Hyracotherium 55-45 million years ago. The oldest known horse was a four-toed browser that foraged on nonfibrous foods. Its molars showed the beginning of horse-like ridges better suited for grazing.

Miohippus 33-99 mya. This small, two-toed browser was responsible for a burst of diverse side branches in the horse family. Its descendants were numerous and distinct.

Merychippus 17-11 mya. The first grazing horse had strong, crested teeth that enabled it to eat abrasive grasses. Even with primitive three-toed feet, its long legs equipped it for quick escapes and long-distance migrations.

Equus 5 mya. The single survivor of the formerly diverse horse genus, its living species include horses, asses, and zebras. Domestication of Equus 3,000 years ago dramatically impacted the world's civilizations by facilitating agriculture, migration, and warfare.
The mystique of the horse seems universal. It is a survivor, a relic of the past, a reminder of a primeval and very different Earth. Today there are eight species of horses, including zebras, donkeys, asses, burros, onagers, kulans, kiangs, and domestic horses, as well as the recently extinct quagga. All eight living species belong to the genus Equus, the Latin word for horse and the source for the term equestrian. However, the horses preserved in the fossil record represent as many as
six to eight genera, with each genus having numerous species. Although scientists once upheld the horse as a model of linear sequence, that model no longer applies.

Despite the horse's ancient success, by 3.7 million years ago the number of genera fell to three in North America. Members included a small form known as Nannippus, a larger relative called Cormohipparion, and Equus. The first two genera represent lineages with a long history starting sixteen million years ago. Both ultimately became extinct, leaving no descendants. In contrast, Equus, a relative latecomer geologically speaking, first appeared only 3.7 million years ago. The genus quickly adapted and diversified, eventually dispersing from North America into Asia, Europe, and Africa where its descendants still survive.

What was it about Equus that made its survival possible when all other types of horses became extinct? Paleontologists look for answers in the anatomy and ecology of Hagerman's Equus simplicidens. By examining the fossilized remains of the earliest known species of Equus, science can better explain why the horse lineage survived.

We refer to the earliest known species of Equus as the "Hagerman Horse" in reference to the large sample from the Smithsonian Horse Quarry, located within Hagerman Fossil Beds National Monument and managed by the National Park Service. However, the scientific history of this species actually goes back to the close of the nineteenth century. In 1892, paleontologist Edward Drinker Cope first described Equus simplicidens. Cope found the original specimen, a single tooth, near Mount Blanco, Crosby County, Texas. Later discoveries of horses from similar age deposits elsewhere in the United States resulted in the description of other species of Equus.
Sometimes these other species were not even considered to be *Equus*. At one time the genus *Plesippus* was used for what are now considered the earliest species of *Equus*. The primitive anatomy of the skeleton of *Plesippus* provided a link between *Dinotherium*, the earlier ancestor, and *Equus*. Such was the case when the Smithsonian visited Hagerman in 1929. The Smithsonian paleontologist who first worked the site now known as the Smithsonian Horse Quarry was James W. Gidley, then the leading student of fossil horses. When Gidley first described the material from Hagerman, he named it *Plesippus shoshonensis* because of the animal's primitive skeletal structure. Later researchers decided that Gidley's species from Hagerman was the same as the previously described *Equus simplicidens* from Texas.

Since many fossil species of *Equus* have often been described based on a single tooth, it has been difficult to determine if all these different species are really valid. If one species is based on an upper tooth and another on a lower, then can we really be sure they are distinct, or do the differences merely reflect the differences between upper and lower teeth? There are many factors that contribute to the variations we see in fossils. They may reflect the age of an individual or be indicative of the differences between males and females. What makes the Smithsonian Horse Quarry sample so important is that it represents a large sample of a single species; it includes males, females, and individuals of all different ages. This site provides a paleontologist with the opportunity to examine the range of variation present in a species. Such a site is a rare occurrence in a fossil record that often consists of bits and pieces rather than whole skulls or skeletons.

