

THE FOSSIL RECORD OF PREDATION IN DINOSAURS

JAMES O. FARLOW¹ AND THOMAS R. HOLTZ, JR.²

¹Department of Geosciences, Indiana-Purdue University Fort Wayne,
2101 Coliseum Boulevard, East, Fort Wayne, Indiana 46805 USA

²Department of Geology, University of Maryland, College Park, Maryland 20742 USA

ABSTRACT—Predatory theropod dinosaurs can usually be identified as such by features of their jaws, teeth, and postcrania, but different clades of these reptiles differed in their adaptations for prey handling. Inferences about theropod diets and hunting behavior based on functional morphology are sometimes supported by evidence from taphonomic associations with likely prey species, bite marks, gut contents, coprolites, and trackways. Very large theropods like *Tyrannosaurus* are unlikely to have been pure hunters or scavengers, and probably ate whatever meat they could easily obtain, dead or alive. Theropods were not the only dinosaur hunters, though; other kinds of large reptiles undoubtedly fed on dinosaurs as well. The taxonomic composition of dinosaurian predator-prey complexes varies as a function of time and geography, but an ecologically remarkable feature of dinosaurian faunas, as compared with terrestrial mammalian faunas, is the very large size commonly attained by both herbivorous and carnivorous dinosaurs. The K/T extinction event(s) did not end dinosaurian predation, because carnivorous birds remained prominent predators throughout the Cenozoic Era

INTRODUCTION

CARNIVOROUS DINOSAURS (Fig. 1) included some of the biggest, most spectacular predators of all time, but also numbered in their ranks a diversity of smaller predators. In this paper we survey what is known about the diets of theropod dinosaurs, and briefly consider morphological differences among taxa that presumably affected the way they dealt with prey. We will also consider non-dinosaurian carnivores that likely fed upon dinosaurs. Finally, we will compare the taxonomic composition of herbivores and carnivores in different dinosaurian faunas, and examine some ecological questions posed by the huge body sizes attained by many predatory dinosaurs.

IDENTIFYING DINOSAURIAN PREDATORS AND PREY

Morphological features.—It is possible to identify most extinct tetrapods as herbivores or carnivores from skeletal morphology by judicious comparison with extant animals of known food

habits. Plant-eaters usually have dentitions suitable for shredding, crushing, slicing, or grinding their fodder (and patterns of tooth wear consistent with such oral processing), capacious guts for housing microbes that assist in breaking down plant fibers, and toes that terminate in blunt nails or hooves rather than claws (cf. Reisz and Sues, 2000). Carnivores, in contrast, have sharp teeth for ripping, cutting, or tearing flesh, narrower gut regions, and sharp claws for restraining and dispatching prey.

On the basis of such criteria, most ornithischians and sauropodomorphs are presumed to have been primarily herbivorous (Farlow, 1997; Ryan and Vickaryous, 1997; Sander, 1997; Upchurch and Barrett, 2000), although some taxa may have been more omnivorous (Barrett, 2000). Most adult theropods were probably vertebrate-eaters, but there are exceptions: therizinosaurs were probably plant-eaters (Russell, 2000), troodontids may have been omnivores (Holtz et al., 1998), and ornithomimids were likely filter-feeders that consumed aquatic plants and/or small invertebrates (Norell et al., 2001).

Even among those theropods that clearly were meat-eaters, there are major morphological

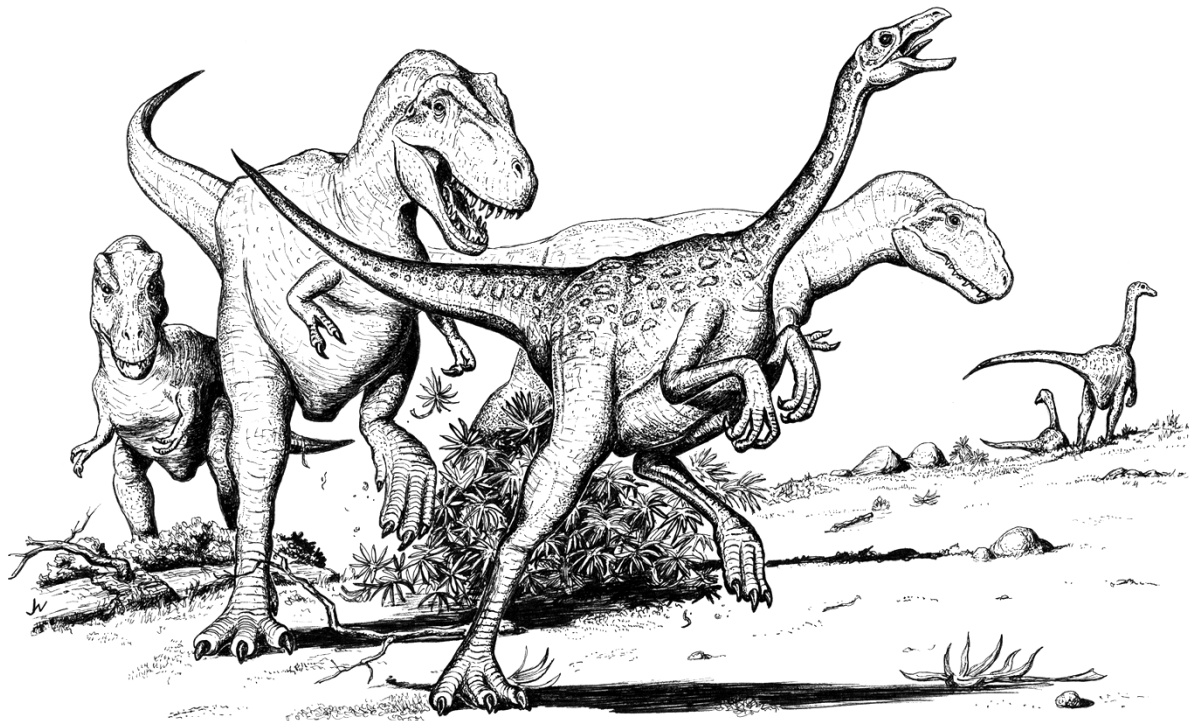


FIGURE 1—Dinosaurian predators and prey. A group of half-grown tyrannosaurids pursue an ornithomimid in the Late Cretaceous of western Canada. The inference that some tyrannosaurids may have lived in groups is drawn from an *Albertosaurus* bonebed (Eberth et al., 2001). Drawing by James Whitcraft.

differences among taxa that presumably reflect differences in attack and feeding behavior and/or diet. For example, the relatively long and narrow, lightly constructed skull and the laterally compressed teeth of *Allosaurus* and many other carnivorous dinosaurs (Rayfield et al., 2001) contrast markedly with the broader, massively constructed muzzle and very stout teeth of *Tyrannosaurus* (Farlow et al., 1991; Molnar, 2000) and its kin; and both morphologies differ greatly from the very long-snouted spinosaurs, whose conical teeth have unusually fine serrations, or lack them altogether (Charig and Milner, 1997; Naish et al., 2001).

Spinosaurids and the Triassic-Jurassic coelophysoids both demonstrate a curvature of the premaxillary-maxillary tooth row similar to that seen in some modern crocodylians; perhaps, as with these extant reptiles, this curvature represents a location in the snout for holding and manipulating smaller prey items or the extremities of larger prey.

Oviraptorosaurs lack teeth, but have strongly constructed skulls that could nonetheless have administered a wicked bite to small prey (Ryan and Vickaryous, 1997). Theropods are diagnosed by the possession of a specialized intramandibular joint between the dentary and postdentary bones (Bakker et al., 1988; Sereno and Novas, 1994; Sereno, 1999; Holtz, 2000). Although this adaptation has yet to be subjected to rigorous biomechanical analysis, it seems likely that it served in part as a “shock absorber” to deal with the forces generated by struggling live prey and/or the dismemberment of carcasses.

