The Lovely Bones

Dinosaur fossils yield their secrets to Cal paleontologists

BY TRACY POWELL

Shamans, oracles, and parlor charlatans throughout history have made a great show of consulting bones. Whether poring over osseous auguries or tallying the carvings on tumbled bone tokens, they have tried to divine what the future might bring. These days, researchers at UC Berkeley and its Museum of Paleontology sift through bones with equal fervor (not to mention more exacting methodology), searching instead for clues to the distant past. From the broadest mapping of fossil caches to the most intimate, microscopic examination of a single slice of bone, these scientists coax from their specimens tantalizing hints about the life and times of those most intriguing of prehistoric beasts: dinosaurs.

In the Beginning

The absence of extant dinosaurs roaming the earth may relieve those of us principally concerned with not getting eaten, but it endlessly vexes paleontologists. Instead of analyzing flesh and blood specimens, they are forced to rely almost exclusively on fossils—fragmented, mineralized, imperfect remnants unable to provide direct examples of behavior or physiology. To combat these limitations, modern paleontologists have developed sophisticated analytical approaches, salvaging astonishing amounts of information from those lovely, cryptic bones.

These approaches range from small-scale, microscopic investigations to continent-spanning surveys of dinosaur fossils. Randall Irmis, a graduate student in Kevin Padian's lab in the Department of Integrative Biology, approaches his research from the broad end of this methodological spectrum. He studies the distribution of different fossil types from the Late Triassic Period (that's 230 to 200 million years ago), drawing sweeping conclusions about the trajectory of dinosaur evolution in the process.

IMAGE COURTESY OF MARK MILLER

IMAGE COURTESY OF RANDY IRMIS

Hayden Quarry, located in the mountains of New Mexico, has yeilded a number of fossils for Randy Irmis and his studies on the evolutionary trajectory of dinosaurs.

This period intrigued Irmis because sometime during that era true dinosaurs supplanted the "pre-dinosaur" reptile species (or the more tongue-twistingly technical "basal dinosauromorphs") from which they had evolved. As dynastic successions go, this transition was both monumental and mysterious: How did a single evolutionary cohort of dinosaur species rise to near-total global domination, thoroughly eclipsing their predecessors? Irmis was especially intrigued by the pace at which this transition occurred. Was it gradual, or the result of an abrupt, competitive *coup d'état*?

To find out, Irmis excavated dinosaur remains at New Mexico's Hayden Quarry site. Carefully examining each fossil's anatomy, Irmis categorized it as pre-dinosaur or dinosaur based on a number of physical characteristics—typically the presence or absence of particular ridges, bulges, and indentations on the bones. He then tracked the extent to which the two different fossil types occurred together, thereby deducing how long the groups coexisted before dinosaurs came to dominate the landscape exclusively.

Surprisingly, he found that dinosaurs lived alongside their basal dinosauromorph brethren far longer than previously thought—at least 15-20 million years, or well into the Late Triassic. (As a bonus, he also discovered an entirely new pre-dinosaur species, a terrier-sized little specimen he dubbed *Dromomeron romeri*.)

These results directly contradicted previous findings from other continents, which had suggested very little overlap between dinosaurs and pre-dinosaurs. To verify that his results were not a fluke, Irmis used his methodology to re-examine additional fossil collections stored at the UC Museum of Paleontology (UCMP) and the Texas Memorial Museum. Reassuringly, these collections shared the Hayden Quarry's overlap of dinosaur and pre-dinosaur species.

Irmis speculates that the exceptionally lengthy overlap he saw in these North American collections may be due to geography. New Mexico, Texas, and Arizona—all the sites from which his fossils were originally unearthed—lay at significantly lower latitudes during the Triassic than sites from other continents, where little to no overlap between dinosaurs and pre-dinosaurs has been reported. Something about low latitudes may therefore have allowed basal dinosauromorph species to persist for longer than they did at higher latitudes. As his research progresses, Irmis hopes to further test this hypothesis at low-latitude sites outside the Americas. A recently concluded prospecting trip to Africa suggests that a dig in Ethiopia may one day help settle the question.

Irmis's broad approach turned up valuable data about large-scale population trends, but wheedling more detailed information about dinosaurs from a mute collection of fossils requires a different approach. For example, Irmis's thesis advisor, Kevin Padian, recently employed more focused approaches to examine fossilized remains, concentrating on their physical arrangement and immediate environmental context in order to tackle a longstanding mystery in the world of fossil analysis: the opisthotonic death posture.

