effected. The spreading of the flight membrane, which is supported by five, six, or seven elongated ribs, is accomplished by the use of a few muscles, particularly the iliocostalis and the intercostals, while the arching and the stiffening of the ribs are performed by the very long, slender muscle slips that run along the length of each rib. The wings in *Draco*, when expanded, provide a flight surface that is very similar in relative extent, and thus of wing loading, to that in the large soaring birds. Perhaps this similarity is due to the fact that the lizards and the birds in question, though quite dissimilar in size, have similar problems of aerodynamics. The significance of the adaptation for gliding in *Draco* is twofold. First, it represents the one example among modern reptiles for aerial locomotion through considerable distances. Second, although in itself perhaps comparatively recent in reptilian evolution, it seems to represent the earliest type of aerial locomotion to be adopted by the vertebrates. Recent studies of fossil lacertilians of Triassic age show adaptations for gliding that are remarkably similar to those in *Draco*. Hence it is probable that the first aerial vertebrates were reptiles equipped to glide from tree to tree on expanded membranes supported by elongated ribs, leaving all four limbs free for arboreal and terrestrial locomotion. Apparently such adaptations for flight preceded by several million years the first attempts at true flight, attained by the pterosaurs. Thus, looking at *Draco*, we are, in effect, looking back through some 200 million years, to view the manner in which backboned animals first took to the air.

BIOGRAPHICAL SKETCH

Remembrances of Edwin H. Colbert, Paleontologist

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Photographs courtesy of the author except where indicated.

My grandfather, Edwin Harris (Ned) Colbert, had a long and distinguished career in vertebrate paleontology. Much of this was at the American Museum of Natural History (AMNH) in New York, where he started as a graduate research assistant, and wound up as Chairman of the Department of Fossil Vertebrates. He made good use of the museum's world-class fossil collections and was involved in a number of great fossil discoveries around the world. One of the most significant was the late Triassic Ghost Ranch Quarry of New Mexico, where he recovered multiple skeletons of the early dinosaur *Coelophysis*, a discovery that profoundly influenced our understanding of early dinosaur evolution. These global travels also took him on a pioneering trip to Antarctica, where his fossil finds supported emerging plate-tectonic theories. His outstanding publication record includes more than 300 published papers and two textbooks. He also wrote a number of popular books on dinosaurs (including a few targeted at young readers), on plate tectonics, a biography, and two autobiographies. In many ways, his legacy to the field of paleontology was as much a consequence of his efforts at reaching out to the general public, as was his scientific output. Rather than summarize this remarkable career, I here attempt a more intimate portrait using the excavation of *Coelophysis* at Ghost Ranch as a vignette to better understand his life.

Ned Colbert in his office at the American Museum of Natural History, ca. 1940s.

When I knew him, my grandfather's research focused on Triassic terrestrial vertebrate faunas from around the world. This research program incorporated newly emerging plate-tectonic theories to explain the distribution of ancient faunas. You can imagine my surprise to find that he wrote a couple of papers on fossil tapirs, a group I now study and one that didn't originate until the Cenozoic! To compound the somewhat inbred feeling that gave me, one of these papers actually reinterprets an earlier tapir-paper by my namesake, great-grandfather William D. Matthew, whose daughter my grandfather had married. Only then did I come to realize the extent of grandfather's work in the middle to late Cenozoic, the study of which was the focus of his Ph.D. dissertation and early career.

My earliest memories of my grandparents predate grandfather's retirement from the AMNH in 1969. My family lived in

My grandfather, brother, and I striking an American Gothic pose. I am on the right.

New York City, and we would often visit on weekends. My mother would take my brother and me to see Grandpa at the AMNH. Like most children, we loved the Jurassic and Cretaceous dinosaur halls that he had designed (now redesigned in a phylogenetic arrangement). I vaguely recollect his Fifth Floor tower office, which commanded a beautiful view of Central Park, and have dim memories of a large mounted theropod skull near his desk. However, I most vividly remember the little plastic dinosaurs he would give us.

I have more concrete recollections of my grandparents after their 1969 move to Flagstaff, Arizona, when I was six. From that year until my graduation from high school, my brother and I would spend part or all of our summer vacations with them. I continued to visit until grandfather passed away in November 2001, at the age of 96. He remained active, having an emeritus position at the Museum of Northern Arizona (MNA). Although he stopped doing active fieldwork near the end of his life, he continued writing, and was working on a book about his Antarctic trip when he died.