Predatory theropod clades differed in the extent to which the forelimbs and hindfoot were likely involved in capturing and killing prey. Theropods retained the ancestral dinosaurian condition of obligate bipedalism, and thus (unlike most other carnivorous reptiles and mammals) the forelimb was freed from the necessity of serving simultaneously

as an organ of locomotion and of prey capture. Basal carnivorous dinosaurs (Serenó, 1993) possessed long fingered hands with elongated penultimate phalanges, an adaptation associated with enhanced grasping ability (Hopson, 2001). Many lineages of theropods retained this condition, and in oviraptorosaur and dromaeosaurid maniraptorans the forelimbs were especially elongated (Middleton and Gatesy, 2000). In contrast, several groups of theropod carnivores reduced the size and/or grasping function of the hand, such as neoceratosaurs (Gilmore, 1920; Bonaparte et al., 1990) and tyrannosaurids (Carpenter and Smith, 2001).

Typical theropod feet have claws, which, while curved, do not have the trenchant shape of the manual talons. In ornithomimosaurs (which are unlikely to have preyed upon other dinosaurs), in fact, the pedal claws are relatively straight and more hoof-like. Several taxa of theropods, however, are characterized by a sickle-shaped ungual on a hyperextensible second digit. These include the dromaeosaurids (Ostrom, 1969), troodontids (Barsbold et al., 1987), the primitive bird *Rahonavis* (Forster et al., 1998), and the neoceratosaur *Noasaurus* (Bonaparte and Powell, 1980). As documented in a spectacularly preserved association (see below), this claw was used in at least some cases to pierce (and presumably rip out) the throat tissue of the victim.

Taphonomic occurrences.—The circumstances of preservation of dinosaur skeletons sometimes suggest predator-prey interactions. Shed theropod teeth are frequently found associated with single or multiple skeletons of herbivorous dinosaurs (Chin, 1997). Perhaps the most spectacular taphonomic association comprises interlocked specimens of a small theropod (*Velociraptor*) with a small ceratopsian (*Protoceratops*). In this assemblage, the sickle claw of the dromaeosaurid is positioned very close to the ventral surface of the cervical vertebrae of the herbivore, and thus would have been within the neck of the plant-eater during the final moments of both animals' lives (Carpenter, 2000).

Bite marks, gut contents, and coprolites.—Dietary inferences based on functional morphology can sometimes be corroborated by trace fossils. Tooth marks in bone indicate that theropods did indeed feed

upon herbivorous dinosaurs, and occasionally on each other (Hunt et al., 1994; Erickson and Olson, 1996; Jacobsen, 1997, 1998, 2001; Chure et al., 2000). A remarkable *Hypacrosaurus* leg bone even has a theropod tooth embedded within it (Fig. 2), as does a limb bone of an azhdarchid pterosaur (Currie and Jacobsen, 1995)!

Some theropod skeletons contain the bony remains of their prey. Specimens of compsognathids have been found with bones of lizards and endothermic vermin (otherwise known as Mesozoic mammals) inside them, indicating that these small theropods ate correspondingly small prey (Ostrom, 1978; Chen et al., 1998; Currie and Chen, 2001), unlike their portrayal in a recent multi-million-dollar motion picture. In contrast, a tyrannosaurid skeleton contained partially digested bones of juvenile hadrosaurids (Varricchio, 2001). The stomach region of a beautiful specimen of *Baryonyx* contained numerous fish scales and teeth (a diet consistent with the dinosaur's cranial anatomy), as well as bones of a young *Iguanodon* (Charig and Milner, 1997). On a grislier note, two individuals of *Coelophysis* contained the bones of what may be smaller individuals of their own species (Colbert, 1989).

Coprolites presumably made by herbivorous dinosaurs contain fragmented plant materials (Chin and Gill, 1996; Chin and Kirkland, 1998). In contrast, Chin et al. (1998) described a 44-cm long coprolite from the Maastrichtian Frenchman Formation that contained angular pieces of bone. The osteohistological texture of the bony inclusions suggests that the bone fragments came from a subadult ornithischian. Given the tremendous size of the coprolite, its most likely maker was *Tyrannosaurus* (or a very sick smaller theropod).

NON-DINOSAURIAN PREDATORS ON DINOSAURS

Dinosaurs originated in the Late Triassic (Heckert and Lucas, 1998; Hunt et al., 1998), and started out as modest-sized animals compared with many of their non-dinosaurian neighbors; it is very likely that Triassic dinosaurs frequently fell prey to (or were scavenged by) large phytosaurs and

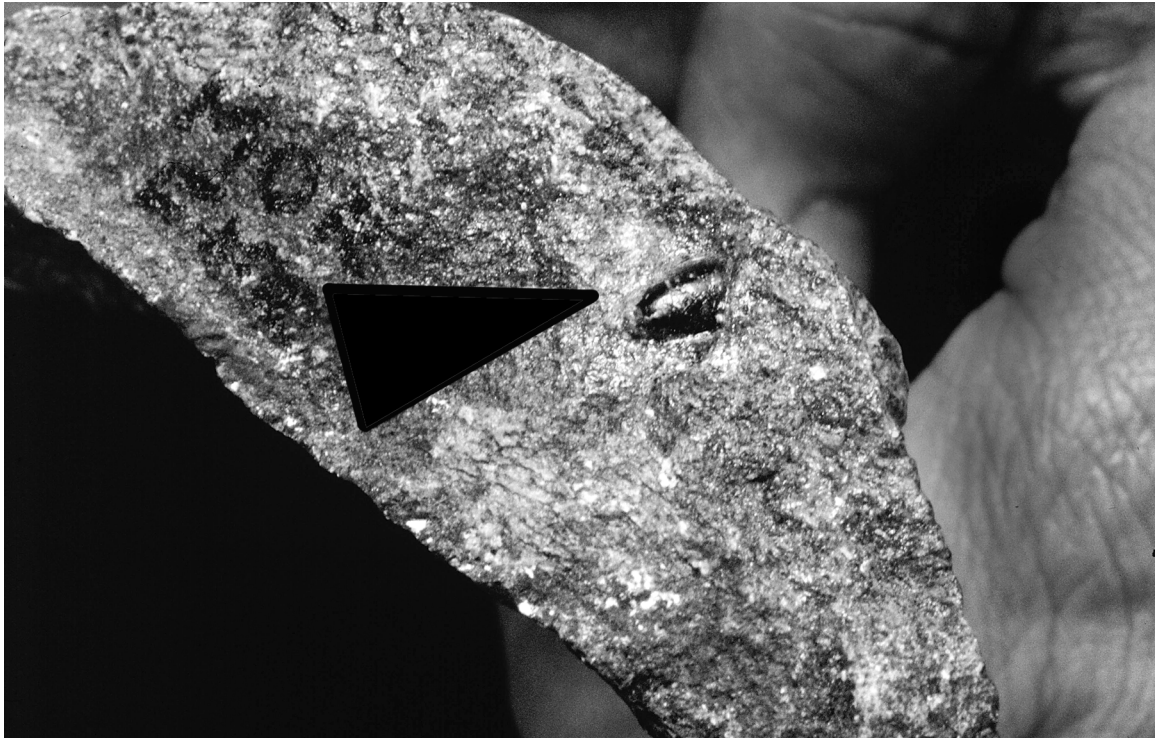


FIGURE 2—Portion of the fibula of an herbivorous dinosaur (Museum of the Rockies 549, *Hypacrosaurus*), with a theropod tooth embedded in it (arrow). The exposed portion of the tooth is about 5 mm long.

other predatory non-dinosaurian archosaurs (Hungerbühler, 2000). Throughout the later Mesozoic, small-bodied dinosaurs (adults or juveniles) were likely eaten by crocodylimorphs (including terrestrial cursorial forms; Kirkland, 1994) and other large reptiles.