The Science of Snuff

"Opisthotonic" is really just a complicated way of saying "head and tail curved backwards over the spine". Because a disproportionate number of dinosaurs have been found preserved in this pose, paleontologists have concocted an impressive repertoire of explanations for the posture over the years.

Many involved postmortem weathering of the carcass: Ligaments and tendons attached to the spine might contract as they dried out, for instance, pulling the body back over itself as it decomposed. Alternatively, water currents could have caused the body to drift and settle in an opisthotonic posture. Or maybe those pea-brained dinosaurs were prone to making headfirst dives into shallow, muddy pools—their contorted crash-landings could then be preserved in the fossil record like some prehistoric sports blooper reel.

Everyone had a favorite explanation—some canny, some crackpot—but for nearly a century nobody bothered to test this motley collection of competing hypotheses methodically. To correct this oversight Padian's collaborator, Museum of the Rockies researcher Cynthia Marshall, undertook a grisly course of research. It has long been clear that dinosaurs were constructed along the same general lines as today's animals—particularly birds, their modern-day cousins. Marshall therefore concluded that dinosaur cadavers would have behaved much like those of modern animals and set to work, meticulously measuring the decaying carcasses of great horned owls, red-tailed hawks, falcons, quail, and even a few dissected slabs of beef from the local grocery store.

Several barrels full of dead birds and some seriously odiferous experiments later, it was clear that postmortem conditions were unlikely to have produced the pose noted in so many fossilized dinosaurs. Bird corpses refused to do the opisthotonic limbo even after months of drying—as *rigor mortis* set in, they just stiffened up in whatever posture they'd been plopped down. Allowing them to decay under high-salt conditions (previously suggested to promote additional tendon shrinkage) produced briny tanks of bobbing bird bodies, but no opisthotonus. Similarly, fresh beef tendons allowed to dry while pinned to a styrofoam board failed to generate enough physical force to dislocate the pins, let alone warp an entire dinosaur skeleton.

It seemed that drying of the corpse could not have produced the opisthotonic posture. Careful examination of the scientific literature allowed Marshall and Padian to similarly discard other explanations. An ill-considered dinosaur nose-dive into the shallow end of the pond, for instance, would be expected to produce a cracked skull or broken neck. Neither is apparent in most of these fossils. Also missing at the site of most opisthotonic fossil finds are ripple marks or a heterogeneous mixture of sediment sizes, both hallmarks of water currents that could have swept dinosaur corpses into the pose.

If not desiccation, water currents, or sheer dinosaur dumbness, then what could explain all those opisthotonic fossils? "Without attempting a Jurassic version of the detective shows *CSI* or *Cold Case*," suggest Marshall and Padian in their 2007 *Paleobiology* paper, "inferences about circumstances of death may be possible for some fossil[s]". As Marshall had observed during prior veterinary training, many contemporary species display the opisthotonic posture, for a variety of unpleasant reasons. Suffocation, diseases such as meningitis or tetanus, or malnourishment can all produce opisthotonus. Thus, rather than telling paleontologists about the conditions the corpse faced after death, the posture may actually betray what the dinosaur experienced as it expired.

Opisthotonic dinos most likely suffered agonizing deaths, contorted in their final moments by asphyxiation, poisoning, or neurological trauma. Though grim, this insight provides a fascinating snapshot of the environmental challenges dinosaurs might have faced. Toxic algal blooms! Noxious volcano fumes! Bacterial epidemics! These scenarios provide hypotheses for opisthotonic fossil finds that can now be tested by examining the bones' immediate environments for clues, such as signature volcanic chemicals or preserved traces of lethal toxins.

