Breathing Life into Tyrannosaurus rex

By analyzing previously overlooked fossils and by taking a second look at some old finds, paleontologists are providing the first glimpses of the actual behavior of the tyrannosaurs

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TYRANNOSAURUS REX defends its meal, a Triceratops, from other hungry T. rex. Troodontids, the small velociraptors at the bottom left, wait for scraps left by the tyrannosaurs, while pterosaurs circle overhead on this typical day some 65 million years ago. Trees and flowering plants complete the landscape; grasses have yet to evolve. inosaurs ceased to walk the earth 65 million years ago, yet they still live among us. Velociraptors star in movies, and *Triceratops* clutter toddlers' bedrooms. Of these charismatic animals, however, one species has always ruled our fantasies. Children, Steven Spielberg and professional paleontologists agree that the superstar of the dinosaurs was and is *Tyrannosaurus rex*.

Harvard University paleontologist Stephen Jay Gould has said that every species designation represents a theory about that animal. The very name Tyrannosaurus rex-"tyrant lizard king"-evokes a powerful image of this species. John R. Horner of Montana State University and science writer Don Lessem wrote in their book The Complete T. Rex, "We're lucky to have the opportunity to know T. rex, study it, imagine it, and let it scare us. Most of all, we're lucky T. rex is dead." And paleontologist Robert T. Bakker of the Glenrock Paleontological Museum in Wyoming described T. rex as a "10,000pound [4,500-kilogram] roadrunner from hell," a tribute to its obvious size and power.

In Spielberg's Jurassic Park, which boasted the most accurate popular depiction of dinosaurs ever, T. rex was, as usual, presented as a killing machine whose sole purpose was aggressive, bloodthirsty attacks on helpless prey. T. rex's popular persona, however, is as much a function of artistic license as of concrete scientific evidence. A century of study and the existence of 22 fairly complete T. rex specimens have generated substantial information about its anatomy. But inferring behavior from anatomy alone is perilous, and the true nature of T. rex continues to be largely shrouded in mystery. Whether it was even primarily a predator or a scavenger is still the subject of debate.

Over the past decade, a new breed of scientists has begun to unravel some of *T. rex*'s better-kept secrets. These paleobiologists try to put a creature's remains in a living context—they attempt to animate the silent and still skeleton of the museum display. *T. rex* is thus changing before our eyes as paleobiologists use fossil clues, some new and some previously overlooked, to develop fresh ideas about the nature of these magnificent animals.

Rather than draw conclusions about behavior solely based on anatomy, paleobiologists demand proof of actual activities. Skeletal assemblages of multiple individuals shine a light on the interactions among T. rex and between them and other species. In addition, so-called trace fossils reveal activities through physical evidence, such as bite marks in bones and wear patterns in teeth. Also of great value as trace fossils are coprolites, fossilized feces. (Remains of a herbivore, such as Triceratops or Edmontosaurus, in T. rex coprolites certainly provide "smoking gun" proof of species interactions!)

One assumption that paleobiologists are willing to make is that closely related species may have behaved in similar ways. *T. rex* data are therefore being corroborated by comparisons with those of earlier members of the family Tyrannosauridae, including their cousins *Albertosaurus*, *Gorgosaurus* and *Daspletosaurus*, collectively known as albertosaurs.

Solo or Social?

Tyrannosaurs are usually depicted as solitary, as was certainly the case in *Jurassic Park*. (An alternative excuse for that film's loner is that the movie's genetic wizards wisely created only one.) Mounting evidence, however, points to gregarious *T. rex* behavior, at least for part of the animals' lives. Two *T. rex* excavations in the Hell Creek Formation of eastern Montana are most compelling.

In 1966 Los Angeles County Museum researchers attempting to exhume a Hell Creek adult were elated to find another, smaller individual resting atop the T. rex they had originally sought. This second fossil was identified at first as a more petite species of tyrannosaur. My examination of the histological evidence-the microstructure of the bones-now suggests that the second animal was actually a subadult T. rex. A similar discovery was made during the excavation of "Sue," the largest and most complete fossil T. rex ever found. Sue is perhaps as famous for her \$8.36-million auction price following ownership haggling as for her paleontological status [see "No Bones about It," News and Analysis, SCIENTIFIC AMERICAN, December 1997]. Remains of a second adult, a juvenile and an infant *T. rex* were later found in Sue's quarry. Researchers who have worked the Hell Creek Formation, myself included, generally agree that long odds argue against multiple, loner *T. rex* finding their way to the same burial. The more parsimonious explanation is that the animals were part of a group.