The Cretaceous saw the evolution of crocodyliforms that were probably large and massive enough to take even big adult dinosaurs. *Sarcosuchus* from the Early Cretaceous of Africa is estimated to have reached a total length of 11–12 meters and a body mass of 8000 kg, as large as any known carnivorous dinosaur (Serenio et al., 2001). *Deinosuchus*, an alligatorid crocodylian from the Late Cretaceous of the southern and western U.S., may have been equally big, and bite marks likely made by this reptile occur in both hadrosaurid and tyrannosaurid bones (Schwimmer, 2002). In the Late Cretaceous of the southeastern U.S., *Deinosuchus* may have displaced large theropods as the dominant

big predator (Schwimmer, 2002), at least near larger bodies of water.

DINOSAUR PREDATOR-PREY INTERACTIONS

Theropod food preferences and the intensity of predation.—Because predation by and on dinosaurs often resulted in the destruction of prey items, it is difficult to quantify the food preferences of theropods, or to assess the intensity of their predation on herbivorous dinosaurs, in the way that can sometimes be done for marine invertebrates (e.g., by determining the relative frequency of drilled bivalve or brachiopod shells). However, some inferences can be made by examining bite marks and coprolites.

In Late Cretaceous skeletal assemblages from Alberta and Montana, the incidence of tooth-marked bone ranges from a few percent to about 14%; the

number is higher for isolated bones than for bones within bonebeds (Fiorillo, 1991; Jacobsen 1997, 1998, 2001; Jacobsen and Ryan, 1998). There is no indication that tyrannosaurids deliberately crushed bones, in the manner of some mammalian carnivores, even though their teeth and jaws were strong enough to handle bone-breaking (Farlow et al., 1991; Erickson et al., 1996; Molnar, 1998; Hurum and Currie, 2000); bone-biting seems to have been incidental to feeding on meat. Hadrosaur bones more frequently show bite marks than do the bones of other herbivorous dinosaurs and theropods.

The presence of juvenile ornithischian bones in tyrannosaurid gut regions and coprolites (Chin et al., 1998; Varricchio, 2001) invites speculation that these large predators preferred to take young as opposed to fully grown individuals of plant-eating dinosaurs. This would have involved less risk of injury to the predator than tussles with large and perhaps dangerous prey. Given that even the largest dinosaurs would have had the capacity to produce large clutches of eggs every year (as opposed to placental mammals, in which larger body size is associated with longer gestation periods; Carrano and Janis, 1991), a stable population size of dinosaurs would have required a high rate of infant mortality. It seems quite likely that a substantial fraction of these juvenile dinosaurs disappeared down the gullets of theropods.

Trackway evidence.—Fossilized trackways offer clues to predatory behavior by theropod dinosaurs. Thulborn and Wade (1984) described a mid-Cretaceous tracksite in Queensland, Australia, in which a host of small bipedal dinosaurs panicked and fled during the approach of a much larger bipedal dinosaur, most likely a large theropod. Whether the bigger dinosaur was actually hunting the smaller animals is uncertain, but at one point it made a sharp change in its direction of travel consistent with the hypothesis that it was trying to drive them in a particular direction.

In 1940 Roland T. Bird collected segments of the trackways of a sauropod and a large theropod dinosaur in the Lower Cretaceous Glen Rose Limestone at what is now Dinosaur Valley State Park near Glen Rose, Texas (Bird, 1985). The theropod

(very likely *Acrocanthosaurus*; Farlow, 2001) repeatedly stepped into and deformed the prints made by the sauropod, and the trails of both animals made a turn at the same point, suggesting that the meat-eater was close behind and following the big herbivore (Farlow, 1987; Thomas and Farlow, 1997).

Dinosaur tracksites suggest that at least some dinosaurs were gregarious some of the time (Ostrom, 1972, 1986; Currie, 1983; Lockley et al., 1986; Thulborn, 1990; Lockley, 1991; Lockley and Hunt, 1995; Lockley and Meyer, 2000), corroborating interpretations about dinosaur sociality based on skeletal assemblages (Coombs, 1990; Horner, 1997; Farlow, 2000; Eberth et al., 2001). Conceivably, herding behavior on the part of herbivorous dinosaurs was an anti-predator strategy (Day et al., 2002), while group hunting by theropods may have permitted them to kill prey too large for a single hunter to take (Farlow, 1976; Maxwell and Ostrom, 1995).

The Paluxy River sauropod trackway collected by R. T. Bird was one of at least a dozen sauropod trails that seem to have been made by a group of the huge plant-eaters. Bird further believed that a group of theropods was following this herd—rather than just one carnivore tracking a single herbivore. Regrettably, the trackway evidence at Dinosaur Valley State Park does not clearly support Bird's interpretation, but neither does it falsify it (Farlow, 1987).

Predation vs. scavenging.—Perhaps the best known predatory dinosaur, *Tyrannosaurus*, has been suggested to have been an obligate scavenger (Horner, 1994; Horner and Lessem, 1993; Horner and Dobb, 1997). Horner (1994) argues that several morphological features of *Tyrannosaurus* would have precluded a predatory lifestyle: 1) relatively small size of the eye that would have prohibited spotting prey at a distance; 2) limb proportions indicative of slow top running speeds, which would have prevented *Tyrannosaurus* from chasing and capturing prey; 3) disproportionately tiny forelimbs that would have been useless for holding prey; 4) relatively broad teeth that depart from the expected blade-like configuration for teeth of a predator.

We do not find these arguments persuasive. The

size of the orbit of *Tyrannosaurus* relative to its skull size is in fact rather large for a reptile of its size (Fig. 3). Furthermore, the dimensions of the orbit suggest that *Tyrannosaurus* had a big eye in absolute terms, which would have increased its light-gathering capacity and thus its acuity (Walls, 1942; Dusenberry, 1992). Even though *Tyrannosaurus* lacks the cursorial hind limb proportions of smaller theropods, and was probably not as good a runner as sometimes portrayed (Farlow et al., 1995b, 2000; Christiansen, 1999; Hutchinson and Garcia, 2002),

its metatarsus/femur or tibia/femur length ratios indicate that it was likely as fleet, or faster, than other big theropods, and certainly faster than the herbivorous dinosaurs that were its likely prey (Gatesy, 1991; Holtz, 1995).

Horner's last two arguments strike us as begging the question. Without explicitly saying so, he is hypothesizing that grasping forelimbs are a necessity for killing prey (which will be news to wolves, seriemas, and secretary birds), and that animals with broad-based teeth are unable to kill prey with them