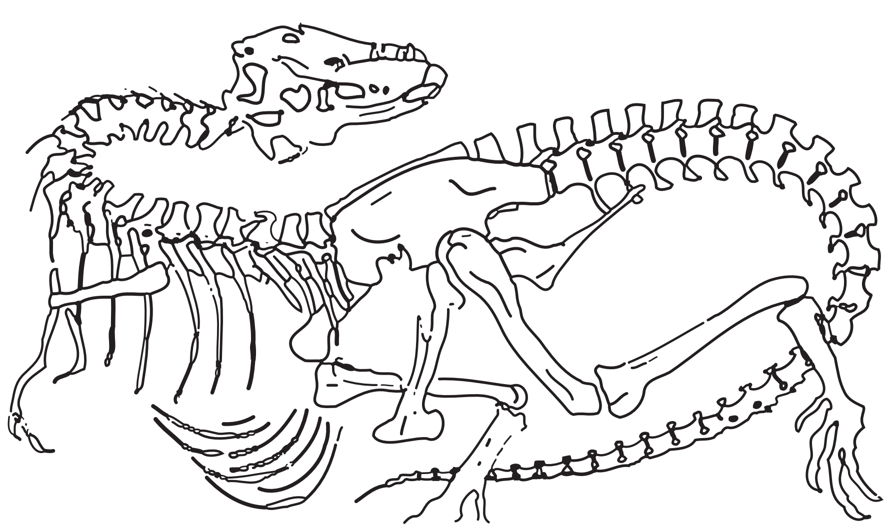
Growing Pains

Though Marshall and Padian gathered valuable information about dinosaur mortality by capitalizing on a fossil's arrangement and environmental context, even closer attention can be lavished upon individual bones to learn more. With detailed studies of fossilized bone structure, Padian and his colleagues use their knowledge of how bones develop in modern organisms in order to piece together biological details about long-deceased species.

A living bone is a busy place. A matrix of cells is embedded in a honeycomb scaffold of calcium, phosphate, and collagen fibers, and shot through with blood vessels industriously shuttling minerals and proteins from place to place. As an organism develops, its bones continually undergo changes in chemistry and architecture that persist long after living bone has transformed into mineralized stone. Damaged bones, for instance, bear signs of the new tissue growth that knit them back together. Similarly, normal bone growth follows a predictable pattern, digesting older bone near the central marrow and depositing new bone on the outer rim. Because this process occurs in a yearly cycle of fast and slow bone deposition, telltale annual rings are laid down—broadly spaced if an animal is growing rapidly, densely spaced if its growth has slowed.

Much as a tree's rings can be read for information about its age and past environmental conditions, the rings and scars of fossilized bones can be interpreted to gain information about a dinosaur's age, health, and behavior. Unfortunately, understanding "dinosaur growth rings" is much more complicated than scanning the clockwork annual depositions of a redwood.

This was clearly demonstrated by Padian's earlier investigations, in which he used a *T. rex*'s bones to establish the dinosaur's age. In collaboration with Jack Horner, a researcher



The cause of the opisthotonic pose in which many dinosaur remains are found is under debate by paleontologists.

Illustration by Minh Nguyen

at the Museum of the Rockies, he used a light microscope to examine thin cross-sections from the specimen's femur, tibia, and fibula (the equivalent of your thigh and shinbones), seeking to count rings of bone growth. Unfortunately, although annual bands of growth were clearly visible, the constant, inward-out remodeling of the living bones had eroded away inner rings even as new growth was added to the outer rim. Thus, a bone with seven rings' worth of growth could have come from a seven-year-old dinosaur, or a seventeen-year-old dinosaur with the innermost ten rings worn away by normal developmental processes.

Had a series of juvenile *Tyrannosaurus* fossils been available, Padian could have directly measured the rate and age at which growth rings began to disappear, then used that information to deduce how many rings had been lost in mature specimens. Unfortunately, since the fossil record has been stingy with pint-sized *T. rexes*, Padian was forced to make a more indirect estimate. By applying what was known about the growth patterns of dinosaurs closely related to *T. rex*, he calculated how many additional rings would have fit into the bones' hollowed-out central spaces. This allowed him to generate a likely age range for each bone's owner.

This approach provided a jumping-off point for graduate student Sarah Werning's more recent research, which addressed a new question: At what age would a *Tyrannosaurus* settle down and hatch up a brood of carnivorous little hellions? There have been no nesting sites excavated, after all, no jackpot discoveries of fossilized little Rex Juniors frolicking at mom's side, nothing that might tell us what family life was like at the top of the Cretaceous food chain. There isn't even a reliable way of telling whether a fossilized dinosaur was male or female! An estimation of when reproductive maturity occurred would provide at least a glimpse into these animals' sexual behavior.

To estimate when *T. rex* and two related dinosaur species reached sexual maturity, Werning and Robert Lee, then a graduate student in the Padian lab, drew upon an unusual feature of avian reproductive biology. In many bird species, new, ephemeral bone tissue forms in the skeleton's interior hollows just before ovulation. Called medullary bone (MB), this tissue acts as a calcium reservoir shortly before egg fertilization, after which it is rapidly dissolved back into the bird's body and its minerals redeployed to the developing eggshell. Thus, though the presence of MB is transitory, it indicates that the bird has reached reproductive maturity.