Partly as a consequence of my grandfather's presence, the MNA Geology program had attracted a number of bright young paleontologists. As a volunteer in the 1970s, I had the opportunity to see my grandfather interact and work with both staff and visiting scientists. My grandfather had a down-to-earth and generally humble demeanor. Only as I got older did I begin to understand the respect and honor accorded 'Ned' by his peers.

Flagstaff was a nice place to retire for many reasons, but I am sure that part of the call was its proximity to the great Triassic-aged rocks in the southwestern desert. In these rocks, he had made his first great Triassic discovery. Before he worked on dinosaurs (and other Mesozoic and Paleozoic vertebrates), Edwin Colbert worked on fossil mammals.

He was a Midwesterner, born in Clarinda, Iowa in 1905, and raised in Maryville, Missouri. He received his undergraduate degree from the University of Nebraska in 1929. There he worked as a research assistant at the paleontology museum. This training spurred him to pursue paleontology as a graduate student at Columbia University under the tutelage of William K. Gregory. His Ph.D. dissertation examined the extensive collection of Cenozoic mammals from the Siwalik Hills of India.

The strength of his dissertation led him to a job at the AMNH, where he continued to publish on Cenozoic mammals. He thoroughly enjoyed these studies, and would have been happy to make a career out of researching fossil mammals, but opportunities for career advancement were slim at the time, especially because of the crowded field working on fossil mammals. So, when recommended for a position as Curator of Fossil Reptiles and Amphibians, he changed his research direction. He had always had an interest in ancient reptiles, and the switch of focus also made available the extensive dinosaur collections housed at the AMNH.

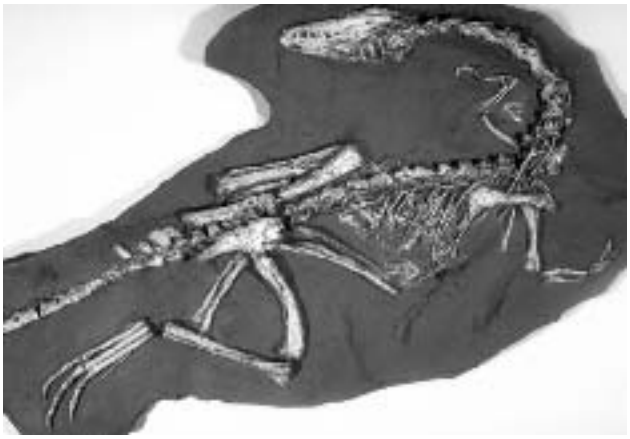
The collections included fragments of a little dinosaur called *Coelophysis* that had been collected in the late 19th century from northwestern New Mexico. Although only preserved as a few postcranial fragments, these fossils provided a glimpse of what the earliest dinosaurs were like, a key to understanding their subsequent modifications. His realization of the significance of these fossils was further solidified when he had the opportunity to do a little fieldwork in the late Permian of north Texas with paleontologist Al Romer. These earlier Permian faunas were characterized by a markedly different assemblage of animals, the dominant components of which were large amphibians and synapsids (the lineage that ultimately gave rise to mammals). By contrast, these animals were represented only as relicts in the Triassic faunas, which were instead dominated by archosaurs (which included many crocodile-like forms and early dinosaurs). A major faunal transition separated

Ned Colbert relaxing at his Flagstaff, Arizona home.

A photomosaic of Ghost Ranch, northern New Mexico. The reddish sediments exposed below the lowest cliff represents the Triassic Chinle Formation.

ERA	PERIOD	MA
CENOZOIC	QUATERNARY	1.8
	TERTIARY	65
MESOZOIC	CRETACEOUS	
	JURASSIC	
	TRIASSIC	248
PALEOZOIC	PERMIAN	
	CARBONIFEROUS	
	DEVONIAN	
	SILURIAN	
	ORDOVICIAN	
	CAMBRIAN	543
PRECAMBRIAN		

A summary of the geologic timescale



Skeleton of *Coelophysis*. Image courtesy of the University of California Museum of Paleontology.

the two time periods, and Colbert was confident that the ancestry of the Dinosauria was to be found in the Triassic.

With this idea in mind, in the summer of 1947, he petitioned for and obtained permits to collect fossils in the extensive exposures of the Triassic Chinle Formation in the Petrified Forest National Park of northeastern Arizona. Colbert and George Simpson, a paleontologist who was Colbert's superior at the museum set out by train for Albuquerque, where they met their field crews and vehicles. The plan was for Simpson, who studied fossil mammals, to collect from the Tertiary sediments in the San Juan Basin of New Mexico. Meanwhile, Colbert, after spending a few days in Simpson's camp, was to drive with his crew to find ancient reptiles and amphibians. Just east of Simpson's camp, however, were some nice exposures of Triassic rocks in an on-and-off dude ranch called Ghost Ranch. This area had been worked years before by Charles Camp, a paleontologist from the University of California. Colbert had spent a summer at Berkeley a few years earlier and had had the opportunity to see Camp's collections from both Ghost Ranch and Petrified Forest. Thus, on a whim, he decided to take his crew there for a week or two of prospecting for fossils before heading west to the Petrified Forest.

