BULLETIN 146

First Occurrence of *Deinonychus antirrhopus* (Dinosauria: Theropoda) from the Antlers Formation (Lower Cretaceous: Aptian-Albian) of Oklahoma

Daniel L. Brinkman
Richard L. Cifelli
Nicholas J. Czaplewski

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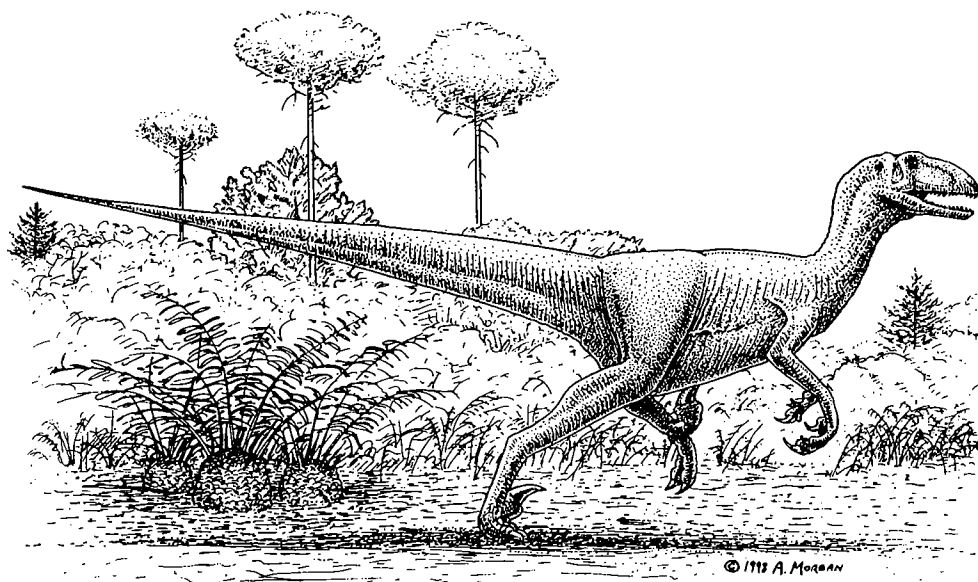
OKLAHOMA GEOLOGICAL SURVEY

CHARLES J. MANKIN, *Director*
KENNETH S. JOHNSON, *Associate Director*

SURVEY STAFF

Cover Illustration

Reconstruction of a subadult individual of *Deinonychus antirrhopus* running across an Early Cretaceous floodplain in what is now southeastern Oklahoma. The low vegetation in the background includes cycads, ferns, and some of the first flowering plants; the trees include Norfolk Island pinelike araucarians, larchlike conifers, and a ginkgo.

Drawing by Armand Morgan, Public Education Division, Yale Peabody Museum

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First Occurrence of *Deinonychus antirrhopus* (Dinosauria: Theropoda) from the Antlers Formation (Lower Cretaceous: Aptian-Albian) of Oklahoma

DANIEL L. BRINKMAN[1]
RICHARD L. CIFELLI[2]
NICHOLAS J. CZAPLEWSKI[2]

ABSTRACT.—We report the discovery of *Deinonychus antirrhopus* in the Antlers Formation of Atoka County, Oklahoma. This species is a medium-sized dromaeosaurid previously known unambiguously from only the Cloverly Formation (Aptian-Albian) of Montana and Wyoming. The specimen discussed herein represents the first reasonably complete material referable to this rare, important taxon outside of the Cloverly Formation. The specimen, together with several presumably shed *Deinonychus* teeth, was found associated with at least three partial skeletons of the ornithopod dinosaur *Tenontosaurus*. This occurrence is only the second known to have produced substantial associated skeletons of the two taxa, the first being the type locality for *Deinonychus* in the Cloverly Formation of Montana. Biostratigraphic evidence suggests that the association in the Antlers Formation may be the geologically older of the two. The Oklahoma occurrence provides corroborative evidence supporting the proposed predator/prey relationship between *Deinonychus* and *Tenontosaurus*.

Although preparation is not complete, every major region of the skeleton is represented in the Oklahoma specimen. This material includes morphology not preserved in any of the described specimens from the Cloverly Formation. In addition to potential geologic age differences between specimens from the Antlers and Cloverly Formations, the individual from Oklahoma is smaller than those from the Cloverly Formation, and its skeletal morphology differs from the Cloverly specimens in a number of subtle ways. However, the fact that at least some of the skeletal elements (e.g., the occiput, coracoid, and phalanges) in the Oklahoma specimen have features generally associated with immaturity strongly suggests that the observed morphological differences are ontogenetic and not taxonomically significant. Thus, the Oklahoma specimen is considered to represent a subadult *D. antirrhopus* and not a second morphospecies. The occurrence of *Deinonychus* (and its presumed prey *Tenontosaurus*) in both the Antlers and Cloverly Formations provides the most compelling biostratigraphic link yet between these two units and indicates broad geographic distributions for at least some taxa of terrestrial vertebrates in the Early Cretaceous of North America.

INTRODUCTION

Standing approximately 1 m tall and reaching nearly 3 m in total length as a fully grown adult, *Deinonychus antirrhopus* is a medium-sized velociraptorine dromaeosaurid from the Early Cretaceous of North America. First discovered in the Cloverly Formation (Aptian-Albian) of Montana and Wyoming, *D. antirrhopus* is characterized by having such velociraptorine features as laterally compressed, serrated teeth with smaller denticles anteriorly than posteriorly, a raptorial manus, a hyperextendable, raptorial second pedal digit, and a long tail stiffened by a series of hypertrophied

prezygapophyseal and chevron processes (Ostrom, 1969a,b; 1970a). Ostrom's (1969a,b; 1974; 1976a) descriptions of this lightly built, agile predator, together with his suggestion that it may have been a gregarious pack-hunter, heralded a revolution in the interpretation of dinosaur paleobiology, sparking intense debate on the activity levels, metabolic rates, and the most appropriate living models for dinosaurs, both on an individual and community-wide basis. This controversy continues unabated (Thomas and Olson, 1980; Bakker, 1986; Farlow, 1990; Chinsamy, 1994 [and papers cited therein]; Chinsamy and others, 1995; Farlow and others, 1995; Barrick and Showers, 1995; Ruben and others, 1996). Furthermore, Ostrom's work on *Deinonychus* enabled him to recognize the fourth specimen of *Archaeopteryx* (Ostrom, 1970b, 1972; Dodson, 1993), the earliest known bird, which led directly to his detailed osteological comparisons of these two taxa. In a series of papers, Ostrom (1973,

[1]Department of Geology and Geophysics, Yale University, New Haven, Connecticut, and Oklahoma Museum of Natural History, University of Oklahoma, Norman, Oklahoma.

[2]Oklahoma Museum of Natural History and Department of Zoology, University of Oklahoma, Norman, Oklahoma.

1975, 1976b) clearly demonstrated that *Deinony-chus* and other closely related small theropods (i.e., maniraptorans *sensu* Gauthier, 1986) shared several unique osteological features with *Archaeopteryx*. In doing so, Ostrom resurrected Huxley's (1868, 1870) hypothesis of a dinosaurian origin for birds and firmly established the now widely accepted view of a theropod-bird link (Gauthier, 1986; Gauthier and Padian, 1989; Benton, 1990 [and papers cited therein]; Barreto and others, 1993; Dodson, 1993; Holtz, 1994, 1996; Chiappe, 1995; Chinsamy and others, 1995; Monastersky, 1996; Padian, 1996). Although Huxley justifiably is credited with developing the dinosaurian hypothesis for the origin of birds, Gegenbaur (1863, 1864) and Cope (1867) were the first to suggest the possible dinosaurian affinities of birds (see discussion by Witmer, 1991).

We report herein on the first substantial remains of *D. antirrhopus* found in Oklahoma. The specimen, Oklahoma Museum of Natural History (OMNH) 50268, was recovered from the Antlers Formation of Atoka County, Oklahoma, on the grounds of the Howard McLeod Correctional Center (HMCC) at OMNH Locality V706, approximately 23 km west–southwest of the town of Ant-

lers (Fig. 1). Although isolated dromaeosaurid bones and teeth possibly attributable to *Deinony-chus* have been reported from presumed Lower Cretaceous deposits in Arizona (Thayer and Ratkevich, 1996), the Cedar Mountain Formation of Utah (Pomes, 1988; Kirkland and Parrish, 1995; Kirkland, 1996), the Potomac Group of Maryland (T. R. Lipka, personal communication, 1997), and the Trinity Group of Texas (Thurmond, 1974; Winkler and others, 1988; Gallup, 1989; Jacobs, 1995), the evidence supporting these reports cannot be evaluated because none of this material has been described or illustrated in detail. OMNH 50268 represents the first reasonably complete material referable to this rare, important taxon outside of the Cloverly Formation. Every major region of the skeleton is represented in the new specimen, and a large block of unprepared material promises to provide additional skeletal elements. It is already clear, however, that the Oklahoma material includes features not preserved in any of the described specimens from the Cloverly Formation. In this report, we briefly describe these new morphologic features, together with the more diagnostic skeletal elements that provide the basis for identification of *D. antirrhopus* in the fauna of
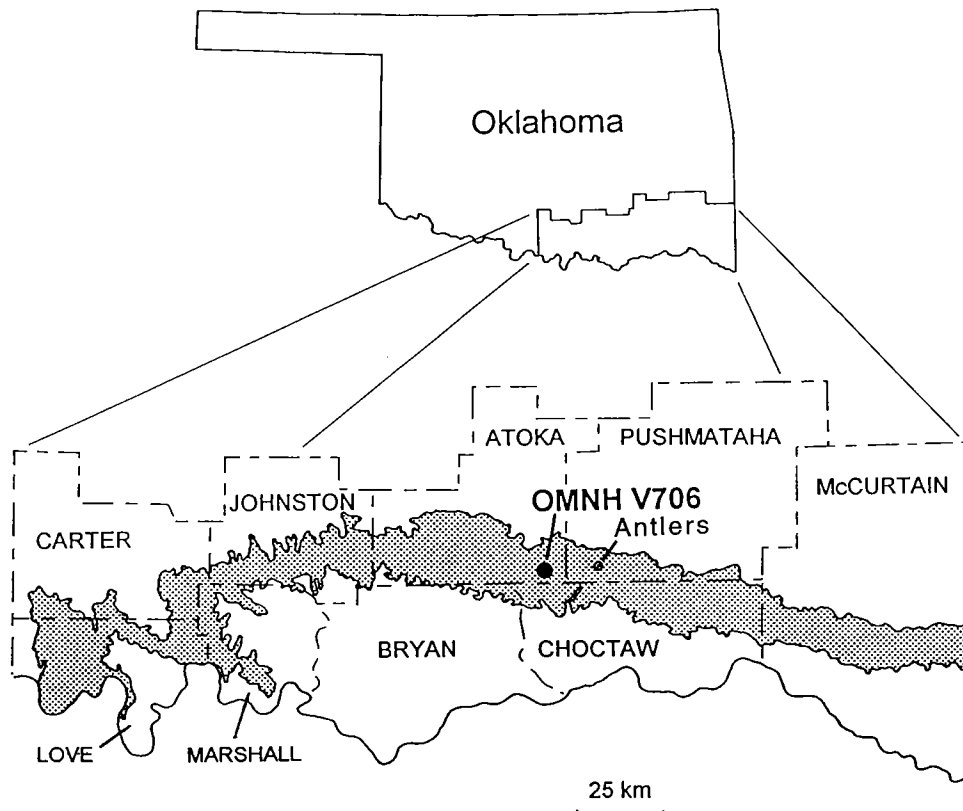

Figure 1. Surface distribution of the Antlers Formation in Oklahoma and the location of OMNH Locality V706. Modified from Hart and Davis (1981), reprinted by permission.

the Antlers Formation, and discuss the biostrati-graphic and biogeographic implications of this discovery.