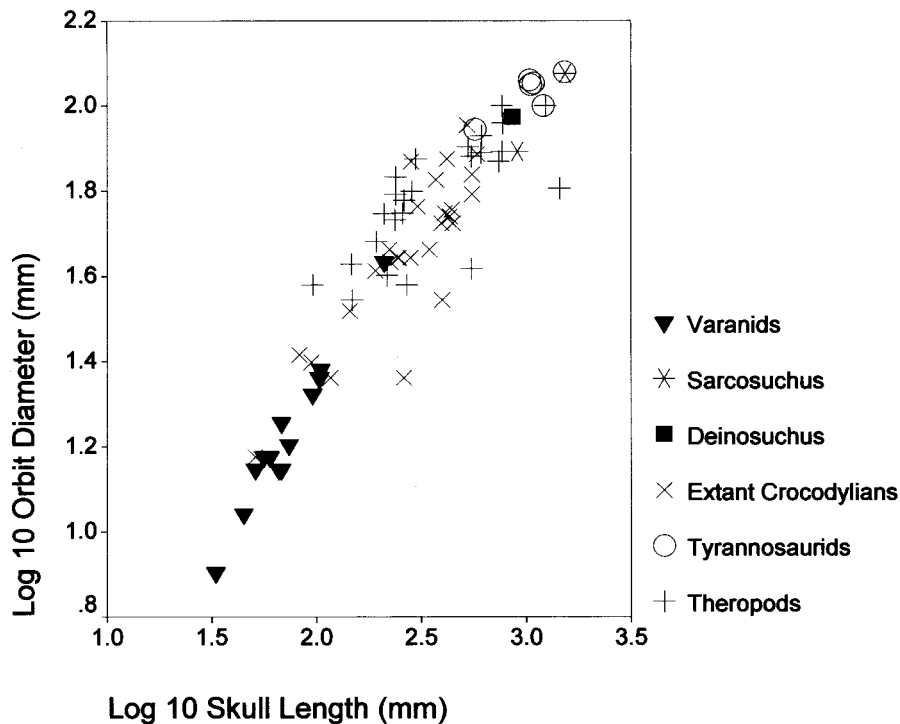


FIGURE 3—Relationship between skull length (occipital condyle to tip of snout) and anteroposterior diameter of the orbit in tyrannosaurids (*Gorgosaurus*, *Daspletosaurus*, *Tyrannosaurus*), theropods other than tyrannosaurids (*Eoraptor*, *Herrerasaurus*, *Coelophysis*, *Dilophosaurus*, *Syntarsus*, *Abelisaurus*, *Carnotaurus*, *Ceratosaurus*, *Acrocanthosaurus*, *Allosaurus*, *Giganotosaurus*, *Monolophosaurus*, *Sinraptor*, *Yangchuanosaurus*, *Dromaeosaurus*, *Velociraptor*, *Erlikosaurus*, *Ingenia*, *Ornitholestes*, *Sauromithoides*, *Dromiceiomimus*, *Gallimimus*, *Garudimimus*, *Struthiomimus*), extant crocodylians (*Alligator*, *Caiman*, *Melanosuchus*, *Paleosuchus*, *Crocodylus*, *Osteolaemus*, *Tomistoma*, *Gavialis*), the extinct crocodylian *Deinosuchus*, the extinct crocodylomorph *Sarcosuchus*, and several extant species of the varanid lizard genus *Varanus* (*acanthurus*, *bengalensis*, *dumerilli*, *exanthematicus*, *gouldii*, *griseus*, *indicus*, *komodoensis*, *niloticus*, *olivaceus*, *prasinus*, *rudicollis*, *salvator*, *timorensis*). Note that tyrannosaurids (including *Tyrannosaurus* itself, represented by the three biggest tyrannosaurid specimens) have orbits (and therefore presumably eyes) as large or larger relative to skull size than those of other carnivorous reptiles.

(which orcas and crocodiles will find surprising). Because the morphology of *Tyrannosaurus* matches the predictions of his hypotheses, Horner concludes that *Tyrannosaurus* could not have been a predator, without first testing those hypotheses.

The brain of *Tyrannosaurus* had respectably large olfactory bulbs (Brochu, 2000), suggesting that the sense of smell was quite acute in this dinosaur. Horner and Dobb (1997) argued that this would have allowed *Tyrannosaurus* to detect the odor of rotting carcasses from afar. This is unquestionably true, but it is also true that a keen sense of smell would have been useful for picking up the scent of live prey, or for behaviors unrelated to food acquisition (Brochu, 2000).

We agree with Horner that *Tyrannosaurus* is unlikely to have engaged in extended, Hollywood-style battles with other large dinosaurs (or huge apes, for that matter). However, surprise, hit-and-run attacks on healthy victims (Paul, 1988), or culling of sick, injured (Carpenter, 2000), or very young dinosaurs, would seem quite likely. In short, we suspect that *Tyrannosaurus* and other carnivorous theropods were, like most extant predators, opportunistic carnivores, eagerly searching for carrion (in which activity the large body sizes of many theropods may have been an advantage; Farlow, 1994), but also killing prey whenever possible.

DINOSAUR FAUNAS

Composition.—Dinosaurs began as minor components of Late Triassic large-tetrapod faunas (cf. Parrish, 1993; Rogers et al., 1993), but by the beginning of the Jurassic Period had become the dominant terrestrial large vertebrates. Over the remainder of the Mesozoic Era the taxonomic composition of herbivorous and carnivorous species in dinosaur faunas varied across time and space, but two particularly noteworthy faunal suites can be recognized. One of these has the herbivorous dinosaur component strongly influenced or even dominated by sauropods (e.g., the Morrison and Wessex Formations) (Table 1); this faunal type is characteristic of much of the world during the

Jurassic and Cretaceous Periods. Sauropods are absent or rare and ornithischians dominant in the second faunal type (e.g., the Dinosaur Park Formation), which occurred in the Late Cretaceous of western North America and eastern and central Asia (Table 1).

Neoceratosaurs, basal tetanurans, and carnosaurs (Holtz, 2000) are the dominant theropod groups in the first faunal type, and coelurosaurs in the second. Medium-sized and large theropods in the first faunal suite come from a variety of lineages, but all large-bodied taxa in the second type are tyrannosaurids. In both faunal types predatory dinosaurs individually are far less abundant than plant-eaters (Farlow, 1997)

Although we do not know which carnivorous dinosaur species specialized on which herbivorous species, the marked differences between the two kinds of faunas suggest the possibility of major differences in predator-prey interactions between them. For example, adult sauropods were considerably bigger than the largest theropods, while most big ornithischians were much closer to tyrannosaurids in body size. Even if tyrannosaurs preferred to attack immature individuals of prey species, it is easy to imagine a single tyrannosaur killing an adult hadrosaur or ceratopsian. It is much harder to visualize a single allosaur slaying an adult apatosaur or brachiosaur. Did large theropods in sauropod-dominated faunas attack only immature sauropods and ignore fully grown adults, or did they engage in group hunting to haul down big sauropods, or did they mainly scavenge sauropod carcasses?

Theropod species in the multi-taxon predator assemblages typical of sauropod-dominated faunas show interesting morphological differences from tyrannosaurids that suggest differences in the style of predation between carnivores in these communities. In the multi-taxon assemblages several large-bodied theropod taxa (basal tetanurans, spinosaurids, and carnosaurs) possessed very powerfully built forelimbs terminating in large talons. It is quite likely that these predators employed their forelimbs as weapons of prey acquisition. In contrast, tyrannosaurids are characterized by greatly reduced forelimbs, and so their style of prey acquisition would

PALEONTOLOGICAL SOCIETY PAPERS, V. 8, 2002

TABLE 1—Comparison of the composition of several dinosaur faunas (X = Xiashaximiao Fm, China, Middle Jurassic; M = Morrison Fm, American West, Late Jurassic [LJ]; T = Tendaguru Grp, Tanzania, LJ; W = Wessex Fm, Isle of Wight, Early Cretaceous [EK]; Y = Yixian Fm, China, EK; C = Cloverly Fm, Wyoming and Montana, EK; B = Bahariya Fm, Egypt, Late Cretaceous [LK]; D = Dinosaur Park Fm, Alberta, LK; N = Nemegt Fm, Mongolia, LK; H = Hell Creek Fm, Montana and Wyoming, LK).

Fauna:	X	M	T	W	Y	C	B	D	N	H
--------	---	---	---	---	---	---	---	---	---	---

Herbivores: "+" indicates that the taxon is present and abundant;
"r" indicates that the taxon is present but rare.

Sauropods	+	+	+	+		r	+		r	
Ornithopods	r	r	+	+	r	+		+	+	+
Marginocephalians				r	+			+	+	+
Thyreophorans	r	+	+	+	r	+		+	+	+

Theropods: "*" indicates that one or all of the species in the taxon may not have been strictly carnivorous; "L" indicates that the taxon is present and includes the largest theropods in the assemblage; "p" indicates that the taxon is present; "?" indicates that the identification of this taxon in the assemblage is tentative at present.