The science of paleontology is constantly reexamining the available fossil evidence, proposing hypotheses regarding the ecology or relationships of extinct animals based on that evidence, and then testing each hypothesis as new evidence becomes available. A hypothesis on the ecology of an extinct species will be weak when only isolated bones and teeth are available. When a large sample of individuals such as that of the Hagerman Horse from the Smithsonian Quarry becomes available, an earlier hypothesis may be strengthened, or as is often the case, revised. Such a large sample provides an opportunity to gain a wealth of information that might not be otherwise possible to glean from the fossil record. Studies of the skeleton of the Hagerman Horse from this sample, and comparison with its modern living relatives, suggest that it is actually more zebra-like than horse-like. More specifically, its skull, teeth, and skeleton are most similar to the living Grevy's zebra, which inhabits arid regions in the northern part of Africa.
Some horse experts consider Grevy’s zebra the most primitive of the living members of the horse family, so some of the features shared with the Hagerman Horse may reflect the generally more primitive skeletal structure of Grevy’s zebra. One of the features they have in common is a long skull with a prominent occipital region, the back of the skull where the neck muscles attach. Also, the folds of enamel on the lower molar teeth are similar. Like modern zebras, the Hagerman Horse has a small hoof in proportion to its body size. While the horse was larger than its ancient ancestors, it was not an especially large animal. Slightly smaller than today’s zebras, it stood about 4.3 feet (13 hands) at the shoulder. Some of its descendants are larger, but not all. The living donkey is smaller than the Hagerman Horse.

Like all modern members of the family Equidae, Hagerman’s Equus simplicidens was one-toed with reduced side toes. The middle toe supported all the animal’s weight. This adaptation to running had already occurred earlier, so Equus was not the only one-toed horse. It merely continued the trend, with the remnant splints of the side toes completely hidden beneath the skin. The main bones for support in the hand and feet (metacarpal and metatarsal) continued to become elongated, increasing the overall length. Longer legs meant a longer stride and more ground covered. “In the horse,” paleontologist W. B. Scott said, “everything has been sacrificed to speed, making the animal a ‘‘cursorial machine.’”

Perhaps one of the most telling features of the skeleton in this early ancestor of modern horses is the upper leg bone, or humerus. One of the very distinct characteristics of living horses is their ability to stand, even sleep, upright for long periods of time. This is possible because of a specialized system of muscles, ligaments, and deep fascia (a connective tissue) known as the stay-apparatus. This serves to transfer the role of supporting body weight from active muscles to non-fatiguing structures in the skeleton of the fore and hind limbs. How can we tell that the Hagerman Horse had this stay-apparatus? Although muscles, ligaments, and fascia all quickly decay after the death of the animal and are not preserved as fossils, these tissues have to attach to bones. They often leave some type of mark, such as ridges and mus-
cle scars, that allows paleontologists to establish their existence. In modern horses there is an extra ridge of bone on the humerus near the shoulder joint that shows where a ligament associated with the passive stay-apparatus attached. This ridge is absent in earlier horses and suggests that they could not stand for long periods or sleep standing upright like modern horses. The earliest horse with a well-developed ridge and hence a well-developed stay-apparatus is *Equus simplicidens*, the Hagerman Horse, and this feature is present in all its living descendants.

What is the importance of this particular anatomical feature? Modern horses are grazers and feed primarily on grasses. Grasses are not as nutritionally rich as other plants, so grazing is not very efficient and requires large amounts of food to be ingested. Grazing horses, in contrast to earlier browsing horses, spend a lot of time standing and feeding in open country in full view of potential predators. The stay-apparatus is one way an animal can conserve muscular energy so that it is available for running and escape should the need arise. Any anatomical feature that aids in escaping predators certainly contributes to the survival of the species.

Being a grazer can be rough on the teeth. Grasses contain little bits of the mineral silica, which has the same composition as quartz sand or glass. These little bits of silica, called phytoliths or literally plant-stones, act as the skeleton of the grass blades.
Any animal, like a horse, chewing these grasses also has to chew bits of silica, resulting in rapid wear of the teeth. How does an animal deal with such an abrasive diet? There are three possible solutions. First, have a tooth that is ever-growing so that even as the tooth is being worn down, more new tooth is being formed. This approach is found in rodents; their front teeth or incisors are used for gnawing and hence are rapidly worn down. For animals that do not have ever-growing teeth, an alternative is to have taller teeth in which the crown, the “business” part of the tooth, takes longer to wear down. The third solution is to have tougher teeth. Teeth are made primarily of two parts, the harder enamel and a softer dentine, better known as ivory.