GEOLOGIC AND TAPHONOMIC SETTING

The Antlers Formation is a southeast-thicken-ing fluvial, deltaic, and strandplain unit laterally equivalent to the Trinity Group of Texas that formed in a generally subtropical, semiarid climate through the accumulation of detritus eroded from the Wichita-Arbuckle-Ouachita highlands to the north (Hobday and others, 1981; Winkler and oth-ers, 1990). The formation, which extends from southwestern Arkansas through southeastern Okla-homa into northern Texas, crops out in an east-west band between 4.8 and 24.1 km wide in south-eastern Oklahoma (Fig. 1) (Hart and Davis, 1981; Darling and Lock, 1984). According to Manley (1965), the formation consists of silty to sandy claystones; fine- to coarse-grained sandstones that are moderately to poorly sorted, unindurated to clayey to locally carbonate-cemented, irregularly crossbedded, and ferruginous; and conglomerates. Based on the estimated dip, lateral outcrop extent, and published thickness estimates from nearby counties, Rennison (1996) estimated the Antlers Formation to be approximately 150 m thick in the area of locality V706.

The Antlers Formation at locality V706 consists predominantly of gray-green or red claystone with irregular lenses of poorly indurated, yellowish to brown sandstone and conglomerate, all of fluvial origin. Preliminary X-ray diffraction (XRD) analy-ses conducted on the claystone at V706 by S.F. Argast of Indiana University–Purdue University at Fort Wayne indicates that this locality is probably in the transitional clay-mineral zone recognized by Manley (1965), and, thus, is in the middle part of the Antlers Formation. This placement is sup-ported by the work of Rennison (1996), who esti-mated the stratigraphic level of V706 to be at ap-proximately 87 m above the base of the forma-tion—thereby placing the fossil locality in the up-per-middle part of the formation.

In addition to OMNH 50268, the claystone at locality V706 has yielded several partial to rela-tively complete skeletons of various sizes of the ornithopod dinosaur *Tenontosaurus*, a partial tooth of the allosauroid *Acrocanthosaurus*, and partial carapaces of the cryptodire *Glyptops*, as well as a rich accumulation of microvertebrate re-mains collected using screenwashing and associ-ated fossil recovery techniques (Cifelli, 1997; Cifelli and others, 1997). Thus far, 18 specimens of *Tenon-tosaurus* sp., including six partial skeletons, have been collected from the claystone at V706. These specimens are currently under study by one of us (DLB) as part of a systematic revision of this genus. Most of the tenontosaur material at V706 was con-centrated in two sites located approximately 30 m apart in a claystone horizon that varies in thick-ness from about 10 to 40+ cm. The distribution of these specimens indicates that a mass death as-semblage on an Early Cretaceous floodplain may be represented.

OMNH 50268 came from the richer, more south-ern of the two tenontosaur concentrations. It was found in proximity to a relatively complete skel-eton of an adult tenontosaur and within 5 m of two partial skeletons of smaller tenontosaurs, one of which is a juvenile, and a pile of associated caudal vertebrae that could belong to either the larger of the two nearby partial skeletons or to yet another individual (Fig. 2). The skeletons of the tenon-tosaurs are either mostly articulated or partially disarticulated but possess associated skeletal ele-ments, whereas the *Deinonychus* skeletal ele-ments are mostly disarticulated but associated. The distribution and three-dimensional orienta-tion of some of the disarticulated skeletal elements (e.g., the left maxilla, three proximal caudal verte-brae, and some ossified tendons of tenontosaur OMNH 16563) suggest slight fluvial transport of these elements from north to south. All four skel-etons have isolated *Deinonychus* teeth associated with them, but the locations of only nine of the 14 teeth could be plotted on Figure 2. Moreover, the left humerus of one tenontosaur, OMNH 50269, has what might be *Deinonychus* tooth marks on its caudal surface (Fig. 3). This possibly tooth-marked humerus was on the underside of the skeleton when found and, thus, may suggest either move-ment of the injured animal before death or tum-bling of the animal's carcass after death but before burial. Currents of water would have been the most likely tumbling agents, though the feeding activities of predators or scavengers cannot be dis-counted. The possible tooth marks consist of eight short (4–13 mm long), narrow (0.5–1.5 mm wide), shallow, subparallel, diagonal grooves or gouges filled with rust-colored, oxidized claystone (Fig. 3). Several unfilled scratches in the same area might be tooth marks as well, but it is also possible that these are preparation tool marks. The purported *Deinonychus* tooth marks resemble those made by a Late Cretaceous velociraptorine, *Saurornith-olestes langstoni*, on the tibia of a pterosaur (cf. Currie and Jacobsen, 1995, fig. 1). The latter veloc-iraptorine was identified by Currie and Jacobsen (1995) on the basis of a taxonomically diagnostic tooth embedded in the pterosaur's tibia near the scratch marks.

The association of isolated, probably shed, *Dein-onychus* teeth with tenontosaur remains is quite common in the Cloverly Formation, and suggests that the former animal fed on the latter (Ostrom, 1969b; Forster, 1984; Maxwell and Ostrom, 1995). However, V706 is only the second locality known to have produced substantial associated skeletons of both taxa. The first, a Yale University locality in the Cloverly Formation of Montana, yielded the partial skeletons of at least four *Deinonychus* indi-viduals together with the partial skeleton of a much larger adult tenontosaur (Ostrom, 1969b;

TENONTOSAURUS
OMNH 50269

TENONTOSAURUS
OMNH 16563

TENONTOSAURUS
OMNH 51091

TENONTOSAURUS
OMNH 53781

N

N. J. Czaplewski

= *Deinonychus* bones
= *Tenontosaurus* bones
D = *Deinonychus* tooth
T = *Tenontosaurus* tooth
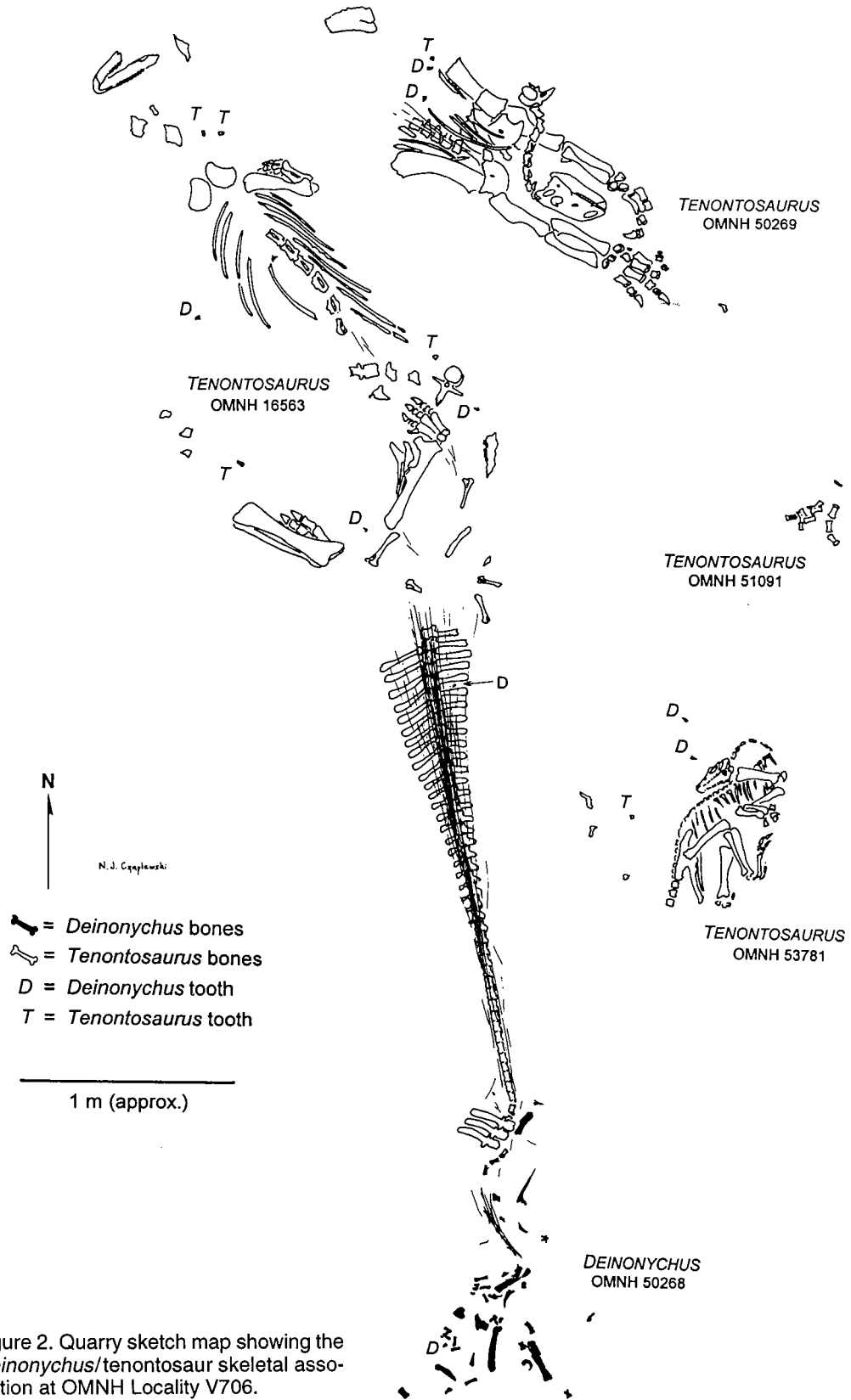
1 m (approx.)

DEINONYCHUS
OMNH 50268

Figure 2. Quarry sketch map showing the
Deinonychus/tenontosaur skeletal asso-
ciation at OMNH Locality V706.

Maxwell and Ostrom, 1995; Maxwell and Witmer, 1996). This intimate association of partial skeletons at the type locality for *Deinonychus* was interpreted by Ostrom (1969b) and by Maxwell and Ostrom (1995) as probable evidence of pack-hunting and gregarious behaviors in *Deinonychus*. Moreover, a partially healed transverse fracture in the penultimate phalanx (II-2) of the right second pedal digit in the type specimen of *Deinonychus* may be indirect evidence in support of pack-hunting/gregarious behaviors in this taxon (Ostrom, 1976a; C. L. Marshall and others, in preparation), as this individual survived for an appreciable amount of time with an injury to one of its purported major defense and food-gathering mechanisms (C. L. Marshall and others, in preparation).

According to Peczkis (1994), an adult *Deinonychus* has an estimated body mass of 70–100 kg, whereas a fully grown *Tenontosaurus*, with a total body length of more than 7.5 m (Dodson, 1980), has an estimated body mass of 1–4 metric tons. Thus, although the skeletal anatomy of *Deinonychus* is clearly indicative of its predatory habits (Ostrom, 1969b), it is unlikely that an individual *Deinonychus* could single-handedly kill an adult tenontosaur considerably larger than itself (Forster, 1984; Norman, 1985). Therefore, the fact that several *Deinonychus* individuals (including the possibly incapacitated animal mentioned above) apparently perished in pursuit of a single tenontosaur at the Yale site in Montana is not surprising given the size disparity between these taxa. Alternatively, such high mortality in pursuit of prey might also indicate a level of ferociousness (toward the prey and each other) in *Deinonychus* not typically seen in modern terrestrial vertebrates

(see also Maxwell and Ostrom, 1995). "Pack-hunting" by *Deinonychus* thus may have resembled an opportunistic feeding frenzy of sharks or piranhas more than the cooperative hunting strategies and subsequent food-sharing behaviors of *Lycaon*, the African hunting dog (see Nowak, 1991). Regardless of whether *Deinonychus* hunted tenontosaurs in packs or not, their common taphonomic association probably represents one of the best-documented predator/prey relationships among dinosaurs (Maxwell and Ostrom, 1995).

MORPHOLOGICAL DESCRIPTIONS

In addition to having as many as 26 teeth, the axial skeleton of OMNH 50268 is represented by the best example yet found of the occiput of *Deinonychus*, a partial right prootic, parts of two mid-dorsal ribs, a nearly complete proximal chevron, and most of what is probably the fifth sacral vertebra. The appendicular skeleton is represented by an exceptionally well-preserved right coracoid, poorly preserved parts of the right humerus and femur, parts of the left and right metacarpals I and II, part of the left and most of the right manual phalanges I-1, most of the left manual phalanx I-2 (ungual), parts of the left manual phalanges II-1 and II-2, the entire left manual phalanx III-2 and right manual phalanx III-3, part of the left metatarsal I, most of the right pedal phalanx II-2, parts of the left and right pedal phalanges II-3 (i.e., the killing claw for which the genus is named), parts of the left pedal phalanges III-3 and IV-3, and the entire left pedal phalanx IV-4.