An even more spectacular find from 1910 further suggests gregarious behavior among the Tyrannosauridae. Researchers from the American Museum of Natural History in New York City working in Alberta, Canada, found a bone bed—a deposit with fossils of many individuals—holding at least nine of *T. rex*'s close relatives, albertosaurs.

Philip J. Currie and his team from the Royal Tyrrell Museum of Paleontology in Alberta recently relocated the 1910 find and are conducting the first detailed study of the assemblage. Such aggregations of carnivorous animals can occur when one after another gets caught in a trap, such as a mud hole or soft sediment at a river's edge, in which a prey animal that has attracted them is already ensnared. Under those circumstances, however, the collection of fossils should also contain those of the hunted herbivore. The lack of such herbivore remains among the albertosaurs (and among the four-T. rex assemblage that included Sue) indicates that the herd most likely associated with one another naturally and perished together from drought, disease or drowning.

From examination of the remains collected so far, Currie estimates that the animals ranged from four to almost nine meters (13 to 29 feet) in length. This variation in size hints at a group composed of juveniles and adults. One individual is considerably larger and more robust than the others. Although it might have been a different species of albertosaur, a mixed bunch seems unlikely. I believe that if *T. rex* relatives did indeed have a social structure, this largest individual may have been the patriarch or matriarch of the herd.

Tyrannosaurs in herds, with complex interrelationships, are in many ways an entirely new species to contemplate. But science has not morphed them into a benign and tender collection of Cretaceous Care Bears: some of the very testimony for *T. rex* group interaction is partially



NIPPING STRATEGY (*above*) enabled *T. rex* to remove strips of flesh in tight spots, such as between vertebrae, using only the front teeth.



MASSIVE FORCE generated by *T. rex* in the "puncture and pull" biting technique (*above*) was sufficient to have created the huge furrows on the surface of the section of a fossil *Triceratops* pelvis (*inset*)

healed bite marks that reveal nasty interpersonal skills. A paper just published by Currie and Darren Tanke, also at the Royal Tyrrell Museum, highlights this evidence. Tanke is a leading authority on paleopathology—the study of ancient injuries and disease. He has detected a unique pattern of bite marks among theropods, the group of carnivorous dinosaurs that encompasses *T. rex* and other tyrannosaurs. These bite marks consist of gouges and punctures on the sides of the snout, on the sides and bottom of the jaws, and occasionally on the top and back of the skull.

Interpreting these wounds, Tanke and Currie reconstructed how these dinosaurs fought. They believe that the animals faced off but primarily gnawed at one another with one side of their complement of massive teeth rather than snapping from the front. The workers also surmise that the jaw-gripping behavior accounts for peculiar bite marks found on the sides of tyrannosaur teeth. The bite patterns imply that the combatants maintained their heads at the same level throughout a confrontation. Based on the magnitude of some of the fossil wounds, *T. rex* clearly showed little reserve and sometimes inflicted severe damage to its conspecific foe. One tyrannosaur studied by Tanke and Currie sports a souvenir tooth, embedded in its own jaw, perhaps left by a fellow combatant.

The usual subjects-food, mates and territory-may have prompted the vigorous disagreements among tyrannosaurs. Whatever the motivation behind the fighting, the fossil record demonstrates that the behavior was repeated throughout a tyrannosaur's life. Injuries among younger individuals seem to have been more common, possibly because a juvenile was subject to attack by members of his own age group as well as by large adults. (Nevertheless, the fossil record may also be slightly misleading and simply contain more evidence of injuries in young T. rex. Nonlethal injuries to adults

would have eventually healed, destroying the evidence. Juveniles were more likely to die from adult-inflicted injuries, and they carried those wounds to the grave.)

