How to Make a Fossil: Part 1 – Fossilizing Bone

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ABSTRACT

Fossils are a physical record of the history of life. Although most people know what a fossil is, few have any idea how fossils form, or they have misconceptions about the process. In this first article, the processes involved in the fossilization of bone are presented, using a Stegosaurus *skeleton as an example. This case study, based on an actual example, begins with the death of the* Stegosaurus *due to illness and stress brought on by a drought. It continues through the stages of decay, which sets the stage for eventual fossilization. Although some strictly chemical processes are involved, experimental work has shown that the vast majority of the fossilization is due to mineral precipitation by bacteria. Bacteria feed on the organic material contained within the bones and attach their metabolic waste on various atoms or molecules, such as iron or carbonate, dissolved in ground water. The result is the formation of minerals, such as iron carbonate (siderite) or calcium carbonate (calcite). It is the formation of these minerals that basically turns "bone to stone."*

INTRODUCTION

It seems fitting that this first issue of the *Journal of Paleontological Sciences* should have an article about how a bone becomes a fossil. Most people interpret the word "fossil" to mean "the remains of an extinct organism". While technically true, what about the unaltered bones of a coyote (*Canis latrans*) from the Ice Age (i.e., Pleistocene - 10,000-1.8 million years), or the feeding trace of a Cambrian trilobite? Perhaps we should refine the definition to "the remains or traces of an organism older than 10,000 years." Indeed, this is currently the most accepted definition by professional paleontologists. Bones that are younger can be referred to as sub-fossils.

Unlike the unaltered bones of the Pleistocene coyote (from Porcupine Cave, Colorado), most fossils have been altered in some way. How such alterations occurred has long been an interest of mine, especially since I felt that the standard chemical and physical model of fossilization could not explain all fossils. Something seemed to be missing. That something has been discovered in recent years through experimental work, including my own. Surprisingly, bacteria and other microbes are now known to play a crucial role in fossilization. How the very small make it possible for us to study the very big is one of several topics I hope to share in a series of articles on fossilization.

HOW TO FOSSILIZE A DINOSAUR: DEATH AND BURIAL

"Take one dinosaur bone and bury rapidly..." But how fast is to bury rapidly? This vague term refers to any amount of time needed to bury a carcass or bone before it is destroyed. How rapidly that destruction would otherwise occur depends a great deal on the environment. A carcass laying frozen on the ground in Siberia will last much longer than one in Death Valley; but one in Death Valley will last longer than one in Louisiana. In each case, there is an increased level of microbial, insect, and physical-chemical activity. Microbial decay is highest when conditions are warm and moist; insect activity when conditions are warm and dry (Gill-King 1997); and physical-chemical when the bone is exposed to chemical and physical forces. Some of the important physical factors include temperature and humidity, and some of the chemical factors include water and soil acidity. The fastest destruction of bone can occur in a matter of minutes (e.g., fire), but such conditions are not considered the norm for bone destruction. The study of what happens to an organism after death is a sub-discipline of paleontology, called taphonomy (Greek *taphos* = burial + *nomos* = law). Taphonomy seeks to answer the many questions surrounding a fossil deposit: What killed the organisms, or why do the fossils occur the way they do? Gross as it may seem, studies of animal and human deaths and what happens to the cadavers provide important background for interpreting what may have happened in the past (Fig. 1; Corfield 1973; Hillman and Hillman 1977; Coe 1978; Conybeare and Haynes 1984; Gill-King 1997). Such studies are examples of where the present is a key to understanding the past (e.g., Carpenter 1987). Taphonomy will help set the stage for understanding the fossilization of the *Stegosaurus* skeleton discussed below.

Figure 1 – (JPS.P.07.0001) *Studies of what happens to modern carcasses helps us to understand fossil deposits. This horse, a drought victim, shows evidence of scavenging.*

The specimen (Denver Museum of Natural History 2818) was mostly articulated, meaning that the bones were in their proper anatomical position (Fig. 2). It was found lying on its back, with the rib cage collapsed into the body region and the skull upside down. The tail was on its left side with its plates preserved in their natural position. A mass of small bone disks, called ossicles, were found on one side of the skull, but they still retained their position relative to one another. Oddly, the forelimbs were missing, carnivorous tooth marks occur on one toe bone and one spike is missing half its length, but shows extensive alteration of the bone surface. The skeleton lay in a grey mudstone containing numerous separated bones of fish, an aquatic turtle, crocodiles, a pterosaur, other dinosaurs and mammals. Charcoal was found scattered throughout the sediments. The abundance of aquatic animals, including the fish, pond turtle and crocodile bones suggest that the grey mudstone was deposited in a pond, whereas the charcoal shows that one or more forest fires had swept through the area. The fire was probably caused by a dry thunderstorm, similar to those that sometimes accompany droughts today. Based on the taphonomic data it is possible to present a reasonable hypothesis about the cause of death and burial of the *Stegosaurus*.