The above material was compared with the holotype and hypodigm specimens of *D. antirrhopus* from the Cloverly Formation at the Yale Peabody Museum (YPM) in New Haven, Connecticut. These comparisons were supplemented with Ostrom's (1969b, 1976a) published accounts of *Deinonychus* specimens at the Harvard University Museum of Comparative Zoology (MCZ) in Cambridge, Massachusetts, and the American Museum of Natural History (AMNH) in New York City, New York. Specimens collected recently from the Cloverly Formation at the Museum of the Rockies in Bozeman, Montana, were not studied. OMNH 50268 compares closely with the above specimens of *D. antirrhopus*, though it is considerably smaller than most of them (Table 1). All measurements in Table 1 were

Figure 3. Possible *Deinonychus* tooth marks on the caudal surface of the humerus of tenontosaur OMNH 50269. Tooth marks indicated by arrows. Proximal end of humerus to the left. Scale bar = 10 mm.

TABLE 1.—MEASUREMENTS (IN MM) OF SELECTED *DEINONYCHUS* BONES AND THE RELATIVE SIZE RANGE OF EACH PARAMETER IN OMNH 50268 COMPARED WITH THOSE IN SPECIMENS FROM THE CLOVERLY FORMATION OF MONTANA

Coracoid	OMNH[a] 50268	YPM[b] 5236	% size[c]
Maximum length	73.27	107.20	68
Maximum ventral width	71.64	99.04	72
Maximum breadth of scapular articulation	16.44	25.59	64

Manus

First metacarpal (MCI)	OMNH 50268L[d]	OMNH 50268R[e]	YPM 5206L	YPM 5206R	% size
Maximum length	31.17	31.04	42.07	42.43	73–74
Maximum proximal width	9.34	11.12E[f]	16.79	16.33	56–68
Maximum distal width	11.49	12.49	18.87	19.62	59–66
Maximum distal breadth	13.50	13.08	19.66	19.85	66–69

First phalanx of the first manual digit (I-1)	OMNH 50268L	OMNH 50268R	YPM 5206L	YPM 5220L	YPM 5220R	YPM 5213R	MCZ[g] 4371	% size
Maximum length	—	54.04E	74.10	—	66.44	72.41	77.30[h]	70–81
Maximum proximal width	—	13.15	21.34	—	17.76	22.10	—	60–74
Maximum proximal breadth	—	13.43	20.11	—	17.57	21.54	—	62–76
Maximum distal width	11.09	11.66	16.18	13.60	13.79	15.60	—	69–86
Maximum distal breadth	10.50	10.42	15.30	12.24	13.13	15.12	—	68–86

Second phalanx of the first manual digit (I-2)	OMNH 50268L	YPM 5206L	% size
Maximum proximal width	29.99	42.00E[i]	71

Second metacarpal (MCII)	OMNH 50268L	OMNH 50268R	YPM 5206L	YPM 5206R	YPM 5220R	% size
Maximum proximal width	12.04	10.46	17.64	17.61	15.60	59–77
Maximum proximal breadth	11.63	11.65	14.89	13.55	13.06	78–89

First phalanx of the second manual digit (II-1)	OMNH 50268L	YPM 5206L	YPM 5216R	% size
Maximum distal width	13.81	17.46	17.58	79
Maximum distal breadth	10.41	15.72	15.30	66–68

Second phalanx of the third manual digit (III-2)	OMNH 50268L	YPM 5206L	% size
Maximum dorsal length	14.56	20.66	70
Maximum proximal width	10.98	14.25	77
Maximum proximal breadth	6.84	10.04	68
Maximum distal width	8.52	11.26	76
Maximum distal breadth	7.26	9.84	74

Third phalanx of the third manual digit (III-3)	OMNH 50268R	YPM 5243R	YPM 5215L	YPM 5209R	% size
Maximum length	39.34	48.24	—	52.12E	75–82
Maximum proximal width	11.21	13.71	14.95	15.63	68–82
Maximum proximal breadth	7.38	9.80	10.83	11.16	66–82
Maximum distal width	8.50	10.20	11.35	11.44	74–83
Maximum distal breadth	7.09	9.30	9.91	9.96	71–76

TABLE 1.—*CONTINUED*

Pes

First metatarsal (MTI)	OMNH 50268L	YPM 5217R	% size			
Maximum distal width	9.56	10.49	91			
Maximum distal breadth	11.50	15.85	73			

Second phalanx of the second pedal digit (II-2)	OMNH 50268R	YPM 5205L	% size			
Maximum length	33.70	49.06	69			
Maximum proximal width	18.53	23.26	80			
Maximum proximal breadth	13.00	18.43	71			
Maximum distal width	17.46	24.78	70			
Maximum distal breadth	10.76	13.89	77			

Third phalanx of the second pedal digit (II-3)	OMNH 50268R	YPM 5205L	MCZ 4371	% size		
Maximum proximal width	29.30	41.00E[i]	44.00E[k]	67–71		

Third phalanx of the third pedal digit (III-3)	OMNH 50268L	YPM 5205	YPM 5217	YPM 5207	% size	
Maximum distal width	11.50	14.54	14.06	15.06	76–82	
Maximum distal breadth	10.16	14.15	12.66	14.92	68–80	

Third phalanx of the fourth pedal digit (IV-3)	OMNH 50268L	YPM 5205L	YPM 5217R	YPM 5207R	% size	
Maximum ventral length	27.26	29.36E	28.26	30.69	89–96	
Maximum proximal breadth	14.44	17.19	16.14	18.51	78–89	
Maximum distal width	11.86	13.36E	12.64	14.10	84–94	
Maximum distal breadth	12.97	15.99	15.07	16.28	80–86	

Fourth phalanx of the fourth pedal digit (IV-4)	OMNH 50268L	YPM 5205L	YPM 5205R	YPM 5217L	MCZ 4371	AMNH[l] 3015	% size
Maximum dorsal length	23.94	28.95	28.73	28.80	32.60[h]	26.30[h]	73–91
Maximum proximal width	12.79	16.10	17.25	14.66	—	—	75–87
Maximum proximal breadth	12.68	15.22	16.20	14.37	—	—	78–88
Maximum distal width	10.79	12.19	13.73	12.80	—	—	80–90
Maximum distal breadth	11.30	12.71	13.31	11.86	—	—	85–95

[a]Oklahoma Museum of Natural History, Norman, Oklahoma.

[b]Yale Peabody Museum, New Haven, Connecticut.

[c]Relative size of a certain parameter in OMNH 50268 compared with the same parameter in specimens from the Cloverly Formation.

[d]Left.

[e]Right.

[f]Estimated.

[g]Harvard University Museum of Comparative Zoology, Cambridge, Massachusetts.

[h]From Ostrom (1976b, Table 1).

[i]Estimated from Ostrom (1969a, fig. 5).

[j]Estimated from Ostrom (1969a, fig. 2).

[k]Estimated from Ostrom (1976b, fig. 7).

[l]American Museum of Natural History, New York, New York.

made using dial calipers accurate to 0.05 mm. Moreover, there are differences between OMNH 50268 and the specimens from the Cloverly Formation in some of the bones' proportions, the degree of development of various bony processes (i.e., sites of muscle attachment) and articular surfaces, the depth of certain fossae, and the shape of the supracoracoid foramen. However, as will be discussed below, these differences are attributed here to ontogeny and are not considered taxonomically significant.

Metapodials and phalanges are the most common elements prepared so far for OMNH 50268. They are shorter and less dorsoventrally deep and less mediolaterally broad than those from the Cloverly Formation (Table 1). In comparison with those of the larger and presumably more mature specimens from the Cloverly Formation, the manual elements of OMNH 50268 tend to be relatively shorter than most of the pedal elements in this individual. In this regard, *Deinonychus* may be similar to *Archaeopteryx* in exhibiting predominantly positive growth allometries in the bones of the manus and negative growth allometries in the bones of the pes during ontogeny (Houck and others, 1990). Thus, both of these taxa appear to have "grown into" their hind feet, a phenomenon which may be related to endothermy (J. A. Gauthier, personal communication, 1997).

TABLE 2.—Tooth Measurements, Serration Density, and Calculated Values of Denticle Size Difference Index (DSDI) for Selected *Deinonychus antirrhopus* Teeth from Oklahoma Museum of Natural History (OMNH) Locality V706

OMNH I. D. #	FABL[a] (mm)	BW[b] (mm)	Serration density Ant. keel[c]	Serration density Post. keel[d]	DSDI[e]
16564[f]	6.65	—	30	20	1.5
16565[f]	7.09	3.52	30	20	1.5
16566[f]	3.64	1.94	50	25	2.0
17709[f]	9.06	4.52	—[g]	20	—
34203[f]	6.19	3.21	30	15	2.0
49410[f]	9.56	4.29	—[g]	20	—
49411[f]	9.24	4.18	—[g]	22.5	—
49412[f]	7.32	3.60	45	20	2.25
49415[f]	7.26	3.32	—[g]	20	—
50268[h](1)	5.70	2.99	30	17.5	1.71
50268[h](2)	6.30	3.09	37.5	20	1.875
52711	6.51	3.30	40	20	2.0
53492[i]	—	3.83	30	20	1.5
54004[j](1)	8.15	4.13	30	15	2.0
54004[j](2)	6.47	3.29	30	20	1.5
54004[j](3)	4.75	2.44	30	20	1.5

[a]FABL = fore–aft basal length measured along the enamel-dentine junction of tooth.

[b]BW = basal width measured along the enamel-dentine junction of tooth.

[c]Number of serrations per 5 mm of anterior keel length (extrapolated from a 1-mm unit length as measured along the middle part of the keel).

[d]Number of serrations per 5 mm of posterior keel length (extrapolated from a 1-mm unit length as measured along the middle part of the keel).

[e]DSDI = anterior serration density divided by posterior serration density.

[f]Tooth found associated with tenontosaur skeleton OMNH 16563.

[g]Anterior serrations destroyed by *in situ* tooth wear and/or weathering.

[h]Tooth found associated with *Deinonychus* skeleton OMNH 50268.

[i]Tooth found associated with tenontosaur skeleton OMNH 50269.

[j]Tooth found associated with poorly preserved tenontosaur bones approximately 24 m NW of OMNH 50268.

AXIAL SKELETON

Isolated Teeth

Fourteen isolated dromaeosaurid teeth have been collected from within 5 m of OMNH 50268, with an additional 12 teeth having been found within 35 m of this specimen. Whereas the more complete tooth crowns appear to have been shed, many of the teeth at this locality consist of partial crowns and, thus, it is difficult to tell whether they were shed during life or lost from the skull after death. However, the great size range represented (Table 2), together with the fact that nearly all of these widely scattered teeth were found either associated with tenontosaur skeletal material or with the bones of OMNH 50268 itself, suggest that they may be the shed teeth of several individuals. Moreover, most crowns exhibit at least some *in situ* tooth wear, especially at the tip and along the distal keels of the larger crowns, thereby increasing the likelihood that at least some of these teeth may have been shed. As in the teeth of tyrannosaurs (Farlow and Brinkman, 1994), tooth wear is more
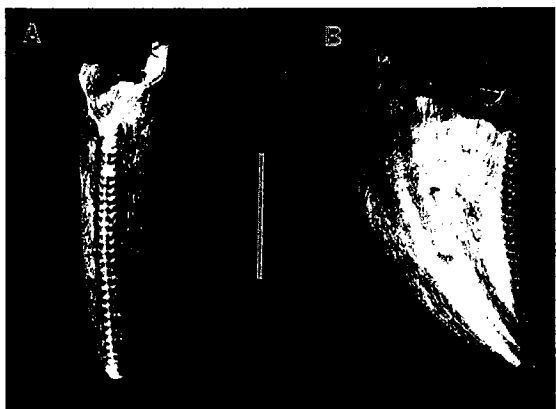
Figure 4. Morphology of a *Deinonychus* lateral tooth associated with OMNH 50268 in (A) posterior and (B) lateral views. Scale bar = 5 mm.

frequent and severe along the anterior keel than the posterior keel. On one tooth in particular (OMNH 17709), the entire anterior keel is worn flat, and it bears a large, flat wear surface on its medial side similar to those in some tyrannosaurs (cf. Farlow and Brinkman, 1994, fig. 3). It is likely that this relatively large, heavily worn crown, at least, was shed by a second, larger *Deinonychus* individual. Furthermore, a batch of nine partial teeth (seven lateral and two premaxillary teeth) found associated with some poorly preserved tenonto-saur bones approximately 24 m northwest of OMNH 50268 may be evidence of at least a second *Deinonychus* individual at the site.