Bites and Bits

I magine the large canine teeth of a baboon or lion. Now imagine a mouthful of much larger canine-type teeth, the size of railroad spikes and with serrated edges. Kevin Padian of the University of California at Berkeley has summed up the appearance of the huge daggers that were *T. rex* teeth: "lethal bananas."

Despite the obvious potential of such weapons, the general opinion among paleontologists had been that dinosaur bite marks were rare. The few published reports before 1990 consisted of brief comments buried in articles describing more sweeping new finds, and the clues in the marred remains concerning behavior escaped contemplation.

Nevertheless, some researchers specu-

lated about the teeth. As early as 1973, Ralph E. Molnar of the Queensland Museum in Australia began musing about the strength of the teeth, based on their shape. Later, James O. Farlow of Indiana University–Purdue University Fort Wayne and Daniel L. Brinkman of Yale University performed elaborate morphological studies of tyrannosaur dentition, which made them confident that the "lethal bananas" were robust, thanks to their rounded cross-sectional configuration, and would endure bone-shattering impacts during feeding.

In 1992 I was able to provide material support for such speculation. Kenneth H. Olson, a Lutheran pastor and superb amateur fossil collector for the Museum of the Rockies in Bozeman, Mont., came to me with several specimens. One was a one-meter-wide, 1.5-meter-long partial pelvis from an adult Triceratops. The other was a toe bone from an adult Edmontosaurus (duck-billed dinosaur). I examined Olson's specimens and found that both bones were riddled with gouges and punctures up to 12 centimeters long and several centimeters deep. The Triceratops pelvis had nearly 80 such indentations. I documented the size and shape of the marks and used orthodontic dental putty to make casts of some of the deeper holes. The teeth that had made the holes were spaced some 10 centimeters apart. They left punctures with eyeshaped cross sections. They clearly included carinas, elevated cutting edges, on their anterior and posterior faces. And those edges were serrated. The totality of the evidence pointed to these indentations being the first definitive bite marks from a *T. rex*.

This finding had considerable behavioral implications. It confirmed for the first time the assumption that T. rex fed on its two most common contemporaries, Triceratops and Edmontosaurus. Furthermore, the bite patterns opened a window into T. rex's actual feeding techniques, which apparently involved two distinct biting behaviors. T. rex usually used the "puncture and pull" strategy, in which biting deeply with enormous force was followed by drawing the teeth through the penetrated flesh and bone, which typically produced long gashes. In this way, a T. rex appears to have detached the pelvis found by Olson from the rest of the Triceratops torso. T. rex also employed a nipping approach in which the front (incisiform) teeth grasped and stripped the flesh in tight spots between vertebrae, where only the muzzle of the beast could fit. This method left vertically aligned, parallel furrows in the bone.

Many of the bites on the *Triceratops* pelvis were spaced only a few centimeters apart, as if the *T. rex* had methodically worked his way across the hunk of meat as we would nibble an ear of corn. With each bite, *T. rex* appears also to have removed a small section of bone. We presumed that the missing bone had been consumed, confirmation for which shortly came, and from an unusual source.

In 1997 Karen Chin of the U.S. Geological Survey received a peculiar, tapered mass that had been unearthed by a crew from the Royal Saskatchewan Museum. The object, which weighed 7.1 kilograms and measured 44 by 16 by 13 centimeters, proved to be a T. rex coprolite. The specimen, the first ever confirmed from a theropod and more than twice as large as any previously reported meat-eater's coprolite, was chock-full of pulverized bone. Once again making use of histological methods, Chin and I determined that the shattered bone came from a young herbivorous dinosaur. T. rex did indeed ingest parts of the bones of its food sources and, furthermore, partially digested these items with strong enzymes or stomach acids.

Following the lead of Farlow and Molnar, Olson and I have argued vehemently that T. rex probably left multitudinous bite marks, despite the paucity of known specimens. Absence of evidence is not evidence of absence, and we believe two factors account for this toothy gap in the fossil record. First, researchers have never systematically searched for bite marks. Even more important, collectors have had a natural bias against finds that might display bite marks. Historically, museums desire complete skeletons rather than single, isolated parts. But whole skeletons tend to be the remains of animals that died from causes other than predation and were rapidly buried before being dismembered by scavengers. The shredded bits of bodies eschewed by museums, such as the Triceratops pelvis, are precisely those specimens most likely to carry the evidence of feeding.