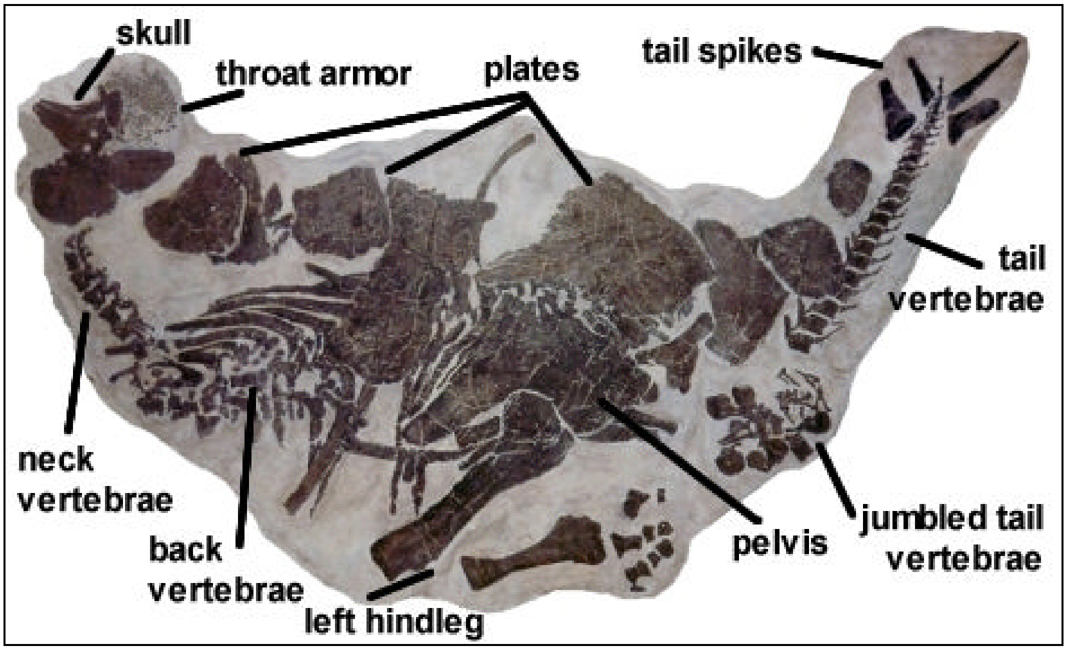

Figure 2 – (JPS.P.07.0002) *Cast of the skeleton of* Stegosaurus *(DMNS 2818) excavated in 1992. This view is of the underside and shows most of the bones in their anatomical position.*

About 150 million years ago, during the Late Jurassic, a *Stegosaurus* lay dying in a small pond. How much water was present, if any, is unknown. A month or so earlier, the *Stegosaurus* had an unpleasant encounter with a large predator, possibly *Allosaurus,* and lost half of a tail spike (Fig. 3A; McWhinney and others 2001; Carpenter and others 2005). Such damage to *Stegosaurus* spikes is not rare. About 10% of 51 spikes analyzed show breakage of the tip during life (McWhinney and others 2001) indicating that *Stegosaurus* did indeed use the spike as a weapon. Further proof came from an *Allosaurus* vertebra with clear signs of having been stabbed by a spike (Fig. 3B,C; Carpenter and others 2005). Not surprisingly, the spike that was broken in half became infected as indicated by the distinctive lace-like (filigree) growth of the bone around the injury. This does not mean that the *Stegosaurus* was regrowing the spike. Rather, the injury was being sealed with new bone (Ham and Harris 1971; Farrow 1999). This bone infection, called osteomyelitis, spread throughout the spike and into the base of an adjacent one. The effects of the infection, however, were eventually felt throughout the body as the infective microbes were spread by the blood and lymph systems. Most likely the infectious microbe causing the infection was the bacterium *Staphylococcus aureus,* which is the most common microbe causing osteomyelitis today (Resnick and Niwayama 1995).

