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Introduction

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It was Roy Chapman Andrews who convinced me as an eleven-year-old to make a career out of hunting dinosaurs. He did not do this directly, of course, but his book *All about Dinosaurs* had such an impact on me that I found myself scrounging up everything I could get on dinosaurs. One of my first prizes in this quest was an Audubon sticker book about prehistoric animals. I often sat and admired the stickers, which were reproductions of the stunningly beautiful color paintings that Charles Knight had done for the Field Museum of Natural History. Such was the power of those images that they worked their way into my dreams, and started to shape my understanding of how dinosaurs interacted with each other and their environments. A year later, a family vacation took us to the hallowed halls of the Field Museum in Chicago, where I stood in open-mouthed wonder in front of the giant murals that had been reproduced in my sticker book. To this day, those paintings are burned deeply into my memory, and Charles Knight is the director of my imaginary Museum of Dinosaur Art!

Charles Knight's influence stretched much further than the minds of eleven-year-olds. Even a quick survey of dinosaur art done before the 1970s reveals that he was the main inspiration for most of the book illustrators and museum artists depicting dinosaurs and other prehistoric beasts. If copying is considered to be a form of flattery, he was clearly well admired by artists depicting prehistoric animals for novels, cartoons, comic books, and a host of other fictional spin-offs.

The artwork created by Knight was so powerful that his images continued to leave a strong impression on both public and scientific minds long after his death. Most people were loath to see their childhood images of prehistory changed when a wealth of new information became available in the 1970s. Ever so slowly at first, the subconscious, inertial reactions

were overcome by new and better evidence that came with the development of the "Dinosaur Renaissance" (Bakker 1975). Once the changes started, they opened up the floodgates for a whole new generation of artists producing completely original dinosaur art (Crumly 2000). The influence of Charles Knight may be less obvious in the work of these new artists, but there can be no denying that they are carrying on traditions with their foundations in Knight's work.

There are many reasons for Knight's long-standing popularity. His drawings and paintings are aesthetically pleasing. But more important, he was able to instill his considerable knowledge of anatomy (of both modern and fossil animals), ecology, and animal behavior into his artwork to create realistic, believable, lifelike scenes.

Knight learned much through his long association with professional paleontologists such as Henry Fairfield Osborn of the American Museum of Natural History. Although he did the best that he could in terms of accuracy, our ideas about prehistoric animals are constantly evolving and changing as new information is acquired from the fossil record. This includes the discovery of more complete fossils, and the acquisition of new or better information through further study of existing specimens and fossil sites. Therefore, even though Knight's illustrations were as accurate as they could have been at the time he did them, changes in our knowledge base have dated some of his illustrations.

Life through the Ages was both illustrated and written by Charles Knight, and was published in 1946. In many ways it was a remarkable book, far ahead of its time. It is only recently that it has become common for illustrators to write their own text for popular books (Paul 1988; Dixon 1993). Knight's text not only provides the reader with information, but also gives some insight into his artwork, explaining the decisions he made in composing the illustrations. Knight was a proponent of using the present as a key to understanding the past, and the book is a precocious combination of prehistoric and recent biology. He was able to make his extinct animals come to life, and after more than half a century, many of the illustrations are still scientifically sound. This is particularly true for those animals with living relatives, such as members of the cat, dog, elephant, and horse families. Restorations of other animals, however, would be done differently by modern artists, who benefit from the changes that have occurred in our knowledge over the last half-century. Similarly, there are many ways that Knight would have done things differently if he were still alive to see how our knowledge of prehistoric animals has changed. Some of the

most profound changes in our understanding of extinct life forms have taken place with dinosaurs. As dinosaur research is the field that I know and love the best, I will use them as an example of how Knight might have done things differently if he were alive today.

Knight starts his book not with dinosaurs, but with the Burgess Shale fauna from British Columbia. In recent years, this and similar soft-bodied Cambrian faunas from other parts of the world have attracted ever-increasing amounts of attention. As Knight stated, "there is still a good deal of dispute as to their actual affinities."