Indeed, Aase Roland Jacobsen of the Royal Tyrrell Museum recently surveyed isolated partial skeletal remains and compared them with nearly complete skeletons in Alberta. She found that 3.5 times as many of the individual bones (14 percent) bore theropod bite marks as did the less disrupted remains (4 percent). Paleobiologists therefore view the majority of the world's natural history museums as deserts of behavioral evidence when compared with fossils still lying in the field waiting to be discovered and interpreted.

Hawk or Vulture?

S ome features of tyrannosaur biology, such as coloration, vocalizations or mating displays, may remain mysteries. But their feeding behavior is accessible through the fossil record. The collection of more trace fossils may finally settle a great debate in paleontology—the 80year controversy over whether *T. rex* was a predator or a scavenger.

When T. rex was first found a century ago, scientists immediately labeled it a predator. But sharp claws and powerful jaws do not necessarily a predator make. For example, most bears are omnivorous and kill only a small proportion of their food. In 1917 Canadian paleontologist Lawrence Lambe examined a partial albertosaur skull and ascertained that tyrannosaurs fed on soft, rotting carrion. He came to this conclusion after noticing that the teeth were relatively free of wear. (Future research would show that 40 percent of shed tyrannosaur teeth are severely worn and broken, damage that occurs in a mere two to three years, based on my estimates of their rates of tooth replacement.) Lambe thus established the minority view that the beasts were in fact giant terrestrial "vultures." The ensuing arguments in the predator-versus-scavenger dispute have centered on the anatomy and physical capabilities of T. rex, leading to a tiresome game of point-counterpoint.

Scavenger advocates adopted the "weak tooth theory," which maintained that *T. rex*'s elongate teeth would have failed in predatory struggles or in bone impacts. They also contended that its diminutive arms precluded lethal attacks and that *T. rex* would have been too slow to run down prey.

Predator supporters answered with biomechanical data. They cited my own bite-force studies that demonstrate that *T. rex* teeth were actually quite robust. (I personally will remain uncommitted in this argument until the discovery of direct physical proof.) They also note that Kenneth Carpenter of the Denver Museum of Natural History and Matthew Smith, then at the Museum of the Rockies, estimate that the "puny" arms of a *T. rex* could curl nearly 180 kilograms. And they point to the work of Per Christiansen of the University of Copenhagen, who believes, based on limb proportion, that *T. rex* may have been able to sprint at 47 kilometers per hour. Such speed would be faster than that of any of *T. rex*'s contemporaries, although endurance and agility, which are difficult to quantify, are equally important in such considerations.

Even these biomechanical studies fail to resolve the predator-scavenger debate—and they never will. The critical determinant of *T. rex*'s ecological niche is discovering how and to what degree it utilized the animals living and dying in its environment, rather than establishing its presumed adeptness for killing. Both sides concede that predaceous animals, such as lions and spotted hyenas, will scavenge and that classic scavengers, such as vultures, will sometimes kill. And mounting physical evidence leads to the conclusion that tyrannosaurs both hunted and scavenged.

Within T. rex's former range exist bone beds consisting of hundreds and sometimes thousands of edmontosaurs that died from floods, droughts and causes other than predation. Bite marks and shed tooth crowns in these edmontosaur assemblages attest to scavenging behavior by T. rex. Jacobsen has found comparable evidence for albertosaur scavenging. Carpenter, on the other hand, has provided solid proof of predaceous behavior, in the form of an unsuccessful attack by a T. rex on an adult Edmontosaurus. The intended prey escaped with several broken tailbones that later healed. The only animal with the stature, proper dentition and biting force to account for this injury is T. rex.

Ouantification of such discoveries can help determine the degree to which T. rex undertook each method of obtaining food, and paleontologists can avoid future arguments by adopting standard definitions of predator and scavenger. Such a convention is necessary, as a wide range of views pervades vertebrate paleontology as to what exactly makes for each kind of feeder. For example, some extremists contend that if a carnivorous animal consumes any carrion at all, it should be called a scavenger. But such a constrained definition negates a meaningful ecological distinction, as it would include nearly all the world's carnivorous birds and mammals.