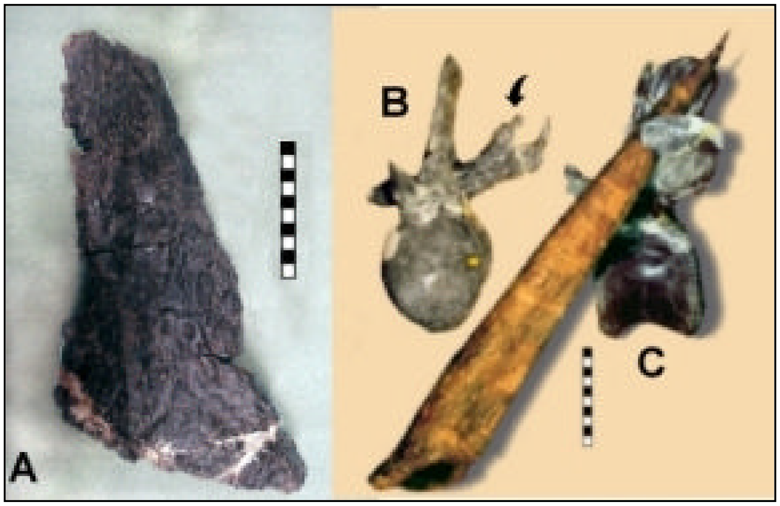

Figure 3 – (JPS.P.07.0003) *Evidence that* Stegosaurus *used its tail spike as a weapon include a damaged spike (A) and a punctured tail vertebra of* Allosaurus *(B), which deflected a fragment of bone (arrow). Note how well a spike fits the puncture (C).*

The timing of the stegosaur's death probably occurred during the dry season or one of the numerous droughts that affected the region. Evidence for the drought includes charcoal found in the sediments beneath the *Stegosaurus* skeleton, which indicates that forest fires must have occasionally raged through the region. Such fires were probably sparked by dry lightning storms. Droughts are also a time of stress for large animals because they have so little food and shade (Corfield 1973; Hillman and Hillman 1977; Conybeare and Haynes 1984; Carpenter 1987). Usually starvation and heat stress kill large animals, not the lack of water because water is often present in permanent rivers and lakes. Large animals, such as the *Stegosaurus*, are closely tied to water for drinking and especially for relief from heat stress (Behrensmeyer and Boaz 1980; Haynes 1991). Being distantly related to crocodiles, *Stegosaurus* had no sweat glands and had to rely on evaporation of water off the skin to cool the body. As rivers dry to a trickle and small lakes dry to mud holes, it becomes harder for larger animals, such as the *Stegosaurus,* to find enough water in which to lie. It seems probable then, that the *Stegosaurus* had sought refuge in a small, drying pond. Its death may have been due to heat stress or to malnutrition, as commonly affect large animals during drought. During a drought, herbivorous animals must travel progressively farther from water for food as local vegetation is eaten or trampled (Conybeare and Haynes 1984). The effects of a prolonged starvation diet, where the body does not receive enough nourishment, causes problems with the body's metabolism and immune system. These problems are greater for sick animals, such as the *Stegosaurus* with the infected spike, and they are often the first to die (Hillman and Hillman 1977).

The *Stegosaurus* apparently died on its left side as indicated by the position of the tail. Decomposition soon set in, the details of which, we know from various studies of modern carcasses (Coe 1977; Coe 1978). Decomposition can be divided into chemical-physical and microbial. Chemical decomposition begins within an hour or two after death when rigor mortis occurs as the glycogen (the storage form of glucose) in the muscles break down into lactic acid. This in turn causes clumping of proteins (actin and myogen) causing the muscles to stiffen. Within a day or two the proteins would break down further and the muscles would relax. Meanwhile, red blood cells would also physically break down, a process called hemolysis. This break down releases hemoglobin, the molecule in the blood cells that transports oxygen. Because hemoglobin is rich in iron, it was probably an important source for the iron found in the fossilized bones (more on this below). Within other tissue cells, such as the membrane lining of the gut, the cells self-destruct, a process called autolysis. That break down is caused by enzymes that are present within the cells. The proteins released by this process are broken down further by enzymes in a process called proteolysis. The result is a rich broth of proteoses, peptones, polypeptides, and amino acids, which is a great medium in which to grow microbes (yeast, fungi and bacteria). The biochemicals provided microbes, especially bacteria, with three essential ingredients: Nutrients (especially carbon, nitrogen, etc.), electrons to convert the biochemicals to a useable state and energy to fuel the conversion. The bacteria break down the biochemicals into molecules and atoms that they can use in metabolism, and in the process release waste that can in turn be utilized by other bacteria or cause mineral precipitation (more below). For the microbes then, the dead *Stegosaurus* was simply a five-ton mound of food.