The laterally compressed, recurved, serrated teeth from V706 (Fig. 4) are nearly identical to the maxillary and dentary teeth described for *D. antirrhopus* by Ostrom (1969b), though they are generally smaller than those from the Cloverly Formation. The teeth from both the Antlers and Cloverly Formations have slightly asymmetrical crowns with essentially straight anterior keels and slightly distomedially deflected posterior keels (Fig. 4; cf. Ostrom, 1969b, fig. 23A). Furthermore, both samples are typically velociraptorine in having much larger denticles on the posterior carinae than on the anterior carinae (Figs. 4, 5) (Ostrom, 1969a,b; Currie, 1995; Rauhut and Werner, 1995). The shape of their denticles are essentially identical to those of the velociraptorine dromaeosaurid *Saurornith-olestes* (Fig. 5; cf. Currie and others, 1990, fig. 8.2).

Following the work of Farlow and others (1991), several measurements were made on the 16 most complete teeth (of the 26 collected) from the death assemblage horizon. These measurements include serration density (i.e., the number of serrations per 5 mm of anterior and posterior keel length), basal width (BW), and fore–aft basal length (FABL) (Table 2). Serration density was measured along the middle part of both keels using a binocular microscope with an ocular micrometer. However,

due to the small size and highly recurved nature of the teeth (Figs. 4, 5), serration density was extrapolated from the number of serrations per 1 mm unit length. Unfortunately, such extrapolation would have exaggerated any counting errors we might have made. Moreover, as denticle size tends to decrease both superiorly and inferiorly from the middle portion of the keel, the number of serrations per unit length of the smaller teeth may be slightly inflated. However, as pointed out by Farlow and others (1991), smaller teeth in general have more denticles per unit length than larger teeth both within and across theropod taxa. BW and FABL were measured along the enamel-dentine junction using dial calipers accurate to 0.05 mm. No attempt was made to determine whether the measured teeth came from the maxilla or dentary, nor was the tooth position along the jaw determined for these teeth. Both of these factors could conceivably affect our data, but would be nearly impossible to determine given the material at hand.

Four teeth from V706 have anterior serration densities beyond the range reported for *Deinonychus* from the Cloverly Formation (Table 2; cf. Rauhut and Werner, 1995, table 1), whereas all but two teeth have posterior serration densities beyond the range reported for *Deinonychus* by Rauhut and Werner (1995). In comparing bivariate plots of serration density and BW (data not shown) against FABL for the Oklahoma teeth and the more complete dromaeosaurid teeth analyzed by Farlow and others (1991), the teeth from the Antlers Formation either plot with *Deinonychus* from the Cloverly Formation or else they follow the same allometric trend as smaller dromaeosaurid teeth from the lower Trinity Group of Texas (Fig. 6). The scatter of points is greater at the small end of the size scale than it is for the large end, but this could be an artifact of our methodology. However, as
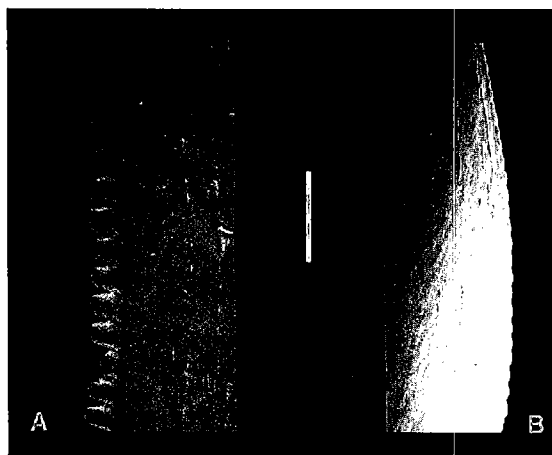

Figure 5. Scanning electron micrograph of (A) posterior serrations and (B) anterior serrations of the same *Deinonychus* tooth as in Figure 4. Tip of tooth toward top of photograph. Scale bar = 1 mm.
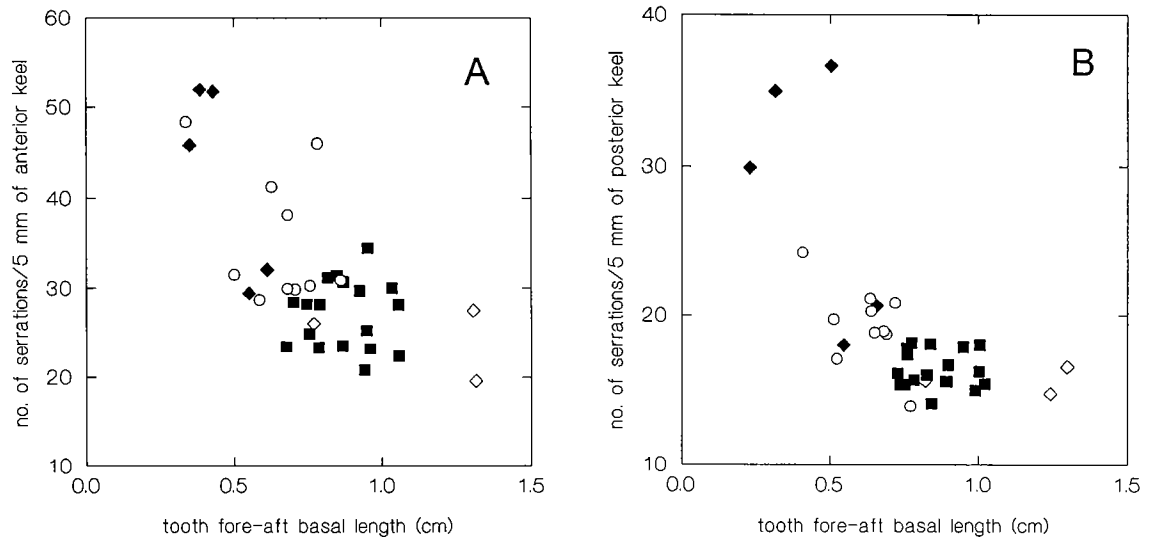
Figure 6. Relationship between serration density and tooth fore–aft basal length in Aptian-Albian–aged dromaeosaurids from the western United States. (A) anterior keel and (B) posterior keel. Key: solid diamond = lower Trinity Group sample, open diamond = upper Trinity Group sample, solid square = Cloverly Formation sample, open circle = OMNH Locality V706 sample. Overlap of symbols reduced using the jitter function of the SPSS graphics program.

discussed by Farlow and others (1991) and Holtz and others (1994), the density of serrations in the teeth of most theropods scales with relation to tooth size along the same allometric curve as that for most other carnivorous vertebrates with serrated teeth. Serration density is thus probably of little use in the systematics of most theropod groups.

The denticle size difference index (DSDI) of Rauhut and Werner (1995) is more important in a systematic account because it is independent of tooth size. This ratio was calculated for the most complete teeth from V706 by dividing their anterior serration densities by their posterior serration densities (Table 2) (Rauhut and Werner, 1995). In situ tooth wear and/or weathering destroyed the anterior serrations of four teeth reported in Table 2, and thus neither the anterior serration densities nor the DSDI values could be calculated for these teeth. Although the serration densities of many of the Oklahoma teeth are greater than those reported for Deinonychus from the Cloverly Formation (Table 2) (Rauhut and Werner, 1995, table 1), all of the teeth from V706 have DSDI values within the range reported for Deinonychus from the Cloverly Formation (Table 2; cf. Rauhut and Werner, 1995, table 2). Thus, we consider the higher serration counts in the teeth from V706 to be size related and not taxonomically significant. As pointed out by Vaughn (1958) for captorhinids, size is not a good character for the recognition of new taxa.

Although we are working with small sample sizes (and, therefore, need to interpret the data

cautiously), it is interesting that the dromaeosaurid teeth from the lower Trinity Group of Texas are considerably smaller (and, thus, have higher serration densities) than those from the upper Trinity Group (Fig. 6). Teeth from the upper Trinity Group are as large or larger than Deinonychus teeth from the Cloverly Formation and, hence, plot nearest to them, whereas most of the teeth from V706 plot between the lower and upper Trinity Group samples (Fig. 6). It is possible that these dromaeosaurids are exhibiting an increase in tooth size through time. If so, this trend could have important biostratigraphic (and, perhaps, taxonomic) implications for dromaeosaurids from the Trinity Group, as well as for those from the Antlers and Cloverly Formations. As will be discussed below, fossils from V706 may be intermediate in geological age between those from the lower and upper Trinity Group, whereas fossils from the Cloverly Formation may be temporally equivalent with those from the upper Trinity Group. Thus, the Deinonychus teeth and associated skeletal elements from V706 may be geologically older than the specimens from the Cloverly Formation. If there has been an increase in average tooth size through time in Deinonychus and other closely related Aptian-Albian dromaeosaurids, then Deinonychus teeth from V706 would be expected to be smaller on average and have higher serration densities than those from the Cloverly Formation and its temporal equivalent in Texas. Our tooth-size data (Fig. 6) may support this hypothesis. Alternatively, specimens clustering together in Figure 6 may represent the haphazard preservation of

similar ontogenetic stages. But until more specimens come to light and until we develop a better understanding of the factors that affect serration-density data, we choose to err on the side of caution and consider the teeth from V706, as well as those from the Trinity Group, to be conspecific with those from the Cloverly Formation. However, treating our sample as a single species does not preclude the possibility of a change in average tooth and/or body size through time. Kurtén (1968), for example, reported various size changes through time in several European species of Pleistocene mammals including the brown bear (*Ursus arctos*) and badger (*Meles meles*).

Occiput

The occiput of OMNH 50268 is generally similar to that described by Currie (1995) for *Dromaeosaurus albertensis*. Although the morphology of the Oklahoma occiput will be discussed in detail by