Animals that eat plants have teeth with a chewing surface formed by alternating ridges of enamel and dentine. The difference in hardness produces low and high areas that trap and hold plants and then cut them. Those animals that eat more abrasive food have more complex ridges of enamel that form a greater proportion of the chewing surface so that it takes longer to wear down. Another way a tooth becomes tougher is by the addition of a third substance, cementum, to the outside of the tooth to make it stronger. While cementum is harder than dentine, it is not as hard as enamel. Yet it does aid in helping the tooth withstand abrasive food.

Which of these adaptations to making the teeth withstand an abrasive diet is present in the Hagerman Horse? All of them. Horses had become grazers long before Equus, so the development of high-crowned (hypodont) teeth for grazing occurred much earlier in the evolution of the horse, though it is best developed in Equus. The permanent teeth also grow longer because there is a delay in the development of roots. Once the roots form, there is no longer any new tooth material produced, and from then on the crown of the tooth is slowly worn away. The teeth of Equus have a more complex folding of the enamel than is seen in the teeth of its ancestors; they also have cementum, so the tooth does not wear down as quickly.

While we can study horse skeletons, their skin, muscles, and other soft tissues are only preserved under extraordinary conditions such as freezing or mummification. Without skin we have no way of knowing whether the Hagerman Horse had stripes like the modern zebra.
Stripes provide protection against predators, a useful adaptation in a herd animal. Since there is evidence that the Hagerman Horse did form herds or at least extended family groups, reconstructing the animal with stripes seems legitimate. But without preserved skin, we cannot say for sure.

Since Cope's discovery in 1892, paleontologists have identified *Equus simplicidens* at forty-seven sites ranging from Idaho to California and South Dakota to Mexico. The variety of environments found within this broad region today makes it safe to imagine that the number of possible habitats in this area also existed in the past. It certainly suggests that the Hagerman Horse was flexible in its habits and adaptable to a variety of environments.

In order to fully understand the ecology of the Hagerman Horse, a thorough knowledge of all the fossil sites where it is found is necessary. Although Hagerman is only one of many sites, it does provide the best record of the environment in which *Equus simplicidens* lived.
Hagerman can be thought of as the keystone to our understanding of this species based on two different criteria. The first one has already been mentioned: the large sample of *Equus simplicidens* found at the Smithsonian Horse Quarry. The second is the rich fossil preserve from the Hagerman site of the many other different species of vertebrates, invertebrates, and plants that shared the environment with the Hagerman Horse when it was alive. While all the other sites may also preserve the flora and fauna, none can compare in the number and diversity of species found. As a result of the work started at Hagerman in 1929 by the Smithsonian and continuing with the work done by numerous other researchers up to the present, 111 species of vertebrates, thirty-nine species of invertebrates, and thirty-four species of plants have been documented. Thus the Hagerman area represents the best-known record of life for the Pliocene (4.8 to 1.9 million years ago) in North America.

In addition to its variety of fossil plants and animals, Hagerman has an added bonus preserved in the bluffs that overlook the Snake River: volcanic ashes. Geologically speaking, the eruption of a volcano and the deposition of volcanic ash on the landscape is an instantaneous event. Each type of volcanic ash has its own distinctive chemistry, reflecting the local rocks that were melted down and blown out of the volcano. This unique fingerprint allows us to match ash layers from the same volcanic eruption to determine that widely separated rock layers were formed at the same time. Not only does the ash allow geologists to show a similar age for different rocks, but in some cases they can even determine exactly when the volcano erupted and deposited that ash layer. Some volcanic ashes similar to the type that came out of Mount St. Helens are rich in the element potassium. Some of the potassium is a radioactive isotope that decays into the inert gas argon. When the volcano erupts, any argon gas present escapes from the hot rock into the air so that when the volcanic ash settles onto the landscape there is no argon present. As time passes, new argon is produced by the decay of the radioactive potassium and remains trapped in the crystals of the minerals in the ash. Since the rate of change from radioactive potassium to argon is constant, there is an increase in the amount of argon present: the more argon present, the older the ash layer. This radiometric clock is the method by which the age of the rocks can be determined.
There are two very distinctive ash layers at Hagerman, and based on their chemical fingerprint we can tell that they came from two very different areas. The older of these two ashes is called the Peters Gulch Ash and was named for the site where it was originally dis-