Microbial decomposition begins slowly soon after death. Without the body's defenses to keep the microbes, especially bacteria, in check, they would thrive at an exponential rate. Bacteria would do exceptionally well in the environment of a warm, moist gut. Most of these bacteria were already present in the body at the time of death (Burn 1934a,b). Because of this, a diseased body decomposes faster than an undiseased one. For the *Stegosaurus*, the bacterium associated with the infected tail spike, *Staphylococcus*, was already widespread throughout the body. This bacterium was joined by the gut flora, especially *Escherichia coli*, which spread by way of the lymph and blood systems (Burn 1934a,b).

The speed of bacterial growth and decay of the *Stegosaurus* was temperature dependant (the body had lots of moisture in the tissue so water was not a concern). Considering that global climate during the Late Jurassic (Demko and Totman Parrish 1998; Totman Parrish and others 2004) was warm and poles ice-free, the air temperature must have been rather high, perhaps over 100°F (38°C) during the drought when the *Stegosaurus* died. We can therefore be certain that bacterial growth was very rapid (as was proteolysis, which is also temperature dependent). Whatever oxygen might have been present within the body (e.g., in the lungs and oxygenated blood) was soon used up by bacteria, and most decomposition must have continued anaerobically, without oxygen. Many bacteria are switch-hitters, in that they will use oxygen for metabolism when it is available, or use alternative sources if it is not available. Fungi, however, require oxygen so continue as decomposers only in those parts of the body where oxygen is present (eyes, ears, nostrils, and mouth if open).

Outwardly, the *Stegosaurus* carcass would have initially shown little sign of the internal decomposition taking place, but within a few hours the body would begin to bloat (Fig. 4). The head, body, tail, and limbs would have swollen as gases became

Figure 4 – (JPS.P.07.0004) *Bloated carcass of the Stegosaurus lying in a pond that was drying out during a drought. The smell of decay attracts a scavenger (right distance)*

trapped beneath the skin. Eventually, even the thick hide at the bottom of the feet would become distended. The gasses originate through fermentation by anaerobic bacteria. These bacteria can function without oxygen to meet their energy needs. Instead, they get the required energy by splitting complex organic molecules into simpler ones through fermentation. The gases produced by this process include sulfur dioxide, hydrogen, carbon dioxide and methane. However, it is the distinctive, sweetish odor of putrefaction, putrescine and cadaverine that draws the attention of scavengers. Insects are often the first to arrive, although during droughts, they can be absent (Hillman and Hillman 1977). Unfortunately, if insects were attracted to the *Stegosaurus*, they left no trace. We do know that a large predator, possibly *Allosaurus*, did arrive. One of the stegosaur's bony hooves from the right hind foot shows parallel grooves caused by the sharp teeth. The marks suggest that the scavenger tugged at the foot although it did not eat it. The scavenger then apparently turned its attention to the distended stomach. Opening the stomach cavity would have vented the decomposition gases and the carcass would have collapsed. That explains why the right rear leg was found partially displaced. As it collapsed across the pelvis it pulled two of the pelvic bones, the ischium and pubis, with it.

Both forelimbs are missing on the *Stegosaurus* skeleton, so the scavenger probably pulled them off at some point. In struggling with the carcass, the *Allosaurus* put a great deal of stress on the base of the tail causing some initial tearing of the tissue and forcing the body to partially roll onto its back. Much of the *Stegosaurus* carcass remained intact, suggesting that the scavenger did not linger over the carcass. Studies in East Africa have shown that during the early phases of a drought, scavengers have a glut of carcasses upon which to feed and tend to only eat select portions (Hillman and Hillman 1977).

With the stomach region open, black putrefaction liquid accumulated in the mud around the carcass and in any surrounding water. Over the next few days, the thin, outer margins of keratinous skin would have begun to dry, crack and curl; most likely the pond was reduced to a patch of mud, and this too soon dried. Within the body cavity, the putrefaction liquid would have evaporated into a black glutinous paste. If there were any insects, some of the larvae would have begun to pupate at this time, while other insect species were just starting to arrive. What remained of the carcass continued to dry. This natural mummification held most of the bones together. We do not know how long this drying lasted, but it continued until the drought was broken. Bacteria became dormant as the tissue dehydrated, but as we shall see, they would eventually awaken.