Coelophysoids		p	p							
Neoceratosaurs		p	L							
Basal Tetanurans	p	p		p?						
Spinosaurids				L			L			
Carnosaurs	L	L	L?	p		L	L			
Basal Coelurosaurids		p		p	p		p?		p	
Tyrannosaurids		p		p				L	L	L
Ornithomimosaurids*					p	p?		p	p	p
Oviraptorosaurids*		p?		p?	p	p		p	p	p
Therizinosaurids*					L			p?	p	
Troodontids*		p?			p			p	p	p
Dromaeosaurids					p	p		p	p?	p
Avialians*		p?			p			p	p	p

have relied on their powerful jaws alone.

Another difference between the faunal types is the overlap of theropod body sizes. In assemblages possessing multiple lineages of large-bodied theropods there is commonly great overlap in the size of the carnivores. For example, in the Morrison Formation the carnosaur *Allosaurus*, the basal tetanuran *Torvosaurus*, and the neoceratosaur *Ceratosaurs* would all include individuals of 1 tonne or greater body mass. Similarly, the Bahariya Formation's spinosaurid *Spinosaurus*, carnosaur *Carcharodontosaurus*, and basal coelurosaur *Deltadromeus* all exceeded 2 tonnes in mass (the first two by a considerable margin). The presence of comparable-sized predators suggests the possibility of competition among these taxa for food, perhaps mitigated by some form of morphologically mediated niche partitioning (Henderson, 2000). Similar size overlap occurs between the adults of medium-sized theropods in these assemblages, which would additionally have been in potential competition with immature individuals of the largest-bodied species.

In marked contrast, all the larger carnivorous dinosaurs in Late Cretaceous assemblages of western North America and eastern and central Asia are tyrannosaurids, and among these there is typically just one or two species present in potential sympatry. Furthermore, there is often a large discontinuity in adult sizes between the tyrannosaurids and the next largest unquestionably carnivorous dinosaurs in the fauna (generally dromaeosaurids), rather than the gradational distribution of adult sizes seen in non-tyrannosaurid-dominated faunas.

Macroecology of carnivorous dinosaurs.—The single most noteworthy feature of most dinosaurs, of course, is their large size. Body size affects or is correlated with numerous physiological and ecological features of animals (Brown, 1995; Brown and West, 2000). Large animals have bigger home ranges than do smaller species, and carnivores require more habitat space than herbivores (Kelt and Van Vuren, 2001). Farlow (2001) used published regressions of home range area against body mass in extant predatory mammals, birds, and lizards to speculate that the home range size of the 2500-kg

carnosaur *Acrocanthosaurus* would have encompassed hundreds or thousands of square kilometers. Kelt and Van Vuren (2001), however, suggested that there may be some upper limit to home range area in mammals, regardless of body size and diet. If true, and if this upper limit holds for other terrestrial vertebrates, it raises the question of how gigantic predators like large theropods could have survived on relatively small (as compared with individual animal size) home ranges.

Because an individual animal's home range area becomes larger with increasing body size, population density (number of individuals / habitat area) must decrease (Damuth, 1987; Brown, 1995; Smallwood, 2001), which in turn mandates large geographic ranges if big-bodied species are to be represented by enough individuals for long-term viability (Calder, 2000). For trophodynamic reasons carnivores must have lower population densities than herbivores, and so the problem of sufficient habitat space should be particularly acute for enormous carnivores (Farlow, 1993; Burness et al., 2001). The huge sizes routinely achieved by carnivorous dinosaurs are therefore ecologically puzzling. Conceivably, theropod gigantism was facilitated by a combination of lower food requirements than expected for elephantine mammalian meat-eaters, along with elevated rates of biological productivity under the greenhouse conditions of the Mesozoic Era (Farlow, 1993; Farlow et al., 1995; Burness et al., 2001). In another scenario (Carrano and Janis, 1991) the greater reproductive capacity of herbivorous dinosaurs relative to placental mammals (due to oviparity of the former) would allow for more available "packages" of dinosaurian meat that could be consumed by theropods while still allowing for a viable sustainable population of prey.

POSSIBLE DIRECTIONS FOR FUTURE RESEARCH

Although progress in understanding predator-prey interactions in dinosaur communities will depend in large part on fortuitous discoveries of particularly informative specimens or assemblages,

we can suggest some approaches that might prove fruitful. One matter worth exploring is the incidence of bite marks in dinosaur bones, or teeth embedded in bone. Such fossils have already been noted for the Late Cretaceous of western North America (Jacobsen, 1997, 1998, 2001), but older formations could also be surveyed. Similarly, paleontologists should keep their eyes open for potential theropod coprolites. With sufficiently large sample sizes of tooth-marked bone and coprolites, it might be possible to determine which species of herbivorous dinosaurs, and which size classes within those species, were preferentially eaten by which predator species. If we were really lucky, we might even find, say, a bite mark unambiguously made by a *Tyrannosaurus* that had healed, which would establish beyond doubt that these predatory dinosaurs at least sometimes attacked live prey. Unfortunately, distinguishing successful predation events from scavenging on the basis of tooth-marked bones is probably impossible, because the victim cannot recover from either.

Structural analysis (including computer modeling) of a variety of theropod skulls in particular faunas (cf. Henderson, 2000; Rayfield et al., 2001) could be used to test whether reconstructions of different biting and/or feeding styles in sympatric theropod species are mechanically feasible, and thus ways in which coexisting species could have subdivided the resource base. Such approaches could be combined with analyses of tooth shape, tooth cutting edges, and wear and breakage patterns, in both *in situ* and shed theropod teeth (Farlow et al., 1991; Farlow and Brinkman, 1994; Abler, 1997). The degree of size and shape overlap of the skulls and teeth of different species of potentially sympatric theropods could be compared with that in modern communities of predatory lizards (e.g., the varanids of Australia) and crocodylians.

With a better understanding of the systematic composition of dinosaur faunas, we could see how the different composition of the prey base in sauropod-dominated and ornithischian-dominated



FIGURE 4—Right lateral view of the pelvis of a moa (Canterbury Museum Av 8317, *Emeus crassus*) showing an elliptical gouge (arrow) dug by the hind toe talon of *Harpagornis*, a huge, extinct eagle. The paper label is 102 mm long. Photograph courtesy of Richard Holdaway.

faunas affected the structure of predatory dinosaur guilds. Do the two kinds of faunas consistently differ in the ratio of the number of herbivore species to carnivore species, or might they differ in the ratio of individual herbivorous animals to carnivorous animals? And can any such differences be related to the mechanisms by which sympatric carnivorous dinosaur species reduced potential niche overlap?

CENOZOIC REPRISE

Because birds are likely a specialized clade of theropods (Gauthier and Gall, 2001), the fossil record of dinosaur predation does not end with the K/T boundary. A diversity of Cenozoic birds has evolved as important predators of invertebrates and small vertebrates. At certain times and places, however, avian faunas have been particularly evocative of the Mesozoic glory days. For example, the phorusrhacoids of Tertiary South America (Andrews, 1901), and possibly the gastornithids of Paleogene Europe and North America (Witmer

and Rose, 1991), were big, flightless, predatory birds startlingly reminiscent of their Mesozoic theropod predecessors.

The real Cenozoic lost world of dinosaurs, however, was New Zealand. In the absence of significant mammalian competition, a host of large and small birds, both volant and flightless, dominated the terrestrial vertebrate fauna (Worthy and Holdaway, 2002). Eleven species of moa, turkey to ostrich-plus in size, clumped through forest and field, cropping the vegetation like scaled-down sauropodomorphs or ornithischians. No ground-based tyrannosaur-avatar threatened the moa. Instead their chief predator was a huge eagle that attacked with talons from the air (Fig. 4), an entirely different style of dinosaurian predator-prey interaction than seen in the Mesozoic world. Dinosaurian dominance of New Zealand remained unchallenged until about a thousand years ago and the arrival of a bipedal, predatory primate far deadlier than any theropod, at which time this faraway land, too, finally fell under mammalian sway.