covered, Peters Gulch, in the southern part of Hagerman Fossil Beds National Monument. Its chemical composition shows this ash originated from a volcano in what is now the Yellowstone area. The age of this ash has been determined to be about 3.7 million years old. While in most places the Peters Gulch Ash forms only a thin layer, in a few places it is almost three feet thick where it washed into ponds on the Hagerman landscape. The surface of the ash has ripple marks reflecting water movement in the pond. Higher up in the layers at Hagerman is another prominent ash layer known as the Fossil Gulch Ash. Fossil Gulch is also found within the monument and is located near the Smithsonian Horse Quarry. Unlike the Peters Gulch Ash, the Fossil Gulch Ash came from the west and probably was produced by a volcano somewhere along the Pacific coast. The exact spot has not yet been identified. It has been dated at 3.2 million years. Since the sediments at Hagerman go below the Peters Gulch Ash and above the Fossil Gulch Ash, we can safely assume that the 600-feet-high bluffs span more than the 500,000 years represented between the two ash layers.
What can we say about life in the Hagerman area between 3.7 and 3.2 million years ago? Based on the plant pollen found preserved in some sediments, southern Idaho 3.5 million years ago was wetter than it is today, with about twice as much annual precipitation. The greater amount of annual precipitation reaching southern Idaho at this time was probably due to the lower elevation of the Coast and Cascade Ranges to the west. Today these mountain ranges capture much of the moisture coming in from the Pacific and create a rain shadow. However, 3.5 million years ago they had not yet been pushed to their present height, so moisture from the Pacific Ocean reached farther inland. This greater
amount of moisture permitted many types of trees such as pine, fir, spruce, juniper, hemlock, and false hemlock, which today are found at higher elevations, to grow on the Snake River Plain where sagebrush now dominates. In many places there were woodlands or somewhat open forest. Along the rivers the riparian vegetation included willow, alder, birch, and elm.

Cross-bedding, overlapping, and sloped sand layers deposited by ancient rivers are common. Like the present-day Salmon Falls Creek, Bruneau River, and Owyhee River, the rivers passing through the Hagerman area originated in Nevada and flowed north. Unlike their modern counterparts, these rivers did not empty into the Snake River that runs by the monument today, since it would not be formed until a million years later. The rivers passing through the Hagerman area emptied into a large lake to the west known as Lake Idaho. While the size of Lake Idaho fluctuated in response to changes in climate, at its largest it was about the size of Lake Ontario. Drainage from Lake Idaho was across Oregon and into northern California. This is known because the nearest living relatives of species of the fish, freshwater snails, and clams unique to the lake are found in the Sacramento Valley today.

Many of the sediments present at Hagerman indicate the presence of wetlands. In the middle part of the Glenns Ferry Formation exposed at Hagerman, ancient pond deposits are common. These are represented by finely layered, brown shales rich in organic material contributed by decaying plants such as cattails. The presence of extensive wetlands is also reflected in the fauna. A variety of frogs is known from Hagerman, as well as a salamander. While no turtles live in the Snake River or its tributaries today, at the time of the Hagerman Horse the fauna included two types of turtles. Most of the birds known from Hagerman are waterfowl. Ducks, geese, swans, pelicans, cormorants, ibis, four types of grebes, herons, and rails were all present. Common mammals included two types of beaver, an otter, and the ancestor to the living muskrat.

The environment at Hagerman was not restricted to wetlands. Savannah grassland habitat was also present, and in addition to the variety of animals associated with wetlands, the Hagerman fauna has species like the horse that would have inhabited more open country. While the various ponds, streams, and rivers would have been important water sources for the Hagerman Horse, its preferred habitat would have been these open grasslands. Sharing the grasslands with the horse were peccaries, a New World relative of the pig, along with llamas, camels, and antelope. None of these grassland species were as common as the wetland forms, suggesting that during part of the time when sediments were being deposited at
Hagerman, open grasslands were not yet as extensive as they eventually became. Smaller mammals in that open country included gophers, ground squirrels, and perhaps one or two types of rabbits. The birds present in this more open country included a burrowing owl.

The first abundant grass pollen found at Hagerman is high in the layers, at about the same level as the Horse Quarry. While horses were present in the Hagerman fauna earlier, they were not common. Perhaps the earlier wetland habitat was only marginally used by the species, and only with the drying of the climate and spread of grasslands did horses become common in the area so that a site with a high concentration of grassland species like the Horse Quarry could be formed.

