not be made on the limited sample, juvenile hadrosaurs appear to have been a readily available food item. Tooth-marked juvenile bones may have a lower preservation potential compared to larger, more durable, and, likely, less frequently ingested adult bones (Fiorillo, 1991; Erickson and Olson, 1996).

Gut contents associated with theropod dinosaurs include whole bones or partial skeletons (Ostrom, 1978; Colbert, 1989; Charig and Milner, 1997; Chen et al., 1998). Ingested bones, like the hadrosaur vertebrae described here and those associated with *Baronyx* (Charig and Milner, 1997), show the corrosive effects of

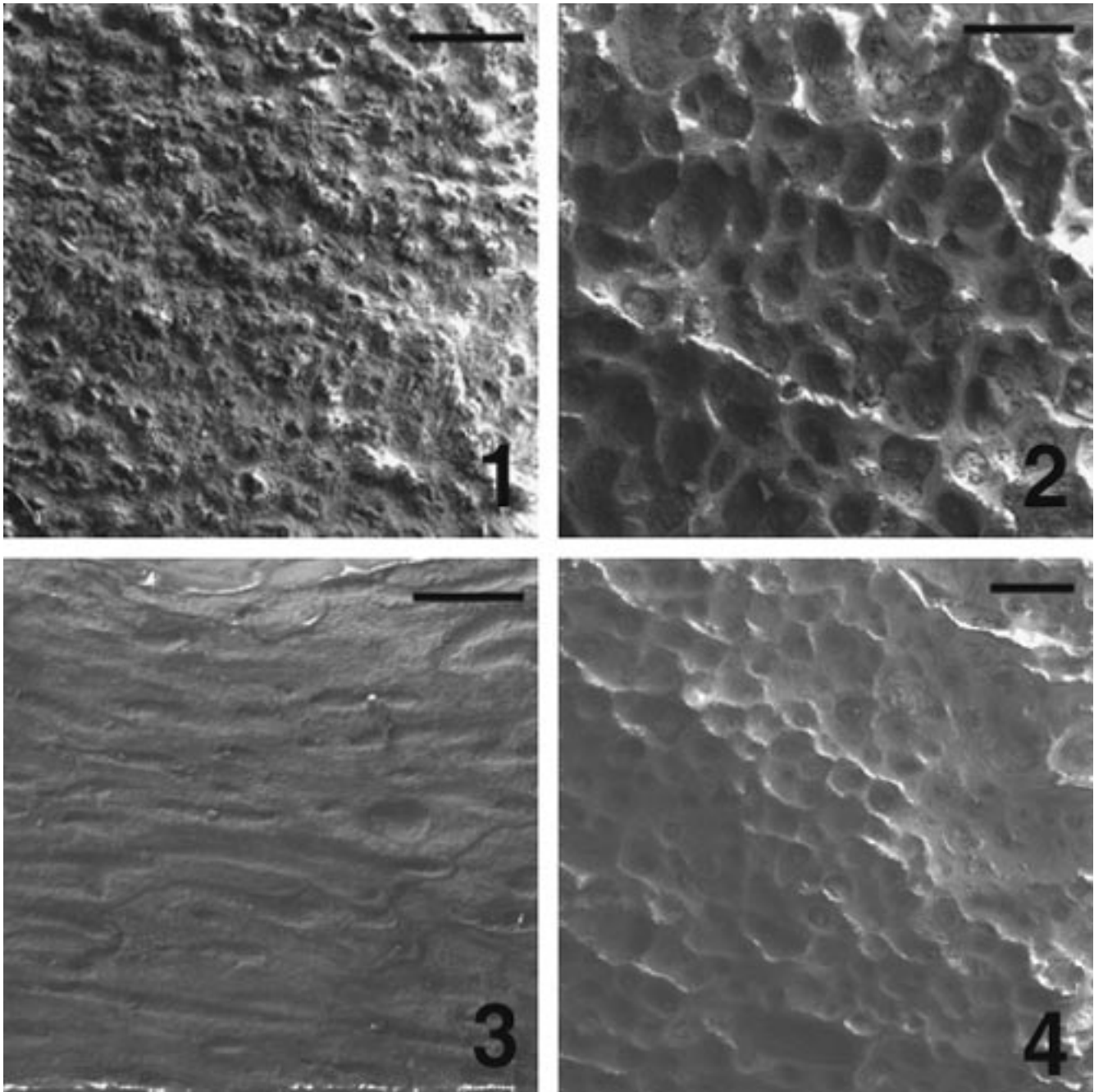


FIGURE 3—SEM photomicrographs of uncorroded and partially digested hadrosaur caudal vertebrae. 1, anterior articular surface of a well-preserved mid caudal from MOR 547, a *Maiasaura* bonebed. 2, anterior articular surface of a corroded proximal caudal (OTM 201-17) associated with the tyrannosaurid. 3, lateral surface of the same well-preserved mid caudal from MOR 547. 4, lateral surface of a corroded distal caudal (OTM 201-61) associated with the tyrannosaurid. Lateral surface photos taken at roughly mid-length. Scale bars equal 0.5 mm. These same three vertebrae in anterior and lateral views are shown in Figure 2.

digestive juices. These gut contents, as well as two studies of tooth-marked dinosaur bones, suggest theropods ingested prey items with a minimum of oral processing (Fiorillo, 1991; Jacobsen, 1998). In contrast, Chin et al. (1998) argued that the distinct fragmentation and angularity of bone within a *Tyrannosaurus rex* coprolite reflect extensive bite- rather than gizzard-induced breakage. Among theropods, *T. rex* may be exceptional. Its dentition, consisting of fewer but both stouter and stronger teeth (Farlow et al., 1991, fig. 2) could easily crush bone (Erickson et al., 1996).