Sauropods were seen by Knight and his contemporaries as "water-living dinosaurs," each of which "spent practically all of its time in the water, feeding on soft vegetation which it bit off with its small finger-like teeth," and which were too heavy to hold up their own weight on land. These incredible animals, which include the longest (*Diplodocus, Seismosaurus*), heaviest (*Argentinosaurus*), and tallest (*Brachiosaurus, Ultrasauros*) species of land-dwelling (terrestrial) animals known, were one of the most successful lineages of dinosaurs. They lived almost worldwide, and their history spanned virtually the entire Jurassic and Cretaceous. It had long been thought that sauropods spent most of their time in the water, which would have supported their enormous body weights. This may have been true for some species, but many lines of evidence (including studies of their distribution and their trackways) have shown that sauropods were capable of walking efficiently on land. In fact, some may have sought their food high in the trees, browsing much like modern giraffes. Sauropod teeth are relatively small and weak compared with overall body size. However, it was not necessary for them to be strong, because they functioned only to comb off branches, and had no role in chewing. The vegetation was swallowed without any further processing in the mouth. The "chewing" was done by gastroliths, stones swallowed and held in a muscular sac in the digestive system. Many modern birds swallow pebbles, which are used for much the same function. Stones are held in the muscular gizzard to grind up seeds and other vegetation. The advantage for sauropods to have used the same system as in birds is that they were able to keep the weight of their teeth to a minimum. This was critical for a sauropod because of the enormous length of the neck, which can be as long as the rest of the body. It would have been mechanically inefficient for a sauropod to have such a long neck if the head were too heavy. Small teeth meant that the skull could be kept small, and having relatively weak jaws that were not involved in chew-

ing meant that the jaw muscles could also be kept small. Selection may even have favored the development of relatively small brains in sauropods as a means of reducing weight. Although the teeth of sauropods may have been relatively weak, they were still more than adequate to ingest a variety of plants, and these did not have to be soft water plants, as was once thought. In fact, sauropod teeth often show extreme wear, and the presence of several generations of germ teeth beneath each functional tooth suggests that teeth were replaced frequently.

Although their feeding strategies may still be a controversial topic, very few modern depictions show sauropods floating in the water. This was once the common belief, and was based on the supposition that sauropods were so large and heavy that they needed to spend most of their lives in water to buoy up their great weights. Evidence—including dinosaur trackway sites, the analysis of skeletal structures, and the recovery of sauropods from regions that were relatively dry when the animals lived there—now suggests that most sauropods were probably more comfortable on land than they were in the water. In spite of his belief that sauropods lived mainly in the water, Knight seemed to hedge his bets in his illustrations, because he often showed them both on land and in the water.

An interesting aside in the text is that sauropods "probably had living young." This idea has most recently been championed by Bakker (1986), whose evidence seems reasonable. However, sauropod eggs are known from many parts of the world (Carpenter 1999), some with embryos inside (Chiappe 1998). The fact that sauropods are known to lay eggs does not, however, eliminate the possibility that some species may have given live birth. This is an attribute that can develop in select species within animal lineages that normally lay eggs, including insects, fish, amphibians, and reptiles.

Knight dealt with *Tyrannosaurus rex* as the final dinosaur because it was "the grandest and fiercest dinosaur"—"the last tremendous example of a mighty race." *T. rex,* probably the best-known dinosaur, may well have been "an enormous eating machine with an insatiable appetite," but among dinosaurs it was reasonably well endowed with a larger than average brain. By the end of the Cretaceous, there was a tendency toward increased brain size for almost all dinosaurs, and it was necessary for the King Tyrant to keep pace with its prey (ceratopsians and hadrosaurs). As Knight pointed out, *T. rex* was the culmination of millions of years of theropod evolution, and it was the most highly specialized large carnivore that we are aware of. In recent years, larger theropods have

been discovered in Argentina (Coria and Salgado 1995), but these carcharodontosaurids had smaller brains, lacked binocular vision, and were stouter, slower animals with relatively short lower leg proportions. No other animal is known with the biting power of *T. rex,* which had enough strength in its jaw muscles to drive the disproportionately long, heavy teeth right into or through the bones of its victims (Erickson and Olson 1996).

The illustration of the two tyrannosaurs fighting would have been done differently if Knight had had access to the information available today. First and foremost, the lizard-like tails would not have been on the ground. They were reconstructed too long in the original American Museum skeletal mounts (complete tails of *Tyrannosaurus* were unknown until recently). Although they may have touched the ground periodically, they were balancing organs that served the animal best by being held in a more horizontal position off the ground. To conserve energy, overlapping parts of the vertebrae and the chevrons beneath them helped to prevent the tail from drooping. The heavily scaled skin of the tyrannosaur drawing is probably incorrect as well. At least three tyrannosaur specimens have been found in recent years with patches of preserved skin. Although the skin is not known from the entire surface of the body, those patches suggest that tyrannosaurid hides had lightly pebbled surfaces. Tyrannosaurs appear to have been social animals that hunted in packs (Currie 2000), and apparently engaged in aggressive behavior with each other (Tanke and Currie 2000). This seems to have consisted mostly of face biting, which may have been related to sexual interaction as in modern animals such as sea otters.