In any ecosystem there are prey and there are predators. One of the outstanding features of the fauna at Hagerman was the variety of carnivores present: thirteen species. They ranged in size from a weasel to a small sabertooth cat. Only the sabertooth cat and the hyenalike dog were large enough to prey on the Hagerman Horse. Two types of dogs were present. The ancestral coyote, like its modern descendant, probably fed on rabbits and mice, both of which were abundant. The other dog, *Borophagus*, belonged to an extinct group. Much like the modern hyena, it was adapted to crushing bones, making it a likely predator of the Hagerman Horse. The Hagerman fauna also included an early ancestor of the black bear that, like its descendant, had flat crushing teeth, indicating it, too, was probably an omnivore. While it may have scavenged carcasses of dead horses, it probably did not actively pursue them.

Toward the top of the bluffs at Hagerman is the Smithsonian Horse Quarry. It seems to have formed at a time when there was a decrease in the amount of wetlands, for there are no carbonaceous shales representing ponds this high in the bluffs. Water was still present, as the quarry itself was formed in the bed of an ancient river.

As the mountain ranges to the west uplifted, the landscape became more arid and the woodlands declined, with grasses becoming increasingly prominent. The continuing success of the horse as it diversified and evolved into new species reflected its adaptations to this open grassland environment.

While the Smithsonian Horse Quarry is an important site, it is not the only place in the Monument where horse remains are found. As with much of the fauna, most other finds of fossil horses consist of isolated bones and teeth. This is not surprising since vertebrate skeletons are easily scattered following the death of an animal; finding a fairly complete skeleton is a rare event. Even more rare is the discovery of large concentrations of numerous individuals of a single species. Although a single tooth or bone can provide important information about an extinct species, it is only when a large sample is studied that we can gain significant insight into the lifestyles and habits of a species. Such a sample allows paleontologists to assess the range of variation within a species. How large are the largest individuals, and how small are the smallest? Is its size related to the sex or age of an individual, and what are the...
important differences that distinguish one species from another? When working with an often fragmentary fossil record, such information is important for determining if a find really represents a new type of animal or merely an extreme version of a previously known species. One of C. L. Gazin's early studies on the Smithsonian Horse Quarry sample looked at some of these questions.

Large samples can originate in two very different ways, and the resulting samples each provide different types of information about the species. Some samples result from long-term, gradual accumulations in one spot. The famous tar pits at Rancho La Brea in Los Angeles, California, are a classic example. They record changes over a long period of time, biologically speaking. Other accumulations are formed more quickly as the result of a catastrophic event that "freezes" in time a snapshot of what the living population was like. The causes of these catastrophic accumulations are varied and can range from floods and droughts to volcanic eruptions or disease.

One type of important information that can be gleaned from a large sample of animals killed in a flood, drought, or other catastrophic event is the herd's population structure. Such a sample provides an opportunity to see the number of individuals of different age classes and the ratio of the sexes in these groups. The question is whether there are clear ways to determine the age of individuals and if there are features of the skull or skeleton that permit us to tell males from females. Fortunately the close similarity between the Hagerman Horse and its modern relatives gives paleontologists important clues.

One very quick and simple way to identify a male horse using either the skull or jaw is to look at the canine, also known as the eye tooth. In stallions this tooth is large and well developed. In mares the tooth is much smaller and in many individuals absent. In modern horses younger than about three years, this tooth has not erupted and is therefore not a useful feature in the very young. About the time young stallions start to become sexually mature, this tooth erupts and becomes visible, thus making determination of the sex of the individual easy.

Horses, like many other mammals, have two sets of teeth, deciduous and permanent. We can observe at what age an animal gets its deciduous teeth, when these teeth are shed, and when each of the permanent teeth are in place. Since this information is available for domestic horses and wild horses such as zebras, we can then determine the age of a
Determining the age of a mammal is not restricted to looking at the teeth. Many bones of the skeleton start out as separate centers of bone formation. As an animal grows and matures, many of these centers fuse together. Different bones fuse at different times in an animal's life. What we know about bone formation in modern horses helps researchers profile the herd uncovered at the Hagerman site.