Ghost Ranch was — and is — a beautiful place. Nestled in a canyon, it boasts spectacular cliffs with rock formations covering the different Mesozoic periods. Triassic-aged rocks are represented by the Chinle Formation, a rock body whose sediments document the passage of a large river system that flowed west from Texas to the coast, which at that time was somewhere in present-day Nevada. Colbert and crew were welcomed there by

the owner, Arthur Pack, who kindly gave them permission to poke around and collect what they found.

Years before, Charles Camp had found numerous skeletons of large crocodile-like animals called phytosaurs from the low badlands of Ghost Ranch. Not surprisingly, then, Colbert and his crew found a nice fossil phytosaur skull on their first day of fossil hunting. They spent about three days collecting it, and then opted to do a little more prospecting before heading west. On a hunch, Colbert decided that they would work some small side-canyons instead of prospecting the flats, as had previously been done. There, George Whitaker, one of Colbert's crew, found some delicate bones, including a small claw, weathering down a talus slope. Excitedly, Whitaker brought the fragments to Colbert, who immediately recognized that they pertained to *Coelophysis*.

Whitaker showed Colbert the spot, and they worked their way up the slope until they discovered the layer from which the bones were weathering. After some cleaning with brushes and awls, they soon realized that they were looking at articulated skeletal remains. At this point, Colbert had to make a decision: Stay in Ghost Ranch and sacrifice the hard-won permits for Petrified Forest, or abandon the site and head west — but the question was really moot, you stick with the fossils in hand.

With these thoughts, Colbert contacted George Simpson and told him of the find. Simpson arrived the next day, and realizing that this was probably the finest Triassic vertebrate site in the world, agreed that they should abandon their Petrified Forest plans. But how much more was to be found? Perhaps the site only extended another couple of inches into the hill, and the steep slope meant that the farther they dug in, the more sediment they would have to remove from above the fossils. This sort of digging was frustrating, as loose dirt and rocks would keep tumbling down from above. More than an annoyance, these rock-falls could easily damage the extremely fragile bones that were emerging (not to mention those working on them!). Accordingly, they spent several days, and considerable effort with picks and shovels, clearing a platform several feet into the slope, a foot or two above the bone-layer.

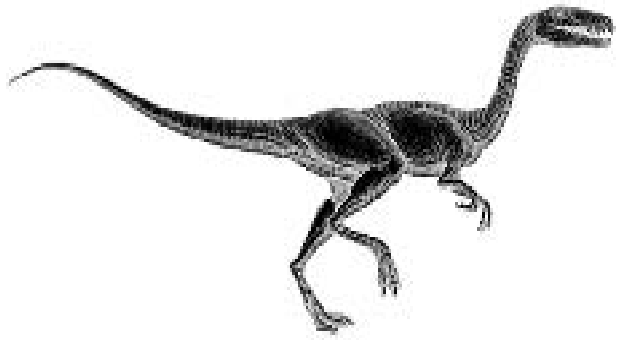
Ned Colbert near some ancient channel sandstones and conglomerates.

Ned and Margaret Colbert at Ghost Ranch, New Mexico. Margaret is the daughter of a prominent paleontologist, William Diller Matthew.

For every two feet they dug into the slope, the hill rose about a foot. So, when they had finished their platform, they had a small cliff six or seven feet tall at the back of the quarry. They then carefully sunk a couple of small test pits at the base of this little man-made cliff. The moment of truth was approaching, and it was with great joy that they were rewarded by the sight of more bones.

The work was long and tedious. The bones were too fragile and too densely packed to remove one-by-one, instead requiring excavation as a series of large blocks that eventually revealed a mass-grave containing the skeletons of hundreds or perhaps thousands of individual *Coelophysis*. Indeed, the bones were so tightly packed that digging channels between the blocks to separate them was impossible without destroying some bones. The field season lasted into September, and the crew also worked all the next summer. They removed a total of thirteen large blocks, which they shipped back to the AMNH for controlled preparation in the lab. Although the bed was still yielding bone, they decided to stop quarrying after the second season, to allow preparation and description of the material, before going back to collect more.