L. M. Witmer and W. D. Maxwell in their forthcoming monographic treatment on the cranium of *Deinonychus*, a brief description of this previously unknown region of the skull is presented here. That the sutures between the supraoccipitals, exoccipitals, and basioccipital are still distinct and not entirely fused in OMNH 50268 is consistent with the immature status of this individual (Fig. 7), though, as pointed out by L. M. Witmer (personal communication, 1997), adult theropods can retain these sutures in their skulls. The supraoccipital is complete except along the eroded dorsal margin. A well-developed, vertically oriented cerebellar fossa is present along the anterior surface of the medial supraoccipital suture just medial to the dural sinus. In addition, the foramen for the caudal petrosal sinus can be seen near the dorsomedial apex of the left supraoccipital in anterior view. Much of the anatomy preserved on the anterior surface of the occiput (including the cerebellar fossa, various sinuses, and two tympanic recesses [see below])
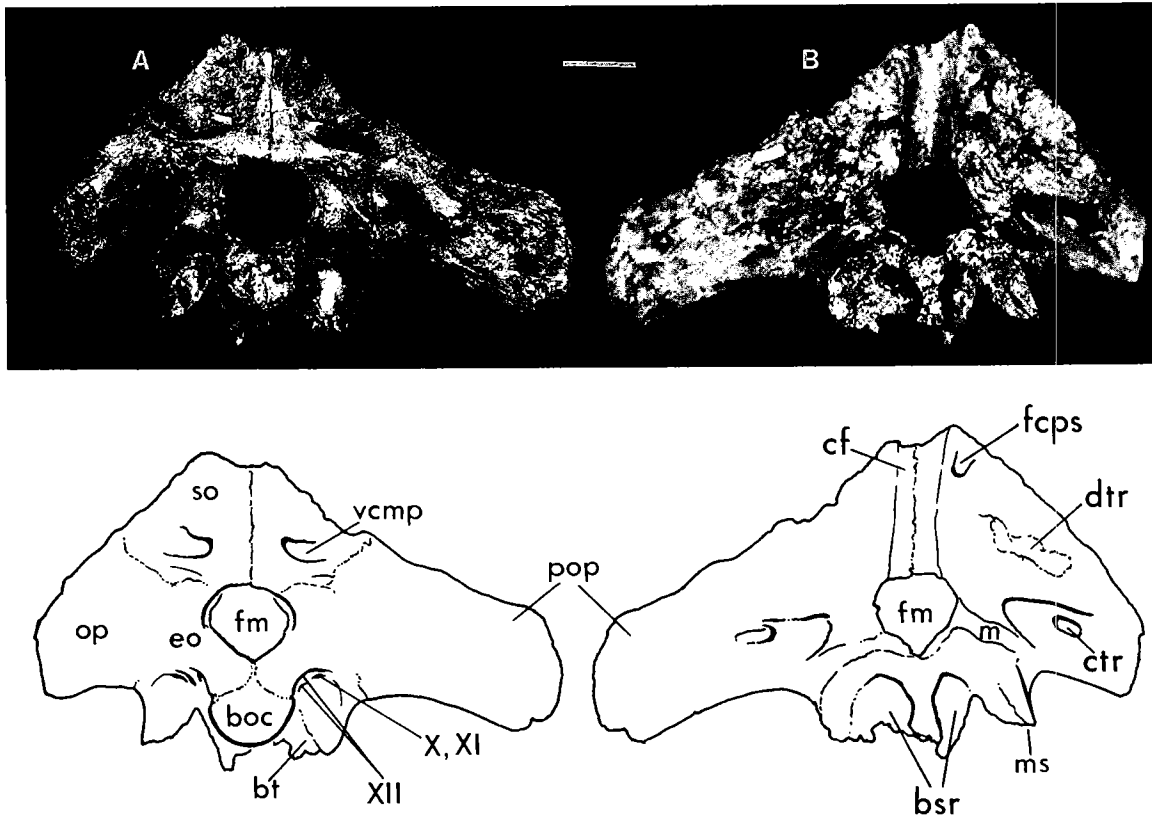

Figure 7. The occiput of OMNH 50268. Photographs and line drawings of (A) posterior and (B) anterior views. Abbreviations: boc = basioccipital, bsr = basisphenoidal recess, bt = basal tubera, cf = cerebellar fossa, ctr = caudal tympanic recess, dtr = dorsal tympanic recess, eo = exoccipital, fcps = foramen for caudal petrosal sinus, fm = foramen magnum, m = metotic fissure, ms = metotic strut, op = opisthotic, pop = paroccipital process, so = supraoccipital, vcmp = posterior canal of middle cerebral vein. Roman numerals represent cranial nerves. Scale bar = 10 mm.

was identified for us by L.M. Witmer (personal communication, 1997). The occipital face in OMNH 50268 slopes anterodorsally as in *Dromaeosaurus* (Currie, 1995), but it is closer to vertical as in most theropods, including *Troodon formosus* (Currie and Zhao, 1993). As in *Dromaeosaurus* (Currie, 1995) and in contrast to *Troodon* (Currie and Zhao, 1993), the posterior canal of the middle cerebral vein is entirely within the supraoccipital of OMNH 50268 (Fig. 7) and not at the supraoccipital-parietal suture. In addition, the interior of the supraoccipital is solid, not hollow. However, the fossa associated with the posterior canal of the middle cerebral vein is relatively larger in OMNH 50268 than in *Dromaeosaurus* (Fig. 7; cf. Currie, 1995, fig. 4C).

The entire right and the base of the left paroccipital processes are preserved in OMNH 50268 (Fig. 7). As in *Dromaeosaurus, Velociraptor,* and *Archaeopteryx* (Currie, 1995), the paroccipital process, which consists of the combined exoccipital and opisthotic bones, projects posterolaterally with a slight distal twist and probably ended distally in cartilage (Fig. 7). A well-developed fossa is preserved on the anterior surface of the paroccipital process lateral to the foramen magnum. In life, this fossa would have been just posterior to the columellar recess (L. M. Witmer, personal communication, 1997), which is missing due to erosion. Along the posterior wall of this fossa is a well-developed caudal tympanic recess; dorsomedially above that is a trace of a dorsal tympanic recess (Fig. 7). These pneumatic recesses, which are similar to and probably homologous with those of *Archaeopteryx* and other birds (Witmer, 1990, 1995), only recently have been reported in *Troodon* (Currie and Zhao, 1993), *Velociraptor* (Norell and others, 1992), and *Deinonychus* (Witmer and Maxwell, 1996). The last report was based on new material from the Cloverly Formation of Montana. Whether these two tympanic recesses communicate is unknown presently, although CT scans similar to those performed on the skulls of *Dromaeosaurus* (Currie, 1995) and *Troodon* (Currie and Zhao, 1993) could be used to address this problem.

The exoccipital takes part in the occipital condyle of OMNH 50268 in much the same way as it does in *Dromaeosaurus* (cf. Currie, 1995). Dorsally, the exoccipitals approach each other above the foramen magnum, but they are separated by the supraoccipital as in *Dromaeosaurus* (Currie, 1995). In posterior view the occipital condyle of *Dromaeosaurus* is essentially kidney shaped (i.e., wider than deep; Currie, 1995); whereas in OMNH 50268 the condyle is as deep as it is wide (Fig. 7). The foramen magnum, on the other hand, is deeper than it is wide in *Dromaeosaurus* (cf. Currie, 1995, fig. 4C), but is wider than it is deep in OMNH 50268 (Fig. 7).

Three foramina, forming the points of a triangle on the posterior surface of the occiput lateral to the occipital condyle, pierce the exoccipital as in *Dromaeosaurus* (cf. Currie, 1995, fig. 4C) and *Troodon* (Fig. 7; cf. Currie and Zhao, 1993, fig. 1D). These foramina are presumably passages for branches of cranial nerves X, XI, and XII (Currie and Zhao, 1993; Currie, 1995). A proximal foramen for cranial nerve XII is visible along the floor of the foramen magnum immediately anterior to the occipital condyle. But a second opening, as reported in *Dromaeosaurus* by Currie (1995), is not readily apparent, though it could be obscured by matrix along the exoccipital-basioccipital suture. Regardless of where it originates, the distal foramen for the first branch of cranial nerve XII is smaller and located ventrally to that of the second branch on the posterior surface of the skull, as in *Dromaeosaurus* (Currie, 1995). About 5 mm dorsal to the proximal opening for cranial nerve XII is an endolymphatic foramen similar to those in *Dromaeosaurus* (Currie, 1995) and *Troodon* (Currie and Zhao, 1993). Anterior to the proximal foramen for cranial nerve XII, along the posteroventral wall of the metotic fissure as in *Dromaeosaurus* (Currie, 1995), is a larger foramen for cranial nerves X and XI. As in *Dromaeosaurus* (Currie, 1995), cranial nerves X and XI pass posteroventrally through this foramen to exit the skull lateral to the foramina of cranial nerve XII.

Most of the basal tubera below the occipital condyle has been destroyed by erosion in OMNH 50268. What remains, however, indicates that ventrally the basal tubera forms the posterior wall of the basisphenoidal recess, as in *Dromaeosaurus* and other theropods (Fig. 7) (Currie, 1995). As suggested for *Dromaeosaurus* by Currie (1995), there are two posterolateral pits (separated by a medium septum) in the roof of the basisphenoidal recess that are bounded posteriorly by the basioccipital. Moreover, along the lateral margin of the basal tubera, the combined exoccipital-opisthotic bones send down a metotic strut, as in *Dromaeosaurus* and other advanced theropods and birds (Witmer, 1990; Currie, 1995), to form the posterior margin of the metotic fissure (Fig. 7). This strut only recently has been reported in *Deinonychus* from the Cloverly Formation (Witmer and Maxwell, 1996). Little bone remains anterior to this level in OMNH 50268, though the partial right prootic also found at V706 fits onto the occiput and confirms the presence of a dorsal tympanic recess in this specimen (L. M. Witmer, personal communication, 1997).

Sacrum

Although it was difficult to decipher because of its incompleteness, Ostrom (1976a) concluded that the only available sacrum of *Deinonychus* (that of MCZ 4371) consisted of five fused vertebrae. In OMNH 50268, most of what is probably the fifth or last sacral vertebra is preserved (Fig. 8). This vertebra is missing its neural spine, much of its anterior surface, and most of its right sacral rib,
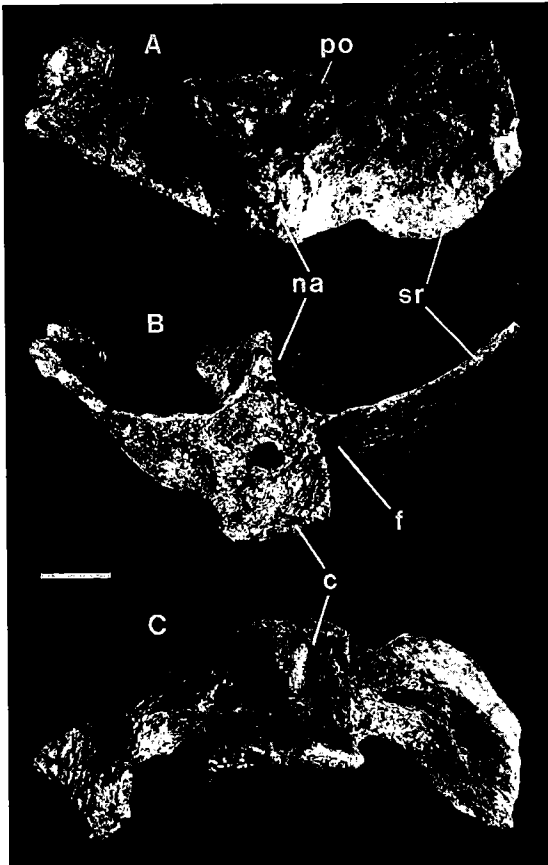
Figure 8. Fifth sacral vertebra of OMNH 50268 in (A) dorsal, (B) anterior, and (C) ventral views. Abbreviations: c = centrum, f = fossa, na = neural arch, po = postzygapophysis, sr = sacral rib. Scale bar = 10 mm.

perhaps due to erosion. Alternatively, the missing bone anteriorly, as well as the missing neural spine, may be indirect evidence of fusion between the fourth and fifth sacrals in OMNH 50268. If so, this might suggest that the animal, though still immature in other features, was a subadult approaching maturity at the time of its death, and that the average adult body size of the Oklahoma *Deinonychus* population was smaller than that of the Cloverly population.

With a fore–aft ventral length of 22.5 mm, the sacral centrum of OMNH 50268 is shorter than the preserved portion of its neural arch. The centrum is weakly opisthocoelous with roughly rectangular-shaped articular faces. The ventral edges of the anterior and posterior ends are slightly concave along the mid-line (Fig. 8). The centrum of OMNH 50268 has unequally expanded articular ends, being wider and deeper posteriorly than anteriorly. Thus, it tapers slightly anteriorly as seen in ventral

view (Fig. 8) and slopes posteroventrally with a slightly concave outline in lateral view. The posterior articular face is slightly concave, slopes craniodorsally, and is covered by smooth, finished bone, thus indicating that it was not fused to the vertebra behind it. Unfortunately, only the ventral edge of the anterior articular surface is preserved in OMNH 50268 (Fig. 8), with the rest presumably either fused to the missing fourth sacral or eroded away. A faint suture line is still visible between the centrum and neural arch on this roughened anterior surface, thereby indicating that complete fusion of these elements had yet to occur in this individual.