One of the early explanations for the large number of individuals at the Smithsonian Horse Quarry was that they had gathered at a water hole. It was thought that over the years as animals came to the water hole, some died and became buried. As the remains accumulated, a large number of animals became preserved at the site. If this explanation for the origin of the site was correct, then it should be reflected in the age distribution of the animals preserved. In gradual accumulations such as this, the individuals most likely to die are the very young and very old. Both are more vulnerable than prime adults to any predators also likely to be found around the water hole. Other possible causes of death might be entrapment in the mud, since these animals might be too weak to escape. Looking at the skulls and jaws, a sample composed of individuals with milk teeth and individuals with heavily worn permanent teeth should be evident.

A study of the age of the animals from the quarry demonstrated that not only were very young and very old individuals present but also all ages in between. The sample did not fit the expected pattern of a gradual accumulation but rather a catastrophic one in which individuals of all ages were killed. While this new information does not provide any explanation as to how the animals died, it certainly suggests that they died within a relatively short time of each other.

Some species of mammals have a reproductive strategy of breeding throughout the year. Others breed seasonally once a year. The Hagerman Horse may have bred seasonally since many of the skulls found in the Smithsonian quarry sample have teeth at the same stage of development and wear. Modern Burchell's zebras living in Africa have a similar age structure to the Hagerman population. They breed once a year and births peak during the wet season when food availability is optimal. The type of vegetation present at Hagerman based on the pollen record suggests that during the Pliocene the annual rainfall was twenty inches a year, with most of it restricted to the winter season. It is not unreasonable to infer that the breeding of the Hagerman Horse was probably closely tied to this seasonal rainfall.

Females in the sample are better represented than males by a ratio of 1.4:1 based on skulls and 2.2:1 based on jaws. These sex ratios are similar to those in the living Burchell's zebra. Burchell's zebra, like many other wild equids, has a social organization composed of
two groups: a reproductive group of a dominant stallion with a number of mares and their young, and separate bands of bachelor males. The pattern in the Horse Quarry sample suggests that the Hagerman Horse had a social structure similar to that of Burchell’s zebra. Zebra bachelor and breeding bands tend to remain separate, and the dominant male is most defensive of his harem while the mares are reproductively receptive. However, since breeding only occurs once a year, the stallion does not have to actively guard his harem all year. In Africa many of these separate bands will come together for the seasonal migration in search of food when the dry season comes. As a result, there are times when hundreds of individuals will be concentrated in a small area. It is very possible that the Hagerman Horse had similar behavior, and that the large number of individuals preserved at the quarry represents portions of one of these migratory congregations of horses.

Although the idea of a catastrophic event killing a large number of horses sounds plausible as an explanation for the origin of the Smithsonian Horse Quarry, we still need to seek evidence that will support this interpretation. While we have looked at the biological evidence of the animals themselves, there is another important source of information. Geological evidence includes the types of sediments in which the horses were buried and how the bones of the horses were positioned within these sediments.

Sediments at the Horse Quarry reveal the presence of moving water. If the site was a water hole as originally thought, then the pattern of sediment deposition would show very fine-grained particles that settled out in quiet water.
As these particles settled to the bottom of the water hole, we might expect to see distinct layers formed, except perhaps near the edge where they would be disturbed by animals walking around. Recent studies of the sediments of the Horse Quarry indicate that the bone layer sits on the bottom of an ancient riverbed. The lowest sediments are the coarsest, including small balls of clay ripped up from the bottom of the channel. From these coarse sediments the particles get smaller in the higher levels above the base of the channel. This pattern of going from coarse to finer sediments indicates a slowing down of the water flow. The finer sediments also display a pattern called cross-bedding in which the layers form crescent patterns. Because the size of sediment particles and the pattern of cross-bedding vary depending on the depth and speed of the water, we can reconstruct the type of river in which the bones were buried. The shape of the ancient river suggests that this was a fairly straight channel that did not meander. The water was slow, moving less than three feet per second, and shallow, less than twenty inches. These were certainly not conditions that could trap, drown, and bury a herd of animals similar in size to the living zebra.