The conventional wisdom at the time that Knight wrote his book was that *T. rex* was descended through a lineage of theropods that became progressively larger from Triassic through Jurassic to Cretaceous times. In recent years, evidence has emerged to suggest that *Allosaurus* and tyrannosaurs are not particularly close in relationship, and that in fact *T. rex* has closer ties with animals such as *Ornithomimus* and *Velociraptor.* Similarities between *Tyrannosaurus* and *Allosaurus* are attributed to mechanical problems related to large size. As large animals, they both had to reinforce and modify their skeletons in similar ways, in spite of the fact that they had different family backgrounds. Curiously, the fact that *Tyrannosaurus* and its kin (*Albertosaurus, Gorgosaurus, Tarbosaurus,* etc.) are overgrown coelurosaurs (a name applied to a suite of generally small, meat-eating dinosaurs) was recognized by Frederick von Huene in 1926 when he established the basic division of flesh-eating dinosaurs into two groups—the diminutive coelurosaurs (including

Compsognathus, Ornithomimus, Troodon, and *Velociraptor*) and the giant carnosaurs (*Acrocanthosaurus, Allosaurus, Megalosaurus*).

Stegosaurus is an animal with a reputation for having a small brain relative to its body size. Knight referred to it as the "stupidest member of a very moronic family." Stegosaurs are now known from Africa, Asia, Europe, and North America, and had a long history within the Jurassic and Cretaceous (Galton 1997). Like ankylosaurs and sauropods, stegosaurs did have relatively small brains, but they still managed to be relatively successful. Fortunately for them, large brains are not essential for survival, and they survived for long enough to spread across the globe. Furthermore, there has always been some doubt concerning the relationship between brain size and "intelligence."

Styracosaurus may have been a formidable animal "with his nose horn and sharp turtlelike beak," but Knight was incorrect when he suggested that it sometimes had to fend off a hungry *Tyrannosaurus.* The two animals both lived in western North America, but *Styracosaurus* was extinct at least five million years before the first *Tyrannosaurus rex* appeared. Nevertheless, *Gorgosaurus* and *Daspletosaurus,* earlier members of the family Tyrannosauridae, probably did hunt and kill *Styracosaurus* whenever they could. "*Styracosaurus* was really a harmless old fellow, a vegetable feeder, armed only for defense against marauding flesh eaters." Knight, like most of his contemporaries, believed that the frills over the necks of horned dinosaurs were to protect them from tyrannosaurs. In recent years, a lot of work has been done on ceratopsian bonebeds in Alberta and Montana. These seem to represent mass death assemblages of herds of *Centrosaurus, Einiosaurus, Pachyrhinosaurus,* and *Styracosaurus.* The spiked frill may have helped protect the neck of an adult *Styracosaurus* to an extent, but the frills of young individuals were short and lacked spikes. There is even some indication that the frills and spikes differed between adult males and females. Given the fact that tyrannosaur jaws were capable of biting through even thicker bones than the neck frill of *Styracosaurus,* and the fact that only the adults had well-developed frill spikes, it seems more likely that the frills developed into such fantastic forms in horned dinosaurs so that they could visually recognize other members of their own species. Dinosaurs were apparently highly visual animals, and seem to have used frills, spikes, crests, horns, and other visual cues to attract potential mates, and perhaps even to establish dominance within social groups. This was probably important at the time *Styracosaurus* lived (about 75 million years ago), because horned dinosaurs were

at their peak of diversity, and many closely related species lived in the same region. It would have been very easy to make mistakes that would have resulted in unproductive matings. The extreme differences in the frills and horns of ceratopsian adults emphasized species differences, making it more likely that adults would recognize and mate with only members of their own species.

"If ever a treasure was unearthed among all the various remains that have come down to us through the years, surely it is *Archaeopteryx,* the answer to the fossil-hunters' prayer." In spite of a virtual "gold rush" of new early bird fossils from northeastern China, including approximately a thousand specimens of the early Cretaceous *Confuciusornis, Archaeopteryx* is as critical to our understanding of bird origins today as it was when Knight wrote this statement in 1946.