Caudally, the neural arch in OMNH 50268 is similar to the fifth sacral of *Coelophysis* (cf. Colbert, 1989, fig. 56) in having well-developed postzygapophyses with a strong medial embayment between them (Fig. 8). In OMNH 50268, the postzygopophyseal articular facets are roughly oval shaped and angled ventromedially at approximately 45°. Thus, the posterior portion of the neural arch of OMNH 50268, as well as the shape of its centrum, resembles those of the proximal caudal vertebrae (cf. Ostrom, 1969b, fig. 38) from which it was presumably derived (Madsen, 1976). In the terminology of Welles (1984), the fifth sacral of *Deinonychus* is a caudosacral.

As in the fifth sacral vertebra of *Allosaurus* (Madsen, 1976), no distinction can be made between the diaphysis and sacral rib in OMNH 50268 (Fig. 8). However, unlike the condition in *Allosaurus*, where the lateral projection arises almost exclusively from the neural arch (cf. Madsen, 1976, pl. 27), in OMNH 50268 most of the sacral rib arises from the side of the centrum (Fig. 8). The sacral rib is a broad, paddle-shaped plate of bone that sweeps caudodorsally. Proximoventrally, it bears a relatively large but shallow, anteroventrally facing fossa that presumably nestled the fourth sacral rib (Fig. 8). In this condition, *Deinonychus* may be similar to *Coelophysis* (cf. Colbert, 1989, fig. 56). But, unlike the condition illustrated for *Coelophysis* (cf. Colbert, 1989, fig. 75), no evidence exists in OMNH 50268 that the lateral margin of the sacral rib contacted the ilium. However, contact with the ilium by the fifth sacral rib might be a growth character linked to increasing coossification of the sacrum with age. According to Ostrom (1969b) the ventral portion of the medial surface of the ilium of AMNH 3015, one of the smallest specimens of *Deinonychus* from the Cloverly Formation, bore the attachment scars for only three sacral ribs, and that there was probably at least a fourth sacral vertebra that did not contact the ilium. Moreover, ankylosis of the sacral complex, or rather lack thereof, has been suggested to be a sexually dimorphic character in *Allosaurus* (Madsen, 1976) and *Coelophysis* (Colbert, 1989), with presumably less ankylosis in the sacrum of reproductive-age females due to the effects of relaxin-like hormones (Madsen, 1976).
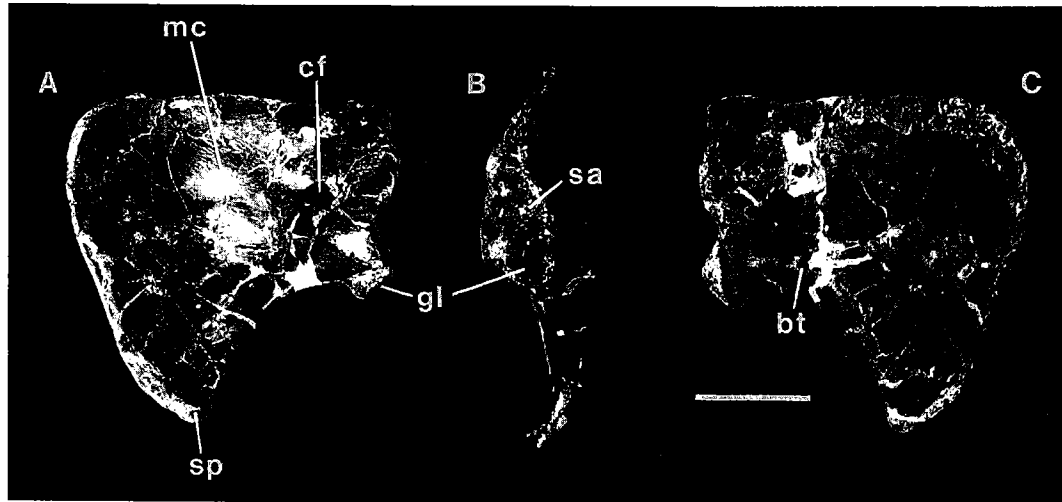
Figure 9. Right coracoid of OMNH 50268 in (A) medial, (B) dorsal, and (C) lateral views. Abbreviations: bt = biceps tubercle, cf = supracoracoid foramen, gl = glenoid, mc = medial concavity, sa = scapular articulation. Scale bar = 20 mm.

APPENDICULAR SKELETON

Coracoid

The right coracoid of OMNH 50268 is similar to YPM 5236, a specimen from the Cloverly Formation described by Ostrom (1974), but differs from the Yale specimen (1) in size (Table 1) and in the shape of its supracoracoid foramen; (2) in the development of its biceps tubercle, sternal process, and glenoid; (3) in the relative thickness of its continuously rounded cranial and ventral borders; and (4) in the development of its medial concavity (Fig. 9). The smaller Oklahoma specimen has a rounder and less dorsoventrally elongated supracoracoid foramen, a less-prominent biceps tubercle laterally, a less strongly hooked sternal process caudoventrally, and a less-flared glenoid lip caudodorsally (Fig. 9; cf. Ostrom, 1974, fig. 1). Moreover, OMNH 50268 has a more rugose, lateral lip built up along its cranial and ventral borders, and the medial concavity beneath its biceps tubercle is less sharply defined, with less-developed bony struts cranially and caudally (Fig. 9). Ventrally, in both coracoids, this medial concavity was either floored by extremely thin bone (now lost) or was fenestrated (Ostrom, 1974).

Unlike YPM 5236, the entire scapular border is preserved in OMNH 50268. The craniodorsal corner of this bone is thin initially but dramatically thickens caudally, starting about one third of the distance to the glenoid, thereby forming a wide, wedge-shaped articular surface for the scapula (Fig. 9). This articular surface is less digitate in OMNH 50268 than it is in the larger YPM 5236. In modern crocodilians, the degree of digitation at this suture increases ontogenetically, with the contact surfaces of immature individuals being relatively smooth and those of mature individuals be-

ing extremely rugose (Brochu, 1995). There is thus basis for interpreting the differences between the fossil coracoids as ontogenetic.

Humerus

Although crushed anteroposteriorly at its distal end and missing much of its proximal end including the head and internal tuberosity, what remains of the right humerus of OMNH 50268 (Fig. 10) compares well with Ostrom's (1969b) reconstruction for AMNH 3015 from the Cloverly Formation. In OMNH 50268, the distal condyles and the inferior half of the deltopectoral crest (including the broad ridge noted by Ostrom along the distal margin of the crest) are preserved as in the Cloverly specimen, as is the entepicondyle (Fig. 10; cf. Ostrom, 1969b, figs. 55, 56). In both specimens, the distal half of the shaft is essentially straight in lateral view. However, OMNH 50268 differs from Ostrom's (1969b) reconstruction of AMNH 3015 in being laterally less bowed in anterior view and in having a transversely narrower deltopectoral crest (Fig. 10).

Manus

Anatomically, the manual elements of OMNH 50268 compare very well with those of *D. antirrhopus* from the Cloverly Formation. However, slight, presumably ontogenetic or individual differences exist in many of the bones' proportions (Table 1). In addition, the fossae for the collateral ligaments in the manual elements of OMNH 50268 tend to be smaller and shallower than those in the Cloverly sample. Moreover, some of the manual elements from the Cloverly Formation have well-developed accessory processes (e.g., the "proximolateral process" of the left phalanx III-2 of YPM 5206) that are only slightly developed in OMNH
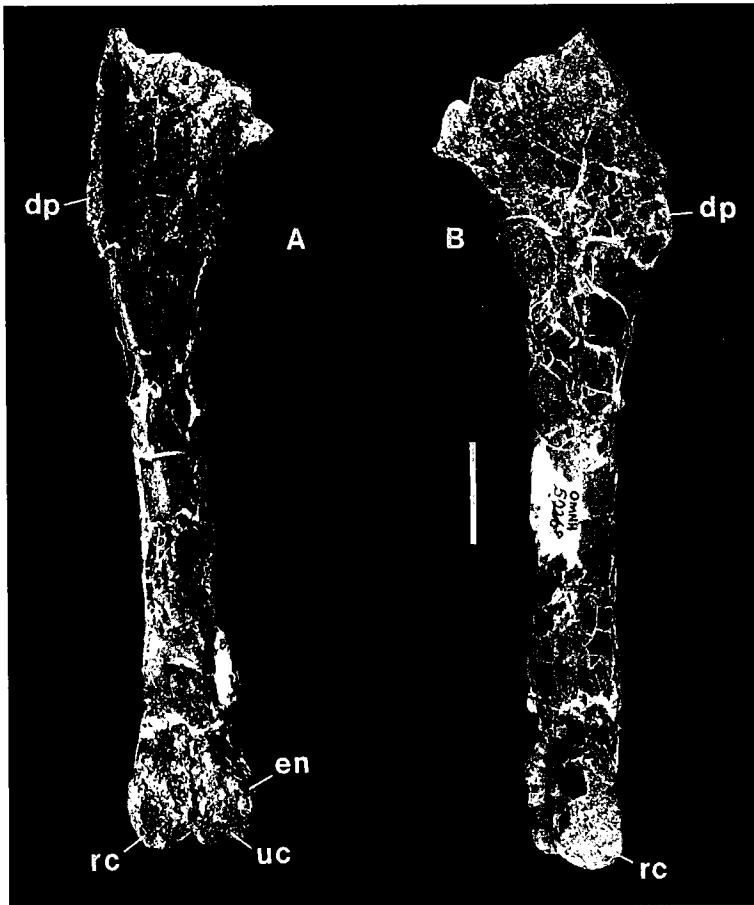
Figure 10. Right humerus of OMNH 50268 in (A) anteromedial and (B) lateral views. Abbreviations: dp = deltopectoral crest, en = entepicondyle, rc = radial condyle, uc = ulnar condyle. Scale bar = 20 mm.

from the Cloverly Formation. The entire femoral head, most of the greater trochanter, and much of the shaft are preserved in OMNH 50268, as is a hint of the "posterior trochanter" (Fig. 12; cf. Ostrom, 1976a, fig. 3). The femoral head is rounded and has a well-developed ligament fossa posteriorly with a distinct inferior lip. The femoral head projects caudomedially from the shaft at approximately 100° as in MCZ 4371 (Fig. 12) (Ostrom, 1976a). The femur of OMNH 50268 is, however, more cranially bowed than that of MCZ 4371 (Fig. 12; cf. Ostrom, 1976a, fig. 3).

Pes

The pedal elements of OMNH 50268 are likewise very similar to those from the Cloverly Formation, though smaller (Table 1). As with the manus, there are probable ontogenetic differences in the proportions of some of the bones, in the development of the various processes, and in the development of the collateral ligament fossae. Most of the specimens from the Cloverly Formation have more substantial bony processes and deeper, better-developed collateral ligament fossae distally. The most diagnostic pedal elements are the right phalanges II-2 and II-3. The penultimate phalanx (II-2) of OMNH 50268 is nearly identical to that of

50268. Perhaps the most distinctive manual element preserved for OMNH 50268 is the left phalanx I-2 (Fig. 11). Although the proximal articular surface of this ungual is missing, what remains is nearly identical to that of YPM 5206. Each has a well-developed flexor tubercle proximoventrally and is strongly recurved with similar claw geometries (Fig. 11; cf. Ostrom, 1969a, fig. 5). However, the manual ungual of OMNH 50268 is more gracile for its entire length than that of YPM 5206 (Table 1), has a slightly greater anterior bulge to its flexor tubercle, and has a more strongly recurved ventral margin than the specimen from the Cloverly Formation (Fig. 11).