When the rainy season did come, it came in earnest and the heavy rains quickly eroded the soils where the vegetation had been stripped and trampled. This eroded earth was flushed into a nearby river where it added to the sediment being transported. The rain swollen river also cut into the banks at meander bends causing the banks to collapse, thereby adding to the sediment load. A few dinosaur bones previously buried in the banks were returned once again to the river and were bounced along the bottom getting their edges abraded in the process. Most of the sandy bottom was moved along as small underwater dunes (Fig. 5A). Any bones too heavy to be transported by the water were buried by the sand passing over them. But as the rain added to the volume

Figure 5 - *A, Underwater dunes of sand being pushed along the bottom of a river channel (Platte River, Nebraska). Any bone lying in the channel would be buried. B, Splay deposit of sand (center of image) deposited by a flood (Pearl River, Mississippi). Similar splays buried the* Stegosaurus. *Arrows show direction of water flow. Images from Google Earth.*

of the river, the river could no longer be contained in its channel. At one point, the river began to spill out of its channel, eroding a notch into the bank called a crevasse. The water gushed through this notch eroding it further and carrying a great deal of sediment with it onto the surrounding, lower floodplain. No longer confined, the water quickly spread and its velocity dropped. Without fast flowing water to support it, the heavier portions of the sediment load, mostly sand, quickly settled out. The sand formed a lobe of sediment that was pushed farther onto the flood plain by the water flowing over it. This lobe of sand, known as a crevasse splay (Fig. 5B), was pushed towards the pond where the *Stegosaurus* lay. The carcass acted like a dam, stopping the splay. If the flood had continued, a great deal more sand would have spilled out from the river channel adding to the splay and burying the *Stegosaurus*.

However, from evidence preserved in the rocks, we know that the river began to wane about the time the crevasse splay reached the carcass. With a gradual drop in water level and velocity, the water was less able to transport sediment. The sediment settled out based on its size, with the finer particles last (technically, it is by mass, but since small particles have less mass, they are the last to settle out). The resulting sediment profile shows stacked layers that are progressively finer, from sand to silt to mud. In the sand layers, stacks of ripple marks, called climbing ripples, formed as deposited sand buried previously formed ripples. We do not know when the next flood came. It may have been soon after the first flood, or later. Regardless, a second sheet of sand poured out of the crevasse and finally buried the *Stegosaurus*. Additional lobes of sediment were eventually added, and when we excavated the *Stegosaurus* skeleton in 1992, we dug through three layers of splay sandstones alternating with mudstone (Fig. 6).

Figure 6 – (JPS.P.07.0005) *Three sandstones deposited as crevasse splays exposed during the excavation of the* Stegosaurus *(encased in plaster of Paris in the lower left). The lowest-most (1) is the initial splay that partially buried the carcass. Note how it tapers towards the left. This sand splay was stopped by the carcass as seen by its absence in the left wall of the quarry.*

HOW TO FOSSILIZE A DINOSAUR: BACTERIA DO THEIR THING

When the carcass was buried by the splay sediments, the tissue began to rehydrate and soften. For bacteria, being buried was a good thing. The carcasses had moved from an unstable environment into one more stable: The bacteria were no longer subjected to fluctuations in daily temperature or moisture. With ground water flowing freely through the sand oxygen was plentiful and decay was rapid. We do not know how long the decay of the tissue took, but eventually only the skeleton remained. Within the skeleton further changes were taking place both chemically and microbially, a process called diagenesis.

The chemical changes generally occur very slowly over a span of several hundred years and involve the inorganic part of the bone, the mineral hydroxyapatite (Hedges 2002). This alteration can result in incorporation of a wide variety of atoms or molecules, including iron, carbonate and uranium. The hydroxyapatite can also be altered to brushite, or the hydroxyapatite can dissolve and reprecipitated into larger crystals. Some bone also can be lost through dissolution.

The greatest changes, however, are the result of microbes, especially bacteria and to a lesser extent, fungi.

Even after decay has removed all of the tissue on the outside of the bone, a considerable amount of organic material remains inside. Bone is not an isolated, inert structure in the body, but is a living structure that must receive oxygen and nutrients via the blood system like any other body tissue. Thus, bone is not solid, but honeycombed with cavities, much of it microscopic. Bone in the center resembles a sponge because of the lattice of bone, hence this part is called spongy or trabecular bone (Fig. 7). This bone is surrounded by a denser layer, called cortical bone. Viewed through a microscope, this bone is pierced by minute tubes called Haversian canals through which blood and nutrients flow during life (Fig. 8). Consequently, even when all the outer flesh has decayed away, there is still a lot of food left within the bone for bacteria. The small size of some bacteria (0.5Φm) enabled them to travel through the smallest bone passages called the canaliculi (20-50Φm). Canaliculi form a vast three-dimensional network of passages between bone cells, or osteocytes, to distribute oxygen and nutrients. Bacteria and fungi can enlarge these passages, thus allowing more access by ground water where it can deliver various molecules (such as iron, etc.) for the microbes to use.