Further, the presence of a gizzard in theropods and its role in bone fragmentation remain largely unexplored.

Extant archosaurs, crocodilians and birds, employ a two-part stomach with a thin-walled, enzyme-producing anterior, the proventriculus, followed by a thick-walled muscular gizzard (Skoczylas, 1978; Kusner, 1990). Gastroliths or “stomach stones” associated with skeletons may indicate the presence of a gizzard (e.g., Gillette, 1991). A variety of ornithischian and saurischian dinosaurs preserve gastroliths: the ankylosaur, *Panoplosaurus*

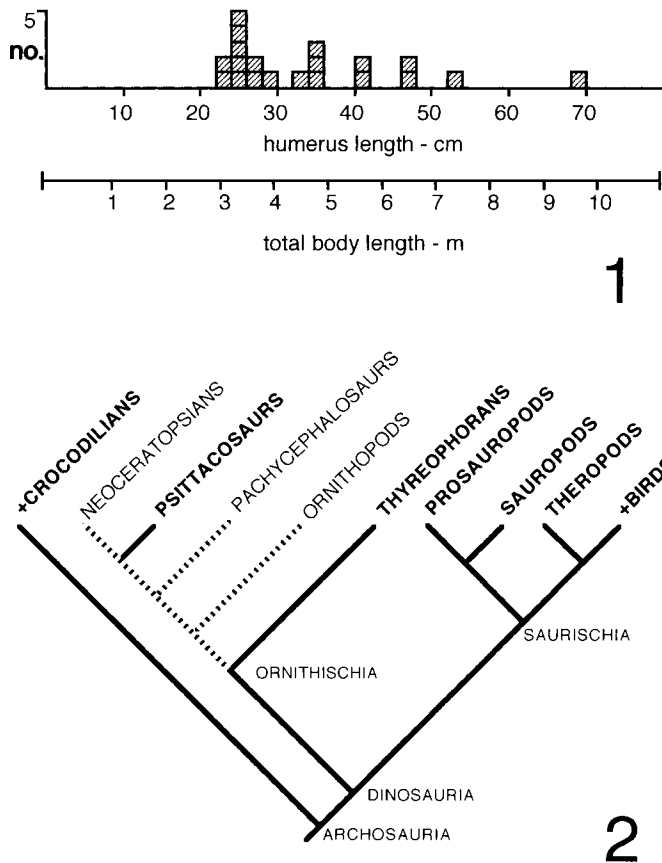


FIGURE 4—1. Size frequency distribution of humerus lengths of hadrosaurs from a *Maiasaura* bonebed, MOR Locality, TM-003. Each square represents a single individual as counted by non-overlapping humeri. Total Minimum Number of Individuals = 20. Note the positive skewness reflecting a dominance of juvenile individuals about 3 m in length. This peak is interpreted as a one-year-old age class (Varricchio and Horner, 1993). Whether this site is catastrophic or attritional in origin does not radically effect the dominance of juveniles. This size-frequency distribution comes close to matching those for extant crocodilian populations (Brandt, 1991). 2. Cladogram suggesting that a muscular gizzard is plesiomorphic for at least Saurischia and probably all Archosauria. Terminal taxa with living members known to possess a gizzard are marked with a "+" and those with representatives preserved with "stomach stones" or gastroliths are in bold face (See text for details). In the figure, "Theropods" equals non-avian theropods. Tree topology based on Sereno (1997).

(Carpenter, 1997b); the ceratopsian, *Psittacosaurus* (Osborn, 1924); the prosauropods *Massospondylus* and *Selosaurus* (Galton, 1990); and the sauropods, *Apatosaurus* (Wieland, 1906; Cannon, 1907), *Barosaurus* (Bird, 1985), and *Seismosaurus* (Gillette, 1991). Surprisingly, several theropod skeletons also occur with stomach stones: the Jurassic *Poekilopleuron* (Eudes-Deslongchamps, 1838), *Baryonyx* (Charig and Milner, 1997), *Caudipteryx* (J. Qiang et al., 1998), and a basal coelurosaurian from the Cretaceous of South Africa (De Klerk et al., 2000). If gastroliths represent a valid indicator of gut anatomy, their phylogenetic distribution among dinosaurs (Fig. 4.2) suggests that a muscular gizzard is plesiomorphic for at least Saurischia and probably for all Archosauria taxa. Additional specimens and embryologic comparisons of extant crocodilians and birds could provide verification of this hypothesis.

Extant archosaurs, crocodilians and birds, typically ingest prey with little mastication and can fully digest bones (Fisher, 1981;

Richardson et al., 1986; Lyman, 1994). As evidenced by gut contents, feeding and digestion in theropod dinosaurs appear very similar to that of their extant relatives. With perhaps some exceptions, predatory dinosaurs appear to have engulfed large chunks of flesh, processing them using the enzymes and muscular capabilities of a two-part, proventriculus-gizzard stomach.

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