Femur

The right femur of OMNH 50268 has been crushed mediolaterally and bowed medially along its mid-shaft and is missing its distal condyles and the tip of the lesser trochanter (Fig. 12). What remains, however, compares well with Ostrom's (1976a) reconstruction for the femur of MCZ 4371
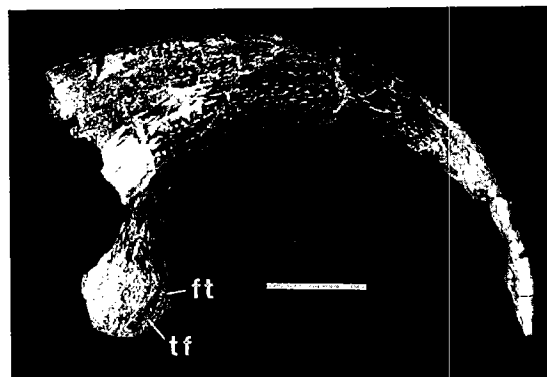

Figure 11. Left manual phalanx I-2 of OMNH 50268 in medial view. Abbreviations: ft = flexor tubercle, tf = tendon fossa. Scale bar = 10 mm.
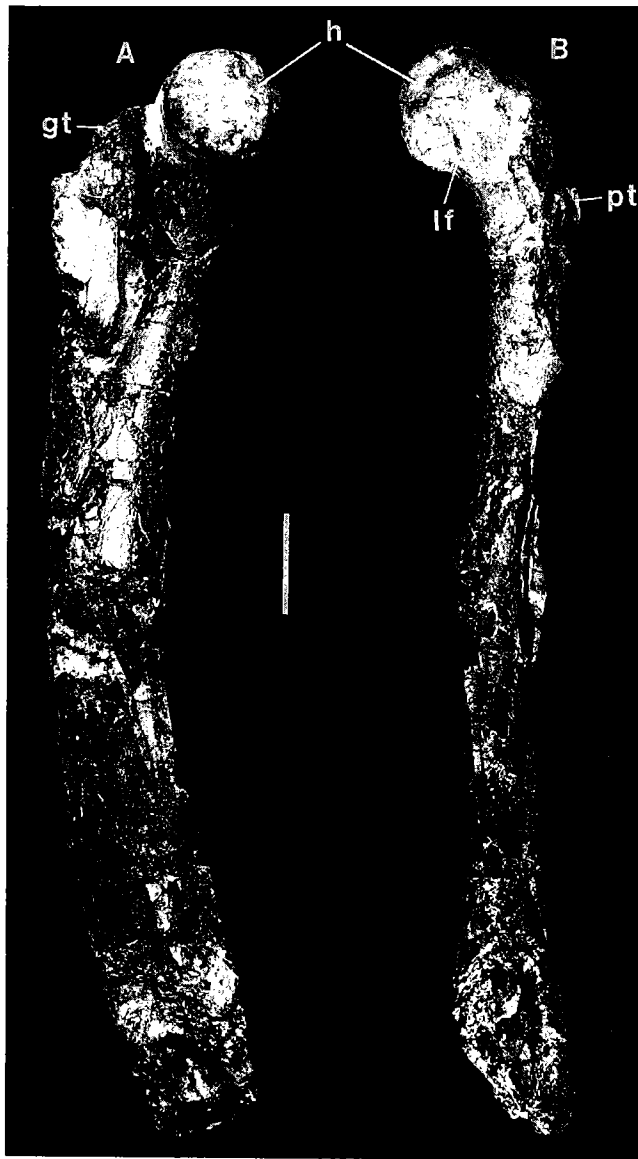
Figure 12. Right femur of OMNH 50268 in (A) medial and (B) posterior views. Abbreviations: gt = greater trochanter, h = head, lf = ligament fossa, pt = "posterior trochanter." Scale bar = 20 mm.

pedal digit II, noting that its proximal and distal interphalangeal joints (of which the proximal and distal ends of II-2 are parts) allowed only extension and flexion, respectively.

Part of the left and most of the right pedal unguals II-3 are preserved in OMNH 50268 (Fig. 14). Unfortunately, their distal ends are either damaged or missing entirely. The two sides differ in that the flexor tubercle of the right ungual bulges slightly more anteriorly than does the left. Perhaps this individual was "right footed," favoring its somewhat more developed right ungual when attacking. The right pedal ungual II-3 of OMNH 50268 is similar to manual ungual I-2 of the same specimen in overall shape and in missing at least some of its proximal articular surface due to erosion (Figs. 11, 14). The pedal ungual of OMNH 50268, however, differs from the manual ungual in being more robust for nearly its entire length, less recurved with a less well-developed flexor tubercle, and in having a better developed tendon pit on the lateral surface of the flexor tubercle (Figs. 11, 14). Kirkland and others (1993) were the first to point out this last distinction in the unguals of both Deinonychus and Utahraptor. However, contra Kirkland and others (1993), the manual unguals I-2 of the Deinonychus specimens from both the Antlers and Cloverly Formations have similar, but shallower and more rugose, tendon fossae anteroventrally on both sides of their flexor tubercles (Fig. 11).

Anatomically, the right pedal ungual II-3 of OMNH 50268 is similar to those of YPM 5205 (cf. Ostrom, 1969a, fig. 2) and MCZ 4371 (cf. Ostrom, 1976a, fig. 7), though it is considerably smaller than both (Table 1; Fig. 14). Ostrom (1976a) noted that the two specimens from the Cloverly Formation had different claw geometries, with the ungual in MCZ 4371 being less strongly curved than that in YPM 5205. Ostrom (1976a) suggested that these different claw geometries could be due to either individual, ontogenetic, or sexual variation. However, because both

YPM 5205, the holotype of D. antirrhopus (Fig. 13; cf. Ostrom, 1969a, fig. 3). Both have a well-developed proximoventral projection or "heel" inferior to the proximal articular facet, and a large and deeply grooved distal articular facet with an unusually large radius of curvature (Fig. 13). However, the smaller Oklahoma specimen differs from YPM 5205 in having less flared proximal and distal ends and in having a relatively more robust shaft (Fig. 13). Ostrom (1969b) attributed a highly specialized, non-weight-bearing, predatory function to

the right and left pedal phalanges II-3 of OMNH 50268 have claw geometries more similar to those in MCZ 4371 than those of YPM 5205, a fourth possibility (chronologic variation) is opened up, with the claws becoming more strongly curved through time. According to Ostrom (1976a), MCZ 4371 was collected from the upper part of Unit V of the Cloverly Formation, whereas YPM 5205 was collected from the lower part of Unit VII (Ostrom, 1970a). As noted earlier, OMNH 50268 most likely was collected from the middle part of the Antlers
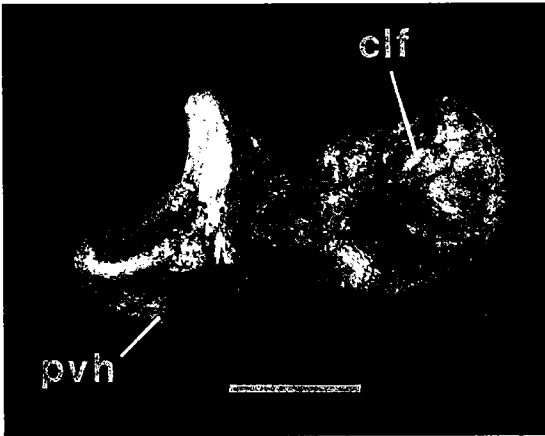
Figure 13. Right pedal phalanx II-2 of OMNH 50268 in lateral view. Abbreviations: clf = collateral ligament fossa, pvh = proximoventral "heel." Scale bar = 10 mm.

Figure 14. Right pedal phalanx II-3 of OMNH 50268 in lateral view. Abbreviations: ft = flexor tubercle, tp = tendon pit. Scale bar = 10 mm.

Formation. Thus, if the middle Antlers Formation is approximately the same age as Unit V of the Cloverly Formation, or if the middle Antlers Formation is older, as its tenontosaur fossils might imply (see below), then we would expect OMNH 50268 to be more similar to specimens from Unit V of the Cloverly Formation than to those from the geologically younger Unit VII (as is the case with pedal ungual II-3).

DISCUSSION

Although OMNH 50268 differs from specimens of *D. antirrhopus* from the Cloverly Formation, ex-

isting evidence suggests that these differences are probably ontogenetic rather than phylogenetic. In addition to their smaller sizes, at least some of the skeletal elements of the Oklahoma specimen (such as the occiput, coracoid, and phalanges) bear evidence of belonging to an immature individual. On this basis, we refer OMNH 50268 to *D. antirrhopus*.

The presence of the same, relatively rare theropod species in both the Antlers and Cloverly Formations raises some interesting Early Cretaceous biostratigraphic and biogeographic issues. Contrary to some published reports (e.g., Clemens and others, 1979; Kielan-Jaworowska, 1982; Jenkins and Schaff, 1988; Winkler and others, 1989; Pomes, 1990; Krause and others, 1990), major epicontinental seaways did not separate North America into eastern and western subcontinents, thus disrupting continuity of terrestrial faunas for appreciable periods of time, until later in the Cretaceous (Jacobs and others, 1991; Steidtmann, 1993). Hence, assessment of the temporal relationships of the Antlers and Cloverly Formations is of great interest in evaluating chronologically and geographically related differences in the Early Cretaceous terrestrial biota of North America.

As mentioned earlier, the Antlers Formation is laterally equivalent to the Trinity Group in Texas. In ascending order, the Trinity Group consists of the Twin Mountains, Glen Rose (which pinches out to the north and west), and Paluxy Formations (Winkler and others, 1989). Northward and westward, beyond the pinch-out of the Glen Rose Formation in north-central Texas, the Twin Mountains and Paluxy Formations merge to become the undifferentiated Antlers Formation, which continues into Oklahoma (Fisher and Rodda, 1966) and beyond (Darling and Lock, 1984). The age of the Trinity Group mammal fauna, which is constrained through correlation of marine invertebrate fossils, has been interpolated to be between 111 and 105 Ma (Jacobs and others, 1991). However, the lowest occurrence of Trinity mammals in Texas is from the Paluxy Church locality in the upper Twin Mountains Formation (Jacobs and others, 1991). Consequently, the age for the basal Trinity Group is probably considerably older than the 111 Ma estimate for the Trinity mammals from Paluxy Church. Thus, the Trinity Group likely extends from the late Aptian to the middle Albian. Gradstein and others (1995) placed the Aptian-Albian boundary at 112.2 ± 1.1 Ma.

Although some workers argue for an Aptian or older age for the Cloverly Formation (Peck and Craig, 1962; Winslow and Heller, 1987; Heller and Paola, 1989; Kvale and Vondra, 1993), others believe that the formation probably extends into at least the early Albian (Ostrom, 1970a; Schwab, 1977; Forster, 1984; Douglass and Johnson, 1984; Scott, 1987). The minimum age of the Cloverly Formation is constrained by the overlying Thermopolis Shale (Ostrom, 1970a; Steidtmann, 1993),

which contains middle late Albian marine invertebrates (Kauffman, 1984), estimated by Jacobs and others (1991) at 100 Ma. Thus, the fauna of the Cloverly Formation could be as much as 5 Ma younger than that of the Trinity Group, but a similar age is not precluded by available constraints (Jacobs and others, 1991). Hence, both units are considered here to be of Aptian-Albian age.

Paradoxically, although reasonably well-represented vertebrate faunas are known from both the Antlers (and its lateral equivalent in Texas, the Trinity Group) and the Cloverly Formations, the faunas are not entirely comparable. The assemblage from the Cloverly Formation is represented mainly by dinosaurs which, thanks to the works of Ostrom (1969a,b; 1970a; 1974; 1976a) and Sues (1980), are known in great detail. In contrast, only four dinosaur taxa (*Acrocanthosaurus*, *Tenontosaurus*, a possible brachiosaurid, and an indeterminate sauropod), and several undescribed small theropod tooth morphotypes, previously have been reported from the Antlers Formation of Oklahoma (Larkin, 1910; Stovall and Langston, 1950; Langston, 1974; Cifelli and others, 1997). Furthermore, an undescribed ornithomimid has been reported from the Antlers Formation of Arkansas (Quinn, 1973; Langston, 1974). Although a diverse vertebrate fauna rich in microvertebrates has been reported from the Trinity Group of Texas (Langston, 1974; Thurmond, 1974; Winkler and others, 1990) as well as from the Antlers Formation of Oklahoma (Cifelli, 1997; Cifelli and others, 1997), and work in progress by ourselves and others promises to add a wealth of primarily microvertebrate taxa to the faunas of both the Antlers and Cloverly Formations, more thorough analyses are necessary to fully understand the biostratigraphic and biogeographic issues raised by these Early Cretaceous faunas.