These microorganisms modified their environment as they metabolized the organic material and released waste material. The role of bacterium in mineral precipitation (Briggs 2003) may be active (i.e., direct) or passive (i.e., indirect). It is direct if the bacterium pulls select elements from the water into the cell for use in metabolism. This direct precipitation can fill the inside of the cell by providing places for mineral molecules to bind to (called nucleation sites); thus the bacterium is fossilized from the inside out. In passive mineralization, spontaneous mineral precipitation occurs outside the bacterium because it has altered the environment around it. Of the two, passive mineralization is more common.

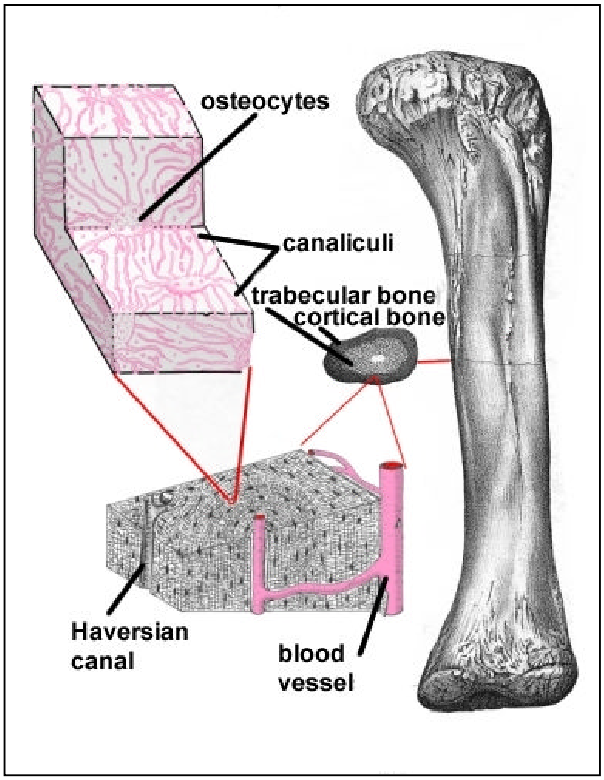

Figure 7. *Structure of bone as illustrated by a Stegosaurus femur. Bone is not solid, but has a lot of open space.*

In the *Stegosaurus* we know that pyrite was formed by bacteria. This pyrite, however, is not the large, gold-colored, metallic crystals, but rather isolated microscopic crystals. The pyrite is a result of bacteria attaching sulfur atoms liberated from the organic material in the bone (such as collagen) to iron atoms dissolved in the ground water or liberated from the hemoglobin of the blood. Both the iron and sulphur are present in very low quantities, which is why the pyrite does not form large crystals. Still it does not take much to produce pyrite, just two atoms of sulfur (abbreviated as S) and one of iron (abbreviated as Fe) having the chemical formula FeS_2. These three atoms form a single molecule of pyrite. At this small size, the pyrite can be too small to be seen under the microscope, but in high enough concentration scattered throughout the bone, it gives the *Stegosaurus* skeleton a black color.

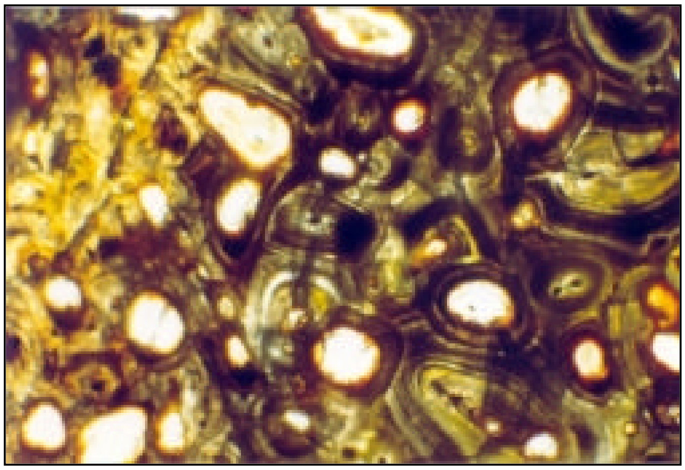

Figure 8. (JPS.P.07.0006) *Microscopic view of a paper-thin slice of* Stegosaurus *spike. The openings are filled with calcium carbonate and the yellow and brown is due to iron.*

The most common mineral deposited within the *Stegosaurus* bones is calcium carbonate. This mineral consists of one atom of calcium, one of carbon and three of oxygen ($CaCO_3$). Bacteria produce calcium carbonate by using calcium ions present in water as a waste receptacle. By attaching their carbon dioxide waste, which is produced by cellular metabolism, to the calcium ion a spontaneous precipitation of calcium carbonate, or calcite occurs (Boquet and others 1973). The calcium carbonate can be seen filling all the empty areas of the bone at both the microscopic and macroscopic (naked eye) levels (Fig. 8). At the macroscopic level, the calcium carbonate is seen as large crystals of calcite, especially in areas once filled with bone marrow. Other minerals precipitated in and around the *Stegosaurus* bones, including various forms of iron and uranium (at very low levels).