In rereading *Life through the Ages,* I was surprised to read that Knight believed that *Archaeopteryx* was a link between theropod dinosaurs and modern birds. He specifically states that "we shall see pictures of dinosaurs and the birdlike forms which we think may have descended from them." It becomes evident later in the book that the "birdlike forms" include *Archaeopteryx* and several toothed birds from the Cretaceous. This statement, as much as any, shows his belief that dinosaurs were involved in the ancestry of birds. This was not a new idea in 1946. The hypothesis had been worked out by Huxley in 1868 and was widely accepted for the rest of that century. In 1916, Heilmann published a thorough analysis of the evidence for bird origins in his native Danish. Although his work did not have much impact at first, this changed dramatically when *The Origin of Birds* appeared in English (Heilmann 1927). He felt that *Archaeopteryx* was anatomically closer to coelurosaurian dinosaurs such as *Compsognathus* than to any other known animals. This demonstrated to him that birds and dinosaurs were closely related. However, several features suggested to him that dinosaurs were not directly ancestral to birds. For example, the clavicle or collar bone had never been reported in a dinosaur. Birds have clavicles, just as most fish, amphibians, reptiles, and mammals do. If dinosaurs lacked clavicles, this was a specialization that indicated they could not be bird ancestors. After all, if they had lost their clavicles, how could their descendants get them back? Because birds retain the clavicle, then, their ancestor must have still had one. Heilmann felt that if dinosaurs had not given rise to birds, then their ancestors, at that time known as thecodonts, must have. Thecodonts at least still had their clavicles. This was the prevailing theory until the 1970s, when several opposing ideas arose. Regardless of Heilmann's view, Knight clearly

thought there was a relationship between birds and dinosaurs. He described *Allosaurus* as "a plucked turkey with a long tail and little front legs with claws instead of wings." "Indeed, as we study them closely, their birdlike affinities become more and more apparent as we shall later see in the *Archaeopteryx* (the bird reptile), a sort of little dinosaur with wings instead of front legs, and feathers, which further enhanced the birdlike appearance."

Between the publication of the Danish and English editions of *The Origin of Birds,* the first wishbone was found in the dinosaur *Oviraptor.* Unfortunately, it was misidentified as a different bone (an interclavicle) for another fifty years. New discoveries and careful reexamination of previously collected specimens have now shown that the wishbone is present in many lineages of theropod families, including tyrannosaurids. The mass of evidence gathered since Knight's book was published strongly favors the hypothesis that birds are the direct descendants of theropod dinosaurs. In fact, the distinction between the two has become blurry with the discovery of at least five species of "feathered" dinosaurs since 1996. Under a modern biological or paleontological classification, birds are even considered to be a subgroup of theropod dinosaurs. In that sense, birds are dinosaurs and dinosaurs are not extinct.

One of Knight's favorite subjects for illustration, birds are compared and contrasted in a suite of sketches. From ancient to modern, he depicted the toothed (yet highly specialized) Hesperornis, the somewhat comparable modern loon, and the gigantic *Phorusrhacus* (*Phororhacos*), looking like some Mark II *T. rex.* As he points out in the text, "our actual knowledge of fossil bird forms is scant, for the fragile skeletons of these flying creatures were easily destroyed." In recent years, fossil sites around the world have produced a wealth of new specimens of early birds. Several of these animals, including more than a thousand specimens of *Confuciusornis* from the Early Cretaceous of China, have feathers for display purposes, including crests on the head and a pair of long tail feathers reminiscent of those of a modern lyretail. Even earlier forms, such as the feathered dinosaur *Caudipteryx* from the same beds, also appear to have developed long feathers on the arms and tail for the purpose of display (Currie 1998). This makes Knight's statement that "there were no beautiful feathered beings in our early world" all the more curious.

Knight showed *Archaeopteryx* sharing a perch with *Rhamphorhynchus,* a pterosaur from the same time and place. It was the old facing the new—the beginning of the end for the pterosaurs. Although flying reptiles were very diverse and successful in coloniz-

ing the air, the new feathered fliers were ultimately more efficient, better fliers that slowly replaced their distant cousins. By the end of the Cretaceous, birds had won out in most niches, although they left the role of giant gliders to flying reptiles such as Pteranodon (shown in the next picture with mosasaurs).