The first detailed comparison of Early Cretaceous terrestrial vertebrate faunas was presented by Ostrom (1970a), who noted the presence in both the Cloverly Formation and the Trinity Group of the aberrant, pustulate-shelled chelonian, *Naomichelys*, and (based on preliminary study of an unpublished specimen from Oklahoma) the ornithopod *Tenontosaurus tilletti*. However, in correlating the Cloverly Formation with the Trinity Group, Ostrom (1970a) noted that the Glen Rose Formation might be younger than the middle or lower Cloverly Formation. Moreover, vertebrate assemblages collected by the OMNH from the Kaiparowits Plateau, a remarkably thick, continuous sequence of Cretaceous rocks in southern Utah (Eaton and Cifelli, 1988), indicate that *Naomichelys*, first described from the Cloverly Formation (Hay, 1908), actually has a much broader stratigraphic distribution than previously appreciated. This genus is present in the Dakota, Straight Cliffs, and Wahweap Formations, and thus is known from the Aptian-Albian through the lower Campanian. In addition, the lungfish *Ceratodus* is

known from both the Cloverly and Trinity faunas; however, this genus is widely ranging and is represented by different morphospecies in the two faunas (Kirkland, 1987). Triconodontid mammals also are known from both the Cloverly Formation (represented by an undescribed species; Jenkins and Crompton, 1979) and the Trinity Group (*Astroconodon denisoni*; Patterson, 1951; Slaughter, 1969). Jacobs and others (1991) suggested that the taxon from the Trinity Group, *A. denisoni*, may be the more primitive (and hence possibly the older) of the two because one of the cusps on its lower molar is lower crowned. Such data must be interpreted cautiously, however, because *A. denisoni* might, on the same basis, be considered contemporaneous with *Priacodon ferox*, from the Upper Jurassic Morrison Formation (cf. Jacobs and others, 1991, fig. 4). Work in progress by one of us (RLC) suggests that the taxon from the Cloverly Formation is quite distinct from *A. denisoni*, to which it may or may not be closely related.

In terms of dinosaurs, two morphospecies of *Tenontosaurus* have been recognized provisionally in the Trinity Group of Texas: *T. dossi*, from the Twin Mountains Formation (Winkler and others, 1997), and *T. tilletti* (first described from the Cloverly Formation; Ostrom, 1970a) from the Glen Rose, Paluxy, and "upper" Antlers Formations (Jacobs, 1995; J. P. Diffily, personal communication, 1995; Winkler and others, 1997). The latter is equivalent to the Paluxy Formation beyond the pinch-out of the Glen Rose Formation. *T. dossi* appears to be more primitive in some respects (e.g., in retaining teeth in its premaxillae; Winkler and others, 1997) than *T. tilletti*, suggesting the possibility of a correlation between the upper Trinity Group and the Cloverly Formation. Moreover, preliminary results of work in progress by one of us (DLB) suggests that the tenontosaur specimen from the Glen Rose Formation (Fort Worth Museum of Science and History [FWMSH] 93B-3; J. P. Diffily, personal communication, 1995) may be conspecific with those from OMNH Locality V706 and several other localities in the Antlers Formation of Oklahoma. These specimens may be, in some respects, morphologically intermediate between *T. dossi* (from the upper Twin Mountains Formation) and *T. tilletti*, as represented by materials from the Cloverly Formation.

The tenontosaurs associated with OMNH 50268, and possibly conspecific with FWMSH 93B-3 from the Glen Rose Formation of Texas, are from a locality interpreted to be in the middle part of the Antlers Formation. A recent isotopic analysis by Rennison (1996) suggests a possible correlation between the lower to middle portion of the Antlers Formation and the lower to middle portion of the Glen Rose Formation. Thus, the middle Antlers Formation may be temporally equivalent to the marine and marginal marine Glen Rose Formation farther to the south. As such, the middle part of the Antlers Formation presum-

ably would be dated as late Aptian through late early Albian like the Glen Rose Formation (Jacobs and others, 1989).

With regard to *Deinonychus*, we have noted the detailed similarities of OMNH 50268 to *D. antirrhopus* from the Cloverly Formation, leading us to refer the Oklahoma specimen to that species. As mentioned, however, it is possible that chronologic variation in pedal claw morphology existed in this species, and, in this respect, OMNH 50268 more closely resembles the specimen from Unit V of the Cloverly Formation than it does those from the geologically younger Unit VII. Furthermore, it is possible that a chronologic increase in average tooth size occurred in Aptian-Albian–aged dromaeosaurids from the western United States, with the Oklahoma teeth being intermediate in size and, thus, possibly, in geologic age as well.

To summarize, constraints imposed by marine invertebrates suggest that both the Antlers and Cloverly Formations are probably penecontemporaneous and that they are most likely of Aptian-Albian age. However, existing evidence based on contained vertebrate faunas is insufficient to conclusively establish detailed age relationships between the two units. Based on somewhat equivocal data provided by the triconodontid mammals and on the evidence provided by the dinosaurs *Tenontosaurus* and *Deinonychus*, we tentatively concur with Jacobs and others (1991) in suspecting that the Trinity Group (and the Antlers Formation of Oklahoma) may be older, at least in part, than the Cloverly Formation, and that there is no reason for believing that the reverse is the case, as has been suggested by Ostrom (1970a) and Clemens and others (1979).

Deinonychus and *Tenontosaurus* are among the most conspicuous and characteristic elements of the Cloverly and Trinity (including the Antlers Formation) faunas. The latter taxon is especially abundant and may become useful as an index fossil when its spatial and temporal distributions are better understood. Both taxa have been reported recently from the middle (not upper, as stated by Lucas, 1993) Cedar Mountain Formation of Utah (Pomes, 1988 [and papers cited therein]; Kirkland, 1992, 1996; Kirkland and Parrish, 1995), as well as possibly from the Arundel Clay facies of the Potomac Group of Maryland (Galton and Jensen, 1979; Weishampel and Young, 1996; T. R. Lipka, personal communication, 1997). The middle Cedar Mountain Formation thus has been assigned an Aptian-Albian age by Kirkland and his co-workers based on its Cloverly-like fauna. Lucas (1993) established a "Cashenranchian land-vertebrate 'age'" for the above faunal association, based on the vertebrate assemblage from the Cashen Ranch, Cloverly Formation, Montana, and considered the faunas of the "upper" Cedar Mountain Formation, Utah, and the Arundel Clay of the Potomac Group, Maryland, among others, to belong to it. However, direct correlation of these faunas is problematic.

For example, preliminary work on the purported specimens of *Tenontosaurus* from the middle Cedar Mountain Formation by R. D. Scheetz (personal communication, 1996) suggests that these specimens are somewhat morphologically intermediate between *T. tilletti* from the Cloverly Formation and an unnamed hypsilophodontid (aff. *Hypsilophodon* sp.; Winkler and others, 1988) from the lower Twin Mountains Formation of Texas, and, thus, appear less derived than *Tenontosaurus*. This somewhat less-derived ornithopod from Utah may be indicative of a slightly older faunal "age" for the middle Cedar Mountain Formation than that for the Cloverly Formation.

The presence of *Tenontosaurus* in the Arundel Clay is likewise problematic. Galton and Jensen (1979) assigned a partial dentary tooth (United States National Museum [USNM] 244564) from the Arundel Clay to ?*Tenontosaurus* sp., noting that it differs from the dentary teeth of *Tenontosaurus* in lacking secondary vertical ridges inferiorly on its crown and in being slightly concave along the base of its single prominent vertical ridge. In these features, as well as in having its single vertical ridge slightly more anterior to the mid-line than in most tenontosaur dentary teeth, USNM 244564 (see Galton and Jensen, 1979, figs. 2H,2I) closely resembles USNM 337977, a smaller, nearly complete ornithischian tooth also from the Arundel Clay. But with a maximum fore–aft crown length of 8.4 mm, USNM 337977 is about half the size of USNM 244564. Variously regarded as either a dryosaur, juvenile tenontosaur, or ceratopsian (Kranz, 1996; Weishampel and Young, 1996), USNM 337977 recently has been given the informal name of "*Magulodon muirkirkensis*" by its discoverer (Kranz, 1996). Although we cannot identify confidently the dinosaur taxon (or taxa) to which these two teeth belong, we can eliminate confidently *Tenontosaurus* from the list of possible taxa for at least USNM 337977. In addition to lacking secondary vertical ridges that extend nearly the entire length of its crown and in not having a convex base to its more anteriorly placed primary vertical ridge, USNM 337977 differs from the teeth of juvenile tenontosaurs in having a relatively taller and narrower crown with smaller marginal serrations inferiorly and larger, more strongly ribbed serrations superiorly on its crown. But, again, none of these ribs extend far enough down the crown to become secondary vertical ridges inferiorly. Moreover, USNM 337977 differs from most tenontosaur dentary teeth in having a slightly taller anterodorsal than posterodorsal margin to its crown. In this regard and in being concave along the base of its primary ridge, USNM 337977 is more similar to a mid-dentary tooth of SMU 70456 (cf. Winkler and others, 1988, fig. 10), a specimen of the unnamed hypsilophodontid from the lower Twin Mountains Formation of Texas, than it is to the dentary

teeth of *Tenontosaurus*. However, USNM 337977 differs from SMU 70456 in having a relatively taller and narrower crown, greater ribbing of its superior serrations, relatively smaller inferior serrations, and a more anteriorly positioned primary ridge. Thus, it may not be closely related to this hypsilophodontid either, though it probably is the tooth of an ornithopod and not that of a ceratopsian. However, Chinnery and others (1998) concluded that USNM 337977 and a second similar but less worn or damaged tooth also from the Arundel Clay are from an indeterminate neoceratopsian.

Although *Tenontosaurus* has yet to be demonstrated conclusively as being present in the Arundel Clay, there is, at least superficially, a striking similarity between much of the rest of the Arundel dinosaur fauna and those from the Cloverly Formation and the Trinity Group (including the Antlers Formation of Oklahoma and Arkansas) (Ostrom, 1970a). Each fauna supposedly contains an *Astrodon*-like sauropod (Ostrom, 1970a; Langston, 1974; Winkler and others, 1990; Weishampel and Young, 1996), an *Acrocanthosaurus*-like large theropod (Langston, 1974; Jacobs, 1995; C. L. Chandler, personal communication, 1997; T. R. Lipka, personal communication, 1997), at least one species of ornithomimid (Ostrom, 1970a; Quinn, 1973; Langston, 1974; Weishampel and Young, 1996), and a *Deinonychus*-like small theropod (Ostrom, 1969a,b; 1970a; Thurmond, 1974; Winkler and others, 1988; Gallup, 1989; Jacobs, 1995; T. R. Lipka, personal communication, 1997). However, much work remains to be done to determine the true affinities of specimens referred to or compared with the taxa listed above. Like the purported specimens of *Tenontosaurus*, it is possible that close inspection of these specimens will fail to support most of their tentative taxonomic assignments. Thus, except possibly for some teeth (Ostrom, 1970a; Langston, 1974; Winkler and others, 1990) and caudal vertebrae (Langston, 1974) of the sauropod *Astrodon* (= *Pleurocoelus*; Hatcher, 1903; Gilmore, 1921; Weishampel and Young, 1996) and some teeth probably attributable to *Deinonychus* (T. R. Lipka, personal communication, 1997), the Arundel Clay shares no unambiguous, biostratigraphically useful lower-level taxa with either the Cloverly Formation or Trinity Group. Furthermore, as stated by Lipka (1996), its contained vertebrate fossils are exceedingly fragmentary and difficult to interpret. Excellent reviews of this issue have been presented by Ostrom (1970a) and Langston (1974) and need not be repeated here. Therefore, pending full publication of the specimens from Utah and Maryland and, more importantly, recovery of a more continuous sequence of terrestrial vertebrate faunas from the Lower and middle Cretaceous, we are skeptical as to the utility of the "Cashenranchian land-vertebrate 'age.'" We also point out that this "age" is probably synonymous with previously defined (and likewise poorly founded) "ages" for the fauna of the Trinity Group, including the Paluxian land-mammal age (Russell, 1975) and the Trinitian North American marine vertebrate age (Russell, 1988; see discussions by Lillegraven and McKenna, 1986; and Jacobs and others, 1991).

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Note: Asterisk (*) indicates cataloged specimen.