We don't know how long it took for fossilization of the *Stegosaurus* skeleton to occur. Experimental work I have conducted has shown that the process does not necessarily take very long (Carpenter 2005). Under ideal situations, a dinosaur could be fossilized in only a few years. The rate seems dependent upon the supply of dissolved atoms and molecules in the water available for bacterial use. This in turn is dependent upon the replenishment rate of the water. The rate is faster for bone buried in sand than for bone buried in mud, because ground water can flow more freely around the sand grains than around the clay particles.

Even after the skeleton was buried and the process of fossilization begun, the environment in which the bones lay continued to change as more sediment was piled on top of the *Stegosaurus* over the years. The growing weight of the sediments caused changes in the pond mud as the water was slowly forced out. Clay particles of the mud were slowly altered as the water squeezed out carried away certain atoms. Without the presence of water molecules, the clay particles were pressed against each other and against other minerals, thereby altering the mud into mudstone or into layered shale. However, the great weight also compressed and distorted the *Stegosaurus* bones because under pressure, clay can flow as the clay particles glide past each other. Where the bones lay in sand, they were much less distorted because sand does not distort or flow due to grain-to-grain contact. Sand is also much more porous than mud because of the voids between the sand grains. These voids allow ground water to flow freely, thereby bringing a steady supply of atoms and dissolved minerals to the bacteria. Eventually, minerals, such as calcium carbonate, can be deposited in these voids, cementing the sand grains together forming sandstone. Not surprisingly, some of the best preserved fossil bones are found in sandstones. The conversion of mud and sand into rock takes a considerable amount of time because a great deal of the transformation relies on pressure from the accumulation of overlying sediments.

Further changes occurred when the great load of overlying sediments was removed through erosion brought on by the uplift of the Rocky Mountains beginning about 68 million years ago, driven very slowly by forces deep within the earth. Over two miles of sediment was deposited over the *Stegosaurus* after its burial, especially during the Cretaceous, when the *Stegosaurus* lay beneath the sea floor of a vast inland sea. All of the overlying sediments were slowly eroded once the Rocky Mountains began development in the Late Cretaceous. Because water always flows towards the lowest spot, rivers and streams carried rock debris downhill. In this very slow manner, millions of cubic feet of rock has been eroded from the Rocky Mountains and deposited by rivers in either the Gulf of Mexico or the Gulf of California. As erosion removed much of the overlying rock above the *Stegosaurus* skeleton, the reduction in pressure allowed the rock to expand causing it to crack. This fracturing increased near the surface as the rock alternated between being wet and dry and hot and cold. Sometime around 10,000 years ago, near the end of the Ice Age (Pleistocene), rivers ran high from melting mountain glaciers and snow fields. The *Stegosaurus* skeleton was near enough to the surface that it began to feel the effects of weathering. Erosion is often preceded by weathering, which is the breakdown of rock by rain, ice expanding along cracks, very dilute carbonic acid in rain (formed by rain drops absorbing carbon dioxide in the atmosphere), and the effects of plant roots along cracks. Once this rock is weakened, erosion by flowing water removes the rock debris. Thus, weathering and erosion go hand in hand. As the *Stegosaurus* neared the surface of the land, weathering broke down some of the pyrite within the bone, causing it to release its sulphur. This sulphur migrated outwards where it combined with calcium and oxygen and was precipitated on the bone as gypsum ($CaSO_4$).

Erosion brought the specimen close to the surface where it was found in 1992 while we were surveying for fossils. Details of that work have been published elsewhere (Carpenter 1998).

CONCLUSONS

All that we know about the history of life we owe to fossils. Remarkably, fossils owe their existence to bacteria and to their capacity of forming minerals. Without bacteria, we would be buried under carcasses, but we would also be without fossils. In my next article in this series I will discuss how soft tissue, such as the creatures from the Burgess Shale, get fossilized.

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REFERENCES

BEHRENSMEYER, A., and D. BOAZ 1980. The recent bones of Amboseli National Park, Kenya, in relation to East African paleoecology. In Behrensmeyer, A., and Hill, A. (eds.), Fossils in the Making. University of Chicago Press, Chicago, 72-92.

BOQUET, E., A. BORONAT, and A. RAMOS-CORMENZANA, A. 1973. Production of calcite (Calcium carbonate) crystals by soil bacteria is a general phenomenon. Nature 245: 537-529.