REFERENCES

- ABLER, W. L. 1997. Tooth serrations in carnivorous dinosaurs, p. 740–743. *In* P. J. Currie and K. Padian (eds.), *Encyclopedia of Dinosaurs*. Academic Press, San Diego.
- ANDREWS, C. W. 1901. On the extinct birds of Patagonia—I: The skull and skeleton of *Phororhacos inflatus* Ameghino. *Transactions of the Zoological Society of London*, 15: 55–86.
- BAKKER, R. T., M. WILLIAMS, AND P. J. CURRIE. 1988. *Nanotyrannus*, a new genus of pygmy tyrannosaur, from the latest Cretaceous of Montana. *Hunteria*, 1(5):1–30.
- BARRETT, P. M. 2000. Prosauropod dinosaurs and iguanas: Speculations on the diets of extinct reptiles, p. 42–78. *In* H.-D. Sues (ed.), *Evolution of Herbivory in Terrestrial Vertebrates: Perspectives from the Fossil Record*. Cambridge University Press, Cambridge, U.K.
- BARSBOLD, R., H. OSMÓLSKA, AND S. M. KURZANOV. 1987. On a new troodontid (Dinosauria, Theropoda) from the Early Cretaceous of Mongolia. *Acta Palaeontologica Polonica*, 32:121–132.
- BIRD, R. T. 1985. *Bones for Barnum Brown: Adventures of a Dinosaur Hunter*. Texas Christian University Press, Fort Worth, TX, 225 p.
- BONAPARTE, J. F., AND J. E. POWELL. 1980. A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, northwestern Argentina (Sauropoda-Coelurosauria-Carnosauria-Aves). *Memoires de la Société Géologique de France, N.S.*, 139:19–28.
- BONAPARTE, J. F., F. E. NOVAS, AND R. A. CORIA. 1990. *Carnotaurus sastrei* Bonaparte, the horned, lightly built carnosaur from the Middle Cretaceous of Patagonia. *Natural History Museum of Los Angeles County, Contributions in Science*, 416:1–41.
- BROCHU, C. A. 2000. A digitally-rendered endocast for *Tyrannosaurus rex*. *Journal of Vertebrate Paleontology*, 20:1–6.
- BROWN, J. H. 1995. *Macroecology*. University of Chicago Press, Chicago, 269 p.
- BROWN, J. H., AND G. B. WEST (eds.). 2000. *Scaling in Biology*. Oxford University Press, Oxford, U.K., 352 p.

PALEONTOLOGICAL SOCIETY PAPERS, V. 8, 2002

- BURNES, G. P., J. DIAMOND, AND T. FLANNERY. 2001. Dinosaurs, dragons, and dwarfs: The evolution of maximal body size. *Proceedings of the National Academy of Science USA*, 98:14518–14523.
- CALDER, W. A. 2000. Diversity and convergence: Scaling for conservation, p. 297–323. *In* J. H. Brown and G. B. West (eds.), *Scaling in Biology*. Oxford University Press, Oxford, U.K.
- CARPENTER, K. 2000. Evidence of predatory behavior by carnivorous dinosaurs. *Gaia*, 15:135–144.
- CARPENTER, K., AND M. SMITH. 2001. Forelimb osteology and biomechanics of *Tyrannosaurus rex*, p. 90–116. *In* D. H. Tanke and K. Carpenter (eds.), *Mesozoic Vertebrate Life*. Indiana University Press, Bloomington.
- CARRANO, M., AND C. JANIS. 1991. Scaling of reproductive turnover in archosaurs and mammals: Why are large terrestrial mammals so rare? *Annales Zoologici Fennici*, 28: 201–216.
- CHARIG, A. J., AND A. C. MILNER. 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum*, 53:11–70.
- CHEN, P., Z. DONG, AND S. ZHEN. 1998. An exceptionally well-preserved theropod dinosaur from the Yixian Formation of China. *Nature*, 391:147–152.
- CHIN, K. 1997. What did dinosaurs eat? Coprolites and other direct evidence of dinosaur diets, pp. 371–382. *In* J. O. Farlow and M. K. Brett-Surman (eds.), *The Complete Dinosaur*. Indiana University Press, Bloomington.
- CHIN, K., AND B. D. GILL. 1996. Dinosaurs, dung beetles, and conifers: participants in a Cretaceous food web. *Palaios*, 11:280–285.
- CHIN, K., AND J. I. KIRKLAND. 1998. Probable herbivore coprolites from the Upper Jurassic Mygatt-Moore Quarry, western Colorado. *Modern Geology*, 23:249–275.
- CHIN, K., T. T. TOKARYK, G. M. ERICKSON, AND L. C. CALK. 1998. A king-sized theropod coprolite. *Nature*, 393:680–682.
- CHRISTIANSEN, P. 1999. Long bone scaling and limb posture in non-avian theropods: evidence for differential allometry. *Journal of Vertebrate Paleontology*, 19:666–680.
- CHURE, D. J., A. R. FIORILLO, AND A. JACOBSEN. 2000. Prey bone utilization by predatory dinosaurs in the Late Jurassic of North America, with comments on prey bone use by dinosaurs throughout the Mesozoic. *Gaia*, 15:227–232.
- COLBERT, E. H. 1978. The Triassic dinosaur *Coelophysis*. *Museum of Northern Arizona Bulletin* 57, 160 p.
- COOMBS, W. P., JR. 1990. Behavior patterns of dinosaurs, p. 32–42. *In* D. B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*. University of California Press, Berkeley, CA.
- CURRIE, P. J. 1983. Hadrosaur trackways from the Lower Cretaceous of Canada. *Acta Palaeontologica Polonica*, 28:63–73.
- CURRIE, P. J., AND P. CHEN. 2001. Anatomy of *Sinosauropteryx prima* from Liaoning, northeastern China. *Canadian Journal of Earth Sciences*, 38:1705–1727.
- CURRIE, P. J., AND A. R. JACOBSEN. 1995. An azhdarchid pterosaur eaten by a velociraptorine theropod. *Canadian Journal of Earth Sciences*, 32:922–925.
- DAMUTH, J. 1987. Interspecific allometry of population density in mammals and other animals: The independence of body mass and population energy-use. *Biological Journal of the Linnean Society*, 31:193–246.
- DAY, J. J., P. UPCHURCH, D. B. NORMAN, A. S. GALE, AND H. PHILIP POWELL. 2002. Sauropod trackways, evolution, and behavior. *Science*, 296:1659.
- DUSENBERRY, D. B. 1992. *Sensory Ecology: How Organisms Acquire and Respond to Information*. Freeman, New York, 558 p.
- EBERTH, D. A., P. J. CURRIE, D. B. BRINKMAN, M. J. RYAN, D. R. BRAMAN, J. D. GARDNER, V. D. LAM, D. N. SPIVAK, AND A. G. NEUMAN. 2001. Alberta's dinosaurs and other fossil vertebrates: Judith River and Edmonton Groups (Campanian-Maastrichtian), p. 49–75. *In* C. L. Hill (ed.), *Guidebook for the Field Trips, Society of Vertebrate Paleontology 61st Annual Meeting, Museum of the Rockies Occasional Paper 3*, Bozeman, MT.
- ERICKSON, G. M., AND K. H. OLSON. 1996. Bite marks attributable to *Tyrannosaurus rex*: preliminary description and implications. *Journal of Vertebrate Paleontology*, 16:175–178.
- ERICKSON, G. M., S. D. VAN KIRK, J. SU, M. E. LEVENSTON, W. E. CALER, AND D. R. CARTER. 1996. Bite force estimation for *Tyrannosaurus rex* from tooth-marked bones. *Nature*, 382:706–708.
- FARLOW, J. O. 1976. Speculations about the diet and foraging behavior of large carnivorous dinosaurs. *American Midland Naturalist*, 95:186–191.
- FARLOW, J. O. 1987. *Lower Cretaceous Dinosaur Tracks, Paluxy River Valley, Texas*. South-Central Section, Geological Society of America, Baylor University, Waco, TX, 50 p.