The exceedingly delicate bones demanded great care in preparation. In fact, preparation of the blocks collected in the summers of 1947 and 1948 was so time consuming that it is incomplete to this day. Enough was revealed, however, to allow Colbert to begin the research process. First of all, the skeleton of *Coelophysis* could now be described thoroughly, revealing itself to be a long-necked, lightly-built biped about 6 to 11 feet in length and standing about 3 feet tall at the hip. It had strong hind legs that were well suited for fast running. Its long bones are hollow, a characteristic for which it was named (*coelo* = hollow, *physis* =



Reconstruction of *Coelophysis*.

form). The skull is gracefully constructed with sharp, recurved, and serrated teeth well adapted for a diet of meat. Although details of the anatomy are specialized, in its overall aspect the skeleton of *Coelophysis* provided a nice model of the earliest theropod dinosaurs.

A brief digression on dinosaur classification is necessary here. The Dinosauria comprises two great groups, the Ornithischia and Saurischia. Ornithischians are herbivorous, and include such animals as the horned and frilled triceratops, duck-billed dinosaurs, armored ankylosaurs, and plated stegosaurs. Saurischians, on the other hand, split into two main lineages, one leading to the giant herbivorous sauropods (e.g., the brachiosaurs) and the other to the theropods, which includes all carnivorous dinosaurs (such as *Tyrannosaurus* and *Velociraptor*) and birds. *Coelophysis* is one of the earliest theropod dinosaurs.

A great size-range was represented in the dinosaurs from the quarry, including fully adult forms and presumed juveniles. A size disparity among adult specimens suggests that *Coelophysis* exhibited sexual dimorphism. One specimen has the remains of a juvenile *Coelophysis* contained within its ribcage. The position of the specimen within the ribcage and its preserved condition suggested to Colbert that it was a victim of cannibalism. The accumulation of skeletons and partial skeletons found at Ghost Ranch begs the question of how they all wound up there. Although other species are represented in the quarry, the prevalence of *Coelophysis* suggested to Colbert that these animals might have lived in a group or herd that met its demise as the result of a flood or some other catastrophic event. In any case, this find gave Colbert the unparalleled opportunity to study variation and growth in a 225-million-year-old animal.

Colbert's formal description of the *Coelophysis* specimens recovered from Ghost Ranch was published as a Bulletin of the Museum of Northern Arizona in 1989 — 42 years after the initial discovery. Although he felt that this description did not do justice to the site, he also realized that it needed to be published. He always seemed a little embarrassed about the amount of time it took from discovery to publication. Of course, he had lots of excuses. Not only were the blocks extremely time-consuming to prepare, but he also had other projects that demanded his time. He continued his descriptions of Triassic life, including the gliding reptile *Icarosaurus*, which led to the study of *Draco*, reprinted here. He also was involved in the creation of the great dinosaur halls in the AMNH and had many other obligations as a museum curator.

Perhaps one of his biggest distractions from the *Coelophysis* project was his trip to Antarctica in 1969, where he recovered Triassic vertebrates. The worldwide distribution of these animals helped solidify the newly emerging theories of plate tectonics, and his description of these fossils and their implications to the past connections of continents occupied most of his research during the 1970s.

The last of his published works dealing with *Coelophysis* was a popular book called "The Little Dinosaurs of Ghost Ranch," which recounted his experiences, and presented the story as a paleontological case study, and on which (in addition to his autobiographies) I have largely based this account.

As mentioned previously, grandfather had a prodigious publication record. Part of his success was a well-defined work ethic. He was able to compartmentalize his life quite effectively, and established personal routines that enhanced his productivity. For example, when I knew him as a 'retiree' in Flagstaff, he would walk to his office for a morning of work, and then walk home for lunch at noon. This was followed by an afternoon nap, and then another hour or two of work in the late afternoon before dinner and relaxation. However, these rather strict routines did not mean that he was inflexible.

He remained open-minded and fair throughout his life. As much as he loved paleontology, I think he loved nature even more. I remember his enjoyment watching the squirrels and birds that would come to the feeder in Flagstaff. Ahead of his time, he did not believe in growing lawns in a desert, and left the Arizona meadow and forest intact on their couple of acres. He learned to identify all of the wildflowers that could be found in their little meadow, and delighted in monitoring their appearance after the Arizona summer monsoons. He always exhorted me to observe living animals in order to better understand long-extinct fossil forms. I remember attending a lecture that he gave to the general public, which ended with a slide of the planet Earth from space. Although this was a talk about dinosaurs, he felt it his duty to remind the audience that this is a small world on which we live, and we should treat it with love and respect.

Ned Colbert preparing for fieldwork in Antarctica. His discoveries of Triassic vertebrates there helped solidify emerging plate-tectonic theories.