BRIGGS, D.E.G. 2003. The role of decay and mineralization in the preservation of soft-bodied fossils. Annual Review of Earth and Planetary Sciences 31: 275-301.

BURN, C.G. 1934a. Experimental studies of postmortem bacterial invasion in animals. Journal of Infectious Disease 54:388-394.

BURN, C.G. 1934b. Postmortem bacteriology. Journal of Infectious Disease 54:395-403.

CARPENTER, K., 1987. Paleoecological significance of droughts during the Late Cretaceous of the Western Interior. In CURRIE, P., and, E.H. KOSTNER(eds.), Fourth Symposium on Mesozoic Terrestrial Ecosystems, Short Papers. Tyrrell Museum of Paleontology Occasional Papers 3:42-47.

CARPENTER, K. 1998. Vertebrate biostratigraphy of the Morrison Formation near Canon City, Colorado. In CARPENTER, K., CHURE, D. and KIRKLAND, J.I. (eds.) The Morrison Formation: An Interdisciplinary Study. Modern Geology 23:407-426.

CARPENTER, K. 2005. Experimental investigation of the role of bacteria in bone fossilization. Neues Jahrbuch für Geologie und Paläontologie Monatshefte 2005 (2): 83-94.

CARPENTER, K., F. SANDERS, L. MCWHINNEY, and L. WOOD,. 2005. Evidence for predator-prey relationships: Example for *Allosaurus* and *Stegosaurus.* Pp. 325-350 in CARPENTER, K. (ed.) The Carnivorous Dinosaurs. Indiana University Press, Bloomington.

COE, J.I. 1977. Postmortem chemistry of blood, cerebrospinal fluid, and vitreous humor. In. Tedescki, C.G., Echert, W.G., and Tedescki, L.G. (eds.) Forensic Medicine II. Physical Trauma. W.B. Sauders Co., Philadelphia, 1033-1060.

COE, M. 1978. The decomposition of elephant carcasses in the Tsav (East) National Park. East African Journal of Wildlife 1:71-86.

CORFIELD, T.F., 1973. Elephant mortality in Tsavo National Park. East African Journal of Wildlife 11:339-368.

CONYBEARE, A. and G. HAYNES. 1984. Observations on elephant mortality and bones in water holes. Quaternary Research 22: 189-200.

DEMKO, T.M., and TOTMAN-PARRISH, J. 1998. Paleoclimatic setting of the Upper Jurassic Morrison Formation. In CARPENTER, K., D. CHURE, and J.I. KIRKLAND, (eds.) The Morrison Formation: An Interdisciplinary Study. Modern Geology 22: 283-296.

FARROW, C.S. 1999. All about new bone. Veterinary Clinics of North America 15: 215-219.

GILL-KING, H. (1997): Chemical and ultrastructural aspects of decomposition. P. 93-108 in HAGLUND, W.G. & M.H. SORG (eds.): Forensic Taphonomy, Boca Raton (CRC Press).

HAM, A.W., and W.R. HARRIS. 1971. Repair and transplantation of bone. In Bourne, G.H. (ed.): The Biochemistry And Physiology of Bone: Development and Growth 3:337-399.

HAYNES, G, 1991. Mammoths, mastodons, and elephants: biology, behavior and the fossil record. Cambridge University Press, Cambridge, 359 pp

HILLMAN, J.C. and A.K. HILLMAN 1977. Mortality of wildlife in Nairobi National Park, during the drought of 1973-1974. East African Journal of Wildlife 15:1-18.

HEDGES, R.E.M. 2002. Bone diagenesis: An overview of processes. Archaeometry 44: 3190328.

MCWHINNEY, L., B. ROTHSCHILD, and K. CARPENTER, 2001. Posttraumatic chronic osteomyelitis in *Stegosaurus* dermal spikes. In CARPENTER, K. (ed.) *The Armored Dinosaurs*. Indiana University Press, Bloomington, 141-156

RESNICK, D. and NIWAYAMA, G. 1995. Osteomyelitis, septic arthritis, and soft tissue infection: mechanisms and situations. In: RESNICK, D. (ed.). Diagnosis of Bone and Joint Disorders. Saunders and Co., Philadelphia: 2325 –2418.

TOTMAN PARRISH, J., F. PETERSON, C. E. TURNER. 2004. Jurassic savannah-plant taphonomy and climate of the Morrison Formation (Upper Jurassic, Western USA). In Turner, C. E., F. Peterson and S.P. Dunagan. Reconstruction of the Extinct Ecosystem of the Upper Jurassic Morrison Formation. Sedimentary Geology 167: 137B162