FARLOW AND HOLTZ— PREDATION IN DINOSAURS

- FARLOW, J. O. 1993. On the rareness of big, fierce animals: Speculations about the body sizes, population densities, and geographic ranges of predatory mammals and large carnivorous dinosaurs. *American Journal of Science*, 293-A:167–199.
- FARLOW, J. O. 1994. Speculations about the carrion-locating ability of tyrannosaurs. *Historical Biology*, 7:159–165.
- FARLOW, J. O. 1997. Trophic groups, p. 755–758. *In* P. J. Currie and K. Padian (eds.), *Encyclopedia of Dinosaurs*. Academic Press, San Diego.
- FARLOW, J. O. 2000. Tracking dinosaur society, p. 232–241. *In* G. S. Paul (ed.), *The Scientific American Book of Dinosaurs*. St. Martin's Press, New York.
- FARLOW, J. O. 2001. *Acrocanthosaurus* and the maker of Comanchean large-theropod footprints, p. 408–427. *In* D. H. Tanke and K. Carpenter (eds.), *Mesozoic Vertebrate Life*. Indiana University Press, Bloomington.
- FARLOW, J. O., AND D. L. BRINKMAN. 1994. Wear surfaces on the teeth of tyrannosaurs, p. 165–175. *In* G. D. Rosenberg and D. L. Wolberg (eds.), *Dino Fest*. Paleontological Society Special Publication 7, University of Tennessee, Knoxville, TN.
- FARLOW, J. O., P. DODSON, AND A. CHINSAMY. 1995a. Dinosaur biology. *Annual Review of Ecology and Systematics*, 26:445–471.
- FARLOW, J. O., M. B. SMITH, AND J. M. ROBINSON. 1995b. Body mass, bone “strength indicator,” and cursorial potential of *Tyrannosaurus rex*. *Journal of Vertebrate Paleontology*, 15:713–725.
- FARLOW, J. O., D. L. BRINKMAN, W. L. ABLER, AND P. J. CURRIE. 1991. Size, shape, and serration density of theropod dinosaur lateral teeth. *Modern Geology*, 16:161–198.
- FARLOW, J. O., S. M. GATESY, T. R. HOLTZ, JR., J. R. HUTCHINSON, AND J. M. ROBINSON. 2000. Theropod locomotion. *American Zoologist*, 40:640–663.
- FIORILLO, A. R. 1991. Prey bone utilization by predatory dinosaurs. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 88:157–166.
- FORSTER, C. A., S. D. SAMPSON, L. M. CHIAPPE, AND D. W. KRAUSE. 1998. The theropod ancestry of birds: new evidence from the Late Cretaceous of Madagascar. *Science*, 279:1915–1919.
- GATESY, S. M. 1991. Hind limb scaling in birds and other theropods: implications for terrestrial locomotion. *Journal of Morphology*, 209:83–96.
- GAUTHIER, J., AND L. F. GALL (eds.). 2001. *New Perspectives on the Origin and Early Evolution of Birds*. Peabody Museum of Natural History, Yale University, New Haven, CT.
- GILMORE, C. W. 1920. Osteology of the carnivorous Dinosauria in the United States National Museum, with special reference to the genera *Antrodemus* (*Allosaurus*) and *Ceratosaurus*. *Bulletin of the United States National Museum*, 110:1–154.
- HECKERT, A. B., AND S. G. LUCAS. 1998. Global correlation of the Triassic theropod record. *Gaia*, 15:63–74.
- HENDERSON, D. M. 2000. Skull and tooth morphology as indicators of niche partitioning in sympatric Morrison Formation theropods. *Gaia*, 15:219–226.
- HOLTZ, T. R., JR. 1995. The arctometatarsalian pes, an unusual structure of the metatarsus of Cretaceous Theropoda (Dinosauria: Saurischia). *Journal of Vertebrate Paleontology*, 14:480–519.
- HOLTZ, T. R., JR. 2000. A new phylogeny of carnivorous dinosaurs. *Gaia*, 15:5–61.
- HOLTZ, T. R., JR., D. L. BRINKMAN, AND C. L. CHANDLER. 2000. Denticle morphometrics and a possibly omnivorous feeding habit for the theropod dinosaur *Troodon*. *Gaia*, 15:159–166.
- HOPSON, J. A. 2001. Ecomorphology of avian and nonavian theropod phalangeal proportions: implications for the arboreal versus terrestrial origin of bird flight, p. 211–235. *In* J. Gauthier and L. F. Gall (eds.), *New Perspectives on the Origin and Early Evolution of Birds*. Peabody Museum of Natural History, Yale University New Haven, CT.
- HORNER, J. R. 1994. Steak knives, beady eyes, and tiny little arms (a portrait of *T. rex* as a scavenger), p. 157–164. *In* G. D. Rosenberg and D. L. Wolberg (eds.), *Dino Fest*. Paleontological Society Special Publication 7, University of Tennessee, Knoxville, TN.
- HORNER, J. R. 1997. Behavior, p. 45–50. *In* P. J. Currie and K. Padian (eds.), *Encyclopedia of Dinosaurs*. Academic Press, San Diego, CA.
- HORNER, J. R., AND E. DOBB. 1997. *Dinosaur Lives: Unearthing an Evolutionary Saga*. Harcourt Brace and Company, San Diego, CA, 244 p.