Due to the evolutionary link between dinosaurs and birds, researchers believed that MB might also indicate reproductive readiness in dinosaurs. This hypothesis turned out to be very labor-intensive: Of the hundreds of fossils paleontologists have examined, only three have been found to contain MB—two of which were identified by Werning and her colleagues. This is an unsurprisingly small proportion, given that MB would only be expected to make a few, fleeting appearances over the course of a female's reproductive life, and only some of these females would make their way into the fossil record.

For each of the three MB-containing specimens found to date, Werning applied Padian's "ring-counting" method and other techniques for estimating the dinosaur's age at the time of death. Her results indicated that *Tyrannosaurus* females were capable of reproducing at *or before* the age of 18. (Researchers have no way of knowing whether the fossil's MB was making its first appearance, or if the

Headbutter's Ball

Image courtesy of Mark Goodwin

Along with the much-maligned scientists who recently demoted Pluto, you have UCMP researcher Mark Goodwin to thank for debunking a treasured scientific myth: Dinosaurs probably did not use their headgear for dueling.

Poring over wafer-thin sections of more than thirty dome-headed dinosaur (pachycephalosaur) skulls with a microscope, Goodwin and his colleagues realized that they bore no signs of the remodeled fractures or healed-over wounds that you would expect from cranial combat. Similarly, though previous reports suggested that the domes were packed with radiating structures that could help diffuse the stress of impact, these structures were only briefly present at early stages of development. Mature specimens (presumably the guilty headbutters) had neither these nor any other adaptations that would help them withstand the smack of skull against skull.

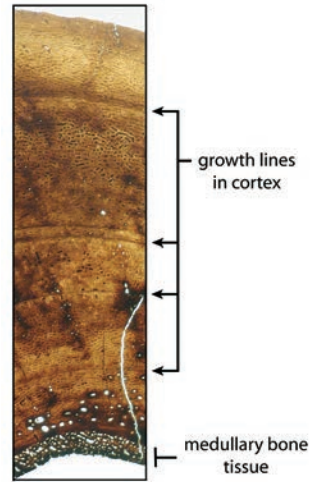
Sad though we may be to relinquish that beloved, B-movie image of two dinosaurs knocking noggins, Goodwin has furnished the scientific world with a consolation prize. His more recent work suggests that the distinctive domes, horns, frills, and ridges that decorate dinosaur skulls may instead help paleontologists identify an individual's developmental stage.

Most parents can attest that teenagers often seem like a different species. But in the case of *Stegoceras*, another, smaller dome-headed dinosaur species, researchers actually *did* mistake a juvenile for a distinct animal, due to differences in both the size and shape of the skull. However, when Goodwin lined up an array of these specimens, it was clear that the skulls came not from distinct species, but rather from individuals of different ages along a developmental continuum. Though a juvenile's skull looks very different from an adult's, the inclusion of intermediate developmental stages clearly illustrates a process of elaborate cranial erosion and deposition as the dinosaur matured. Those aptly named dome-headed dinosaurs did not start life with their lofty pates in place; only continuous remodeling of the skull during adolescence produced that big, irresistible bulb.

Goodwin suggests that, rather than combat, these dinosaurs' distinctive silhouettes may have signaled which individuals belonged to the same species, helping them to identify potential rivals or herd members. Particularly given that these features were expressed near the onset of adulthood, that come-hither headgear may also have indicated a dinosaur's readiness to mate

Intriguingly, Goodwin has also found remnants of collagen fiber in the bone of some *Triceratops* skulls. In modern bird bills, such fibers anchor a tough, skinlike layer of keratin to the underlying bone. He therefore speculates that the unique skull morphology of these decorated dinosaurs may have only been part of the show; like modern birds such as cassowaries and toucans, brightly colored keratin may have completed their display.

Images courtesy of Matt Wedel and Andrew Lee



(left) Dinosaurs bones, like those of Tenontosaurus, *grow in much the same way that trees add rings to their trunks and branches. Pneumaticity helped large dinosaurs save on weight, much the same way it does for modern birds. (center) A turkey vertebra with the front sanded off. (right) An* Apatosaurus *vertebra that has been similarly eroded.*

dinosaur had already reproduced multiple times prior to its death.) *Allosaurus* and *Tenontosaurus*, the other two dinosaur species examined, exhibited MB by about ten and eight years, respectively. This means that in all three species, dinosaurs reached reproductive maturity at only one-third to one-half of their projected adult size—years before they had finished growing.