Knight shared with many of his contemporaries the idea that dinosaurs were "slow-moving dunces" that were "unadaptable, and unprogressive." None of these descriptive terms are correct for the Dinosauria overall, but they might be applied to certain species in the same way that mammalian sloths are slow, and dodo birds were unadaptable. Although dinosaurs were generally not large-brained animals, some species had brain sizes that were within the lower limits for modern mammals and birds. *Troodon,* from the Late Cretaceous of North America, had a brain six times larger than that of a crocodile of equivalent body weight. Regardless of brain size, dinosaurs seem to have been extremely well adapted to their world, and indications suggest that they were intelligent enough to have developed complex behaviors and social structures that are generally thought of only in the context of birds and mammals. Many dinosaurs, including the wiry *Velociraptor* and the long-legged ostrich-mimic dinosaurs, seem to have been well adapted for moving quickly. And even the diminutive *Sinosauropteryx* was fast enough to catch and consume lizards and mammals. Throughout their history, dinosaurs had been highly adaptable, and had maintained their role as the dominant land animals even though they were sharing their world with mammals, birds, crocodiles, turtles, lizards, and many other animals that still live with us today. Over the last few decades, the image of dinosaurs has been completely "made over," and it is no longer appropriate to consider them "stupid, unadaptable, and unprogressive."

Knight painted a pretty bleak picture of the end of the Cretaceous period, "with huge, bizarre and ungainly shapes rising and subsiding in the landscape, the earth covered with harsh and brittle scrub under tall palmettos, while both on the ground and in the trees, small, sinister, bright-eyed mammals awaited the slow but inevitable finale of the great Reptilian Era." In truth, most of the Late Cretaceous environments inhabited by dinosaurs were not dissimilar from many modern environments. Flowering plants had already appeared millions of years earlier, and the variety of habitats available for dinosaurs to live in was almost as varied as our modern world. Insects, fish, turtles, lizards, crocodiles, birds, and mammals would have been hard to distinguish from modern forms on the basis of superficial examination. Al-

though dinosaurs would have appeared unusual to us at first, they in fact filled in niches that are today occupied in many parts of the world by equally bizarre animals. Think of the African veldt, for example, with a variety of species of crested duckbilled dinosaurs instead of antelopes and gazelles. Or herds of horned dinosaurs rather than the great herds of bison that used to cover the plains of North America. Is a giraffe any less bizarre than a long-necked sauropod? And was there anything so strange in dinosaurs as the elephant's nose? It was certainly a different world from any we know today. But it was not so foreign from modern environments that we could not relate to it.

During Knight's entire career, dinosaurs were considered to be reptiles that were best understood by studying modern reptiles such as crocodiles and lizards. To Knight and many of his contemporaries, dinosaur extinction made sense because "Nature had apparently grown weary of the great scaly cold-blooded monsters. They had been in existence too long. . . . And so the world was to grow away from these slow-moving dunces, and little warm-blooded beings, furry, alert and aggressive, were to supersede them."

Although the present may be the key to the past, it does not always unlock the door that you expect it to. It had long mystified people that dinosaurs, which were mere reptiles, could dominate the world for at least 140 million years. This was especially perplexing when one considers that mammalian history stretched back as far as or farther than the earliest dinosaurs. In other words, mammals were contemporaries of dinosaurs, and not just successors. With the beginning of the Dinosaur Renaissance (actually more like a "revolution"), paleontologists finally started to challenge the concept that dinosaurs were nothing more than overgrown lizards and crocodiles. We started to question whether or not dinosaurs really were cold-blooded (Bakker 1975; Desmond 1975). We became aware of more "intelligent" dinosaurs with brains as large as some mammals and birds (Russell 1997). We learned unexpected things about dinosaurian behavior (Horner 1997). The widespread acceptance of phylogenetic systematics, in conjunction with the fact that birds are probably the direct descendants of theropod dinosaurs, even leads us to question whether or not dinosaurs are extinct. Dinosaurs (if we include birds) are still more speciose than mammals, and in that sense are still more successful. Dinosaurs were different in many ways from modern lizards and crocodiles, and in some ways it is more appropriate to compare them with modern birds and mammals. But even that must be done with great

caution, because dinosaurs were unique animals that were well adapted to the Mesozoic world, not to our world. Today, paleontologists tend to look at both birds and crocodiles, the two closest living relatives of dinosaurs, for clues to define the limits of dinosaurian biology. Dinosaurs may also, however, have had traits that were unique to them.

Life through the Ages is a wonderful retrospective view of science as it was more than half a century ago. Yes, there are the occasional errors, and it needs to be read with a grain of salt. But it helps us understand the mindset of an era when paleontology was still a young science. It is also a window into the mind of one of the greatest artists of prehistoric life. None can deny the tremendous impact his images had on the development of at least the public perception of the history of life.

People are probably more interested in Charles Knight now than they have been in the last half-century. He was even introduced as a fictional "character" in the Imax film entitled *T. rex: Back to the Cretaceous.* Knight's artwork, published here and widely available for the first time in five decades, should inspire a whole new crop of prehistoric artists!

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T. rex: Back to the Cretaceous. Imax film.