PALEONTOLOGICAL SOCIETY PAPERS, V. 8, 2002

- HORNER, J. R., AND D. LESSEM. The Complete *T. rex*: How Stunning New Discoveries Are Changing Our Understanding of the World's Most Famous Dinosaur. Simon and Schuster, New York, 244 p.
- HUNGERBÜHLER, A. 2000. Taphonomy of the prosauropod dinosaur *Sellosaurus*, and its implications for carnivore faunas and feeding habits in the Late Triassic. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 143:1–29.
- HUNT, A. P., S. G. LUCAS, A. B. HECKERT, R. M. SULLIVAN, AND M. G. LOCKLEY. 1998. Late Triassic dinosaurs from the western United States. *Geobios*, 31:511–531.
- HUNT, A. P., C. A. MEYER, M. G. LOCKLEY, AND S. G. LUCAS. 1994. Archaeology, toothmarks and sauropod dinosaur taphonomy. *Gaia*, 10:225–231.
- HURUM, J. M., AND P. J. CURRIE. 2000. The crushing bite of tyrannosaurids. *Journal of Vertebrate Paleontology*, 20:619–621.
- HUTCHINSON, J. R., AND M. GARCIA. 2002. *Tyrannosaurus* was not a fast runner. *Nature*, 415:1018–1021.
- JACOBSEN, A. R. 1997. Tooth marks, p. 738–739. *In* P. J. Currie and K. Padian (eds.), *Encyclopedia of Dinosaurs*. Academic Press, San Diego.
- JACOBSEN, A. R. 1998. Feeding behavior of carnivorous dinosaurs as determined by tooth marks on dinosaur bones. *Historical Biology*, 13:17–26.
- JACOBSEN, A. R. 2001. Tooth-marked small theropod bone: an extremely rare trace, p. 58–63. *In* D. H. Tanke and K. Carpenter (eds.), *Mesozoic Vertebrate Life*. Indiana University Press, Bloomington.
- JACOBSEN, A. R., AND M. J. RYAN. 1999. Taphonomic aspects of theropod tooth-marked bones from an *Edmontosaurus* bone bed (Lower Maastrichtian, Alberta, Canada). *Journal of Vertebrate Paleontology*, 19(3):55A.
- KELT, D. A., AND D. H. VAN VUREN. 2001. The ecology and macroecology of mammalian home range area. *American Naturalist*, 157:637–645.
- KIRKLAND, J. I. 1994. Predation of dinosaur nests by terrestrial crocodilians, p. 124–133. *In* K. Carpenter, K. F. Hirsch, and J. R. Horner (eds.), *Dinosaur Eggs and Babies*. Cambridge University Press, Cambridge, U.K.
- LOCKLEY, M. G. 1991. *Tracking Dinosaurs: A New Look at an Ancient World*. Cambridge University Press, Cambridge, U.K., 238 p.
- LOCKLEY, M. G., AND A. P. HUNT. 1995. *Dinosaur Tracks and Other Fossil Footprints of the Western United States*. Columbia University Press, New York, 338 p.
- LOCKLEY, M. G., AND C. MEYER. 2000. *Dinosaur Tracks and Other Fossil Footprints of Europe*. Columbia University Press, New York, 323 p.
- LOCKLEY, M. G., K. J. HOUCK, AND N. K. PRINCE. 1986. North America's largest dinosaur trackway site: implications for Morrison Formation paleoecology. *Geological Society of America Bulletin*, 97:1163–1176.
- MAXWELL, W. D., AND J. H. OSTROM. 1995. Taphonomy and paleobiological implications of *Tenontosaurus-Deinonychus* associations. *Journal of Vertebrate Paleontology*, 15:707–712.
- MIDDLETON, K. M., AND S. M. GATESY. 2000. Theropod forelimb design and evolution. *Zoological Journal of the Linnean Society*, 128:149–197.
- MOLNAR, R. E. 2000. Mechanical factors in the design of the skull of *Tyrannosaurus rex* (Osborn, 1905). *Gaia*, 15:193–218.
- NAISH, D., S. HUTT, AND D. M. MARTILL. 2001. Saurischian dinosaurs 2: Theropods, p. 242–309. *In* D. M. Martill and D. Naish (eds.), *Dinosaurs of the Isle of Wight*. Palaeontological Association Field Guide to Fossils 10, London.
- NORELL, M. A., P. J. MAKOVICKY, AND P. J. CURRIE. 2001. The beaks of ostrich dinosaurs. *Nature*, 412:873–874.
- OSTROM, J. H. 1969. Osteology of *Deinonychus antirrhopus*, an unusual theropod from the Lower Cretaceous of Montana. *Peabody Museum of Natural History Bulletin* 30, Yale University, 165 p.
- OSTROM, J. H. 1972. Were some dinosaurs gregarious? *Palaeogeography, Palaeoclimatology, Palaeoecology*, 11:287–309.
- OSTROM, J. H. 1978. The osteology of *Compsognathus longipes* Wagner. *Zitteliana*, 4:73–118.
- OSTROM, J. H. 1986. Social and unsocial behavior in dinosaurs, p. 41–61. *In* M. H. Nitecki and J. A. Kitchell (eds.), *Evolution of Animal Behavior*. Oxford University Press, Oxford, U.K.
- PARRISH, J. M. 1993. Distribution and taxonomic composition of fossil vertebrate accumulations in the Upper Triassic Chinle Formation, Petrified Forest National Park, p. 393–396. *In* S. G. Lucas and M. Morales (eds.), *The Nonmarine Triassic*, New Mexico Museum of Natural History and Science Bulletin 3, Albuquerque.

FARLOW AND HOLTZ— PREDATION IN DINOSAURS

- PAUL, G. S. 1988. *Predatory Dinosaurs of the World: A Complete Illustrated Guide*. Simon and Schuster, New York, 464 p.
- RAYFIELD, E. J., D. B. NORMAN, C. C. HORNER, J. R. HORNER, P. M. SMITH, J. J. THOMASON, AND P. UPCHURCH. 2001. Cranial design and function in a large theropod dinosaur. *Nature*, 409:1033–1037.
- REISZ, R. R., AND H.-D. SUES. 2000. Herbivory in late Paleozoic and Triassic terrestrial vertebrates, p. 9–41. *In* H.-D. Sues (ed.), *Evolution of Herbivory in Terrestrial Vertebrates: Perspectives from the Fossil Record*. Cambridge University Press, Cambridge, U.K.
- ROGERS, R. R., C. C. SWISHER III, P. C. SERENO, A. M. MONETTA, C. A. FORSTER, AND R. N. MARTÍNEZ. 1993. The Ischigualasto tetrapod assemblage (Late Triassic, Argentina) and $^{40}\text{A}/^{39}\text{A}$ dating of dinosaur origins. *Science*, 260:794–797.
- RUSSELL, D. A. 1997. Therizinosauria, p. 729–730. *In* P. J. Currie and K. Padian (eds.), *Encyclopedia of Dinosaurs*. Academic Press, San Diego.
- RYAN, M. J., AND M. K. VICKARYOUS. 1997. Diet, p. 169–174. *In* P. J. Currie and K. Padian (eds.), *Encyclopedia of Dinosaurs*. Academic Press, San Diego.
- SANDER, P. M. 1997. Teeth and jaws, p. 717–725. *In* P. J. Currie and K. Padian (eds.), *Encyclopedia of Dinosaurs*. Academic Press, San Diego.
- SCHWIMMER, D. R. 2002. *King of the Crocodylians: The Paleobiology of Deinosuchus*. Indiana University Press, Bloomington, 220 p.
- SERENO, P. C. 1993. The pectoral girdle and forelimb of the basal theropod *Herrerasaurus ischigualastensis*. *Journal of Vertebrate Paleontology*, 13:425–450.
- SERENO, P. C. 1999. The evolution of dinosaurs. *Science*, 284:2137–2147.
- SERENO, P. C., AND F. E. NOVAS. 1993. The skull and neck of the basal theropod *Herrerasaurus ischigualastensis*. *Journal of Vertebrate Paleontology*, 13:451–476.
- SERENO, P. C., H. C. E. LARSSON, C. A. SIDOR, AND B. GADO. 2001. The giant crocodyliform *Sarcosuchus* from the Cretaceous of Africa. *Science*, 294:1516–1519.
- SMALLWOOD, K. S. 2001. The allometry of density within the space used by populations of mammalian Carnivora. *Canadian Journal of Zoology*, 79:1634–1640.
- THOMAS, D. A., AND J. O. FARLOW. 1997. Tracking a dinosaur attack. *Scientific American*, 277(6):74–79.
- THULBORN, R. A., AND M. WADE. 1984. Dinosaur trackways in the Winton Formation (Mid-Cretaceous) of Queensland. *Memoirs of the Queensland Museum*, 21:413–517.
- THULBORN, T. 1990. *Dinosaur Tracks*. Chapman and Hall, London, 410 p.
- UPCHURCH, P., AND P. M. BARRETT. 2000. The evolution of sauropod feeding mechanisms, p. 79–122. *In* H.-D. Sues (ed.), *Evolution of Herbivory in Terrestrial Vertebrates: Perspectives from the Fossil Record*. Cambridge University Press, Cambridge, U.K.
- VARRICCHIO, D. J. 2001. Gut contents from a Cretaceous tyrannosaurid: implications for theropod dinosaur digestive tracts. *Journal of Paleontology*, 75:401–406.
- WALLS, G. L. 1942. *The Vertebrate Eye and Its Adaptive Radiation*. Cranbrook Institute of Science Bulletin 19, Bloomfield Hills, MI, 785 p.
- WITMER, L. M., AND K. D. ROSE. 1991. Biomechanics of the jaw apparatus of the gigantic Eocene bird *Diatryma*: implications for diet and mode of life. *Paleobiology*, 17:95–120.
- WORTHY, T. H., AND R. N. HOLDAWAY. 2002. *The Lost World of the Moa: Prehistoric Life of New Zealand*. Indiana University Press, Bloomington, 720 p.