Sly references to teenage pregnancy aside, this research has several important implications for dinosaur biology. For one, it indicates that their growth patterns were more similar to reptiles and large mammals, which reach reproductive maturity relatively early, than to birds and small mammals, which typically attain full size before reproducing. In living species, such accelerated reproduction usually occurs in animals that experience high adult mortality. This observation led the researchers to suggest that dinosaurs may have evolved early reproductive strategies in order to offset harsh conditions and low rates of adult survival.

Airheads

Clearly, bones can tell us complex stories about dinosaurs' behavior and environment. But structures such as MB or growth rings only provide part of the plotline—many other skeletal characteristics are also mined for information. Like Werning, former UCMP researcher Matt Wedel (he recently accepted a lectureship at UC Merced) examines dinosaur bones closely, searching for morphological similarities between dinosaurs and their avian descendents. But rather than medullary bone, he looks for evidence of pneumaticity, or the hollowing out of bones by air-filled sacs.

Most schoolchildren can tell you that birds' skeletons are hollow, rendering them lightweight enough to soar over earthbound, heavy-boned clodhoppers like us. These hollow, or pneumatic, spaces in the bone come in the form of many small, air-filled cavities that riddle the skeleton. Pneumatic spaces form early in development, when four flexible, membrane-bound chambers attached to the lungs begin to sprout extra projections that balloon forcefully into the growing bone, forming hollow pockets. Though the remaining scaffold of bone is strong, it is extremely lightweight, and the skeleton can be as much as 85% air space by volume in birds like the pelican.

To verify that dinosaurs and birds shared a pneumatized skeletal system, Wedel examined the internal structure of dinosaur backbones, using both vertebral cross-sections and X-ray images taken using a standard medical CT scanner. His recent efforts focus on some of the largest dinosaur species—*Apatosaurus*, *Diplodocus*, and *Sauroposeidon* (a fifty-ton whopper whose individual vertebrae can clear four feet).

His research suggests that while an average dinosaur bone runs about 60% air space by volume, neck vertebrae from these gigantic sauropod species can reach 90% air—"up in the styrofoam range," as Wedel describes it. Such high levels of pneumatization often accompanied increased body size in sauropod evolution. Wedel therefore believes that these humongous dinosaurs offset their extra skeletal mass by increased pneumatization, which would simultaneously preserve the strength and minimize the weight of their massive bones.

Beyond the presence of pneumatized bone in dinosaurs, Wedel has also shown that pneumatization occurred via the same process as in modern birds. Shortly after hatching, for example, a chicken's air sacs begin their pneumatic invasions at opposite ends of the spine. Over the first few months of a chick's life, these intrusions invade bone progressively closer to the middle of the spine, rather like two trains chugging towards each other on the same track. Occasionally, the two converging engines of pneumatization lose momentum and stop before meeting in the middle, leaving the central vertebrae more solid than their neighbors. By determining that the central vertebrae of some adult dinosaurs were significantly less pneumatized than vertebrae closer to the head and tail, Wedel confirmed that the same developmental pattern seen today in birds was already at work in their distant ancestors, millions of years ago.

In future research, Wedel hopes to determine just how typical this sauropod pattern of pneumatization was amongst dinosaurs, inspecting specimens such as *Allosaurus* for similar developmental trends. Because the same sacs that cause pneumatization are involved in oxygen exchange, he is also working to mine this data for further information about dinosaurs' respiratory systems. Were dinosaurs sluggish titans, or athletes? The amount of oxygen they could extract from each lungful of air would determine how much physical activity their bodies could sustain. By clarifying whether they used their air sacs to breathe in the same highly efficient way that birds do, he hopes to better understand dinosaurs' metabolic capabilities.

Rock On

Seeking further insights into dinosaur biology, Mark Goodwin, Wedel's colleague at UCMP, employs an even more intimate approach to studying fossils: examining their individual chemical components. This includes looking at characteristics such as the types of minerals present or the proportion of certain isotopes present in a bone. (Isotopes are elemental variants in which the atom has the expected number of protons, but a different number of neutrons.)

Scientists have long used bone chemistry to test hypotheses about dinosaurs' diets, physiology, and habitat. But many of these studies assumed that chemical data from fossils directly represented the original chemistry of the bones during the animal's lifetime. Goodwin suspected that this assumption was too simplistic. As a bone becomes fossilized, its organic portions are degraded by bacteria and replaced by minerals in the environment, transforming the bone's physical and chemical properties. Goodwin therefore believed that conditions in the burial environment could profoundly influence a fossil's chemistry—in which case chemical data might inform scientists less about dinosaurs' lifestyles than about the postmortem environment of the fossil.