BONE MICROSTRUCTURE reveals the maturity of the animal under study. Older individuals have bone consisting of Haversian canals (*large circles, left*), bone tubules that have replaced naturally occurring microfractures in the more randomly oriented bone of juveniles (*right*). Microscopic examination of bone has shown that individuals thought to be members of smaller species are in fact juvenile *T. rex*.

In a definition more consistent with most paleontologists' common-sense categorization, a predatory species would be one in which most individuals acquire most of their meals from animals they or their peers killed. Most individuals in a scavenging species, on the other hand, would not be responsible for the deaths of most of their food.

Trace fossils could open the door to a systematic approach to the predatorscavenger controversy, and the resolution could come from testing hypotheses about entire patterns of tyrannosaur feeding preferences. For instance, Jacobsen has pointed out that evidence of a preference for less dangerous or easily caught animals supports a predator niche. Conversely, scavengers would be expected to consume all species equally.

Within this logical framework, Jacobsen has compelling data supporting predation. She surveyed thousands of dinosaur bones from Alberta and learned that unarmored hadrosaurs are twice as likely to bear tyrannosaur bite marks as are the more dangerous horned ceratopsians. Tanke, who participated in the collection of these bones, relates that no bite marks have been found on the heavily armored, tanklike ankylosaurs.

Jacobsen cautions, though, that other factors confuse this set of findings. Most of the hadrosaur bones are from isolated individuals, but most ceratopsians in her study are from bone beds. Again, these beds contain more whole animals that have been fossilized unscathed, creating the kind of tooth-mark bias discussed earlier. A survey of isolated ceratopsians would be enlightening. And analysis of more bite marks that reveal failed predatory attempts, such as those reported by Carpenter, could also reveal preferences, or the lack thereof, for less dangerous prey.

Jacobsen's finding that cannibalism among tyrannosaurs was rare-only 2 percent of albertosaur bones had albertosaur bite marks, whereas 14 percent of herbivore bones did-might also support predatory preferences instead of a scavenging niche for T. rex, particularly if these animals were in fact gregarious. Assuming that they had no aversion to consuming flesh of their own kind, it would be expected that at least as many T. rex bones would exhibit signs of T. rex dining as do herbivore bones. A scavenging T. rex would have had to stumble on herbivore remains, but if T. rex traveled in herds, freshly dead conspecifics would seem to have been a guaranteed meal.

Coprolites may also provide valuable evidence about whether *T. rex* had any finicky eating habits. Because histological examination of bone found in coprolites can give the approximate stage of life of the consumed animal, Chin and I have suggested that coprolites may reveal a *T. rex* preference for feeding on vulnerable members of herds, such as the very young. Such a bias would point to predation, whereas a more impartial feeding pattern, matching the normal patterns of attrition, would indicate scavenging. Meaningful questions may lead to meaningful answers.

Over this century, paleontologists have recovered enough physical remains of *Tyrannosaurus rex* to give the world an excellent idea of what these monsters looked like. The attempt to discover what *T. rex* actually *was* like relies on those fossils that carry precious clues about the daily activities of dinosaurs. Paleontologists now appreciate the need for reanalysis of finds that were formerly ignored and have recognized the biases in collection practices, which have clouded perceptions of dinosaurs. The intentional pursuit of behavioral data should accelerate discoveries of dinosaur paleobiology. And new technologies may tease information out of fossils that we currently deem of little value. The *T. rex*, still alive in the imagination, continues to evolve.

The Author

GREGORY M. ERICKSON has studied dinosaurs since his first expedition to the Hell Creek Formation badlands of eastern Montana in 1986. He received his master's degree under Jack Horner in 1992 at Montana State University and a doctorate with Marvalee Wake in 1997 from the University of California, Berkeley. Erickson is currently conducting postdoctoral research at Stanford and Brown universities aimed at understanding the form, function, development and evolution of the vertebrate skeleton. Tyrannosaurus rex has been one of his favorite study animals in this pursuit. He has won the Romer Prize from the Society of Vertebrate Paleontology, the Stoye Award from the American Society of Ichthyologists and Herpetologists, and the Davis Award from the Society for Integrative and Comparative Biology. He will shortly become a faculty member in the department of biological science at Florida State University.

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