To help clarify the extent to which burial environment can alter bone chemistry, Goodwin conducted two studies. The first profiled fossils from a collection of hadrosaurs and marine reptiles buried in the same marine sediments. Though these hadrosaurs' bones were presumably chemically similar in life, some were buried in freshwater sediments deposited by rivers and streams near where they lived, while others ended up buried in deep ocean marine sediments. "These unfortunate few were likely 'bloat and float' carcasses that washed out to sea," explains Goodwin. By showing that the isotope profiles were different between the two groups of bones, Goodwin demonstrated that postmortem burial environment impacts fossil chemistry.

Goodwin further illustrated this point by examining chemical variation between dinosaur skeletons from diverse latitudes, ranging from southern Alaska to the American southwest. For these more detailed chemical analyses, Goodwin used a diamond saw to excise thin sections of fossilized bone, which were then cemented to slides and placed in a proton induced X-ray emission machine (PIXE, pronounced "pixie"—the technology even Tinker Bell could love). PIXE works by running a focused beam of protons across a sample, which responds by emitting X-rays. The exact X-ray signature varies according to the elements and isotopes present, informing researchers which chemical constituents are present, in what quantities, and where exactly in the sample they are located. The result was a detailed, three-dimensional chemical map of each bone sample.

Goodwin's data made a strong case for the burial environment's contribution to fossil chemistry. Many of the dinosaur bones were enriched in iron and manganese, with a corresponding depletion in calcium and phosphorous—a product of the fossilization process, in which minerals from the environment replaced the bones' original material. Similarly, a fossilized *Dilophosaurus* (perhaps more familiar as "that spitting dinosaur" from *Jurassic Park*) sitting in the red, iron-oxide rich landscape of Arizona contained massive levels of arsenic—up to 46,270% higher than fresh bone tissue and significantly higher than similar fossils found in other locations. Other researchers had proposed that such elevated arsenic levels were evidence the dinosaur had died of arsenic poisoning. Goodwin instead suggested that the postmortem environment was responsible: As iron replaced the bone's original chemical compounds during mineralization, naturally occurring arsenic in the environment was adsorbed and concentrated onto the iron, saturating the bones as they aged.

> "The bone is like a sponge; it's very porous."

Goodwin asserts that though it *is* possible to recover informative chemical data from fossils—the harder, more durable tissue of tooth enamel is a particularly valuable alternative to bone—researchers must be cautious about drawing scientific conclusions based on fossil chemistry. Far from simply providing a paleobiological or environmental record from when the dinosaur was alive, these fossils also chronicle their own myriad chemical interactions with the burial environment after death.

Such interactions complicate the use of fossilized bones to answer questions about dinosaur life histories. But they also make fossils fascinating archives of the prevailing geological conditions during the millennia in which they formed. In this sense, Goodwin's research has revealed fossils and the fossilization process to be both more complex and more informative than previously imagined.

Skeleton Crew

Popular depictions of the average dinosaur researcher restrict her to two primary activities: *tap-tap-tap*ping away at half-buried skeletons with a pick, or proudly standing in front of a fully assembled, dramatically posed skeleton, like a child completing an outsized set of Triassic Tinker-Toys. But as these UC Berkeley researchers demonstrate, a paleontologist's work is much more varied, requiring exhaustive analysis of fossils at every possible level of examination.

From large-scale observations such as the geological conditions where the fossils are discovered, the types of fossils found nearby, and the bodily arrangement of individual skeletons, right down to microscopic analysis of a bone's tissue structure and chemical profiling of ts chemical constituents, a wide range of scientific techniques are exhausted in order to extract every last scrap of information.

The result is a forensic masterpiece. With each experiment, researchers paint an increasingly detailed picture of the life and times of dinosaurs—how they came to dominate the landscape so thoroughly, and how they went about their daily business of survival, procreation, and death. Through modern scientific innovation and good, old-fashioned paleontological sleuthing, these scientists reconstruct the circumstances of a prehistoric world and its mysterious, magnificent inhabitants.

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Want to know more? Check out:
Randy Irmis' field notes:
`http://www.ucmp.berkeley.edu:80/science/profiles/irmis_0705.php`

and Matt Wedel's blog post on pneumaticity:
`http://svpow.wordpress.com/2007/11/03/tutorial-3-pneumaticity`