Very few complete skeletons have been found. Of the more than 200 individuals collected since 1989, only about eight are represented by fairly complete skeletons. Although there are thousands of horse bones in this one small area, they tend to be scattered and isolated. This is not to say that parts of skeletons did not stay together; often skulls and jaws are still attached, and occasional strings of vertebrae are found. Usually when bones are found in place still in their original anatomical connections, they are from the lower legs such as the wrist and ankle. Had the Smithsonian Horse Quarry formed when a large number of individuals drowned in a flood, then their quick burial should have resulted in mostly complete skeletons instead of scattered bones. Any explanation for the origin of the quarry needs to look at two different events: what killed the animals, and what caused their bones to accumulate in a small area on the bottom of an ancient riverbed.
Since few articulated skeletons are found in the quarry, it is safe to assume that enough time passed between the death of the animals to allow their carcasses to rot enough for bones to become separated. Once a bone becomes exposed, it will start to weather and undergo a distinctive pattern of decomposition as the organic part decays. While some skulls are broken in such a way that they may have been stepped on, the surface of most bones does not show any type of weathering that would suggest they sat exposed to the elements for long periods of time. They were probably exposed less than a year before being buried. If we consider the anatomy of a horse and the relationship of bones to muscles, it is quickly obvious that the lower part of the legs does not have much muscle. The skin covers a few tendons, but that is about all that is present. After the animal dies, the skin dries and shrinks, forming a tight package that holds the bones of the wrist and ankle in place. In other parts of the body, such as the upper parts of the leg where there are more muscles to decompose, it is easier for the bones to become separated. The above pattern only applies to an animal that dies on dry land, not in water. An animal submerged in water would have its soft tissues quickly decay so that all of the skeleton would become separated.

How bones are transported in a moving current depends on their size and shape and the speed of the water. Horses have about 205 bones in their skeleton, ranging in size from the largest like the skull, jaws, and hips to the smallest such as the wrist and ankle bones or those in the tail. By measuring the compass direction of the long bones of the leg we can determine if the current helped align the bones in a preferred orientation. Measurements of the long axis of the troughs in the cross-bedded sands show that the current flowed from northeast to southwest. Therefore, there should be a pattern of two sets of bone orientation. One set of bones would align with the current and a second set with the bones positioned at right angles. This pattern is not present in the Horse Quarry bone assemblage. Although there is some indication that many bones were rolling with the current, it was not strong enough to sort the long bones into two groups oriented at right angles to each other.

Because all bones of the skeleton are present and the water current was too weak to remove small bones or move larger bones into the typical bimodal pattern of orientation, we can conclude two things. Where the bones are buried is close to where the animals died, and the bones were not washed downstream from someplace else. If river current cannot account for the large number of bones deposited at the quarry, then why are so many horse skeletons concentrated in one spot? The idea that there was a large number of animals due to a seasonal migration has been proposed, but the evidence shows the river was neither deep nor fast enough to cause drowning. Also, if the bones were not transported any great distance, then the carcasses most likely decomposed in the river bottom before the water rose. Therefore, the animals did not likely die adjacent to the river.

Although many kinds of catastrophes kill herd animals, the explanation that best fits the Hagerman data is catastrophic drought. The summers on the Snake River Plain during the Pliocene were cooler and the winters were warmer than those of today. The average temperature during the late fall, winter, and early spring did not extend below 10°C (50°F). If rainfall was seasonal and mostly fell during the winter, then any delay or reduction in rain might have a dramatic effect on the river. If the river was as broad and shallow as the geology suggests, it would have dried up quickly. The river may have already been at its lowest at the end of the dry summer season. Excavations at the quarry show there were low areas that would have
Mystery of Mysteries

Darwin's solution to evolution's mystery was a tree of life that accounted for everything but chaos. For all the organic diversity his tree allowed, Darwin remained fixed on the idea of orderly progression through competitive replacement. The evolution of the horse shows a different sequence, an unpredictable and divergent path twisted by powerful biological complexities and subject to intricately random events.
Hippidion
2 mya-10,000
years ago

Neophipparion
16-5 mya
been deep pools, and these may have held small amounts of water even after most of the river had disappeared.

All living horses are water-dependent. Dominant stallions of Grevy’s zebra select and defend territories with the best water and food supplies in the arid parts of Africa. Burchell’s zebras have a seasonal migration to areas with water and plants when the dry season comes.

There is no reason to think that the Hagerman Horse was any different in its physiology. If the animal’s foaling season was tied to the yearly rains, then any delay in those rains would have a severe effect on the population. If it was the beginning of the foaling season and the winter rains had not yet arrived, then mares would have been drawn to any remaining water and edible riparian plants. The presence of skeletons of young horses only weeks old in the quarry suggests that death occurred at this time. The high concentration of horses around the last remnants of water in the dried riverbed probably depleted the remaining vegetation. Horses then died from either starvation or thirst as the last pools of water and available vegetation disappeared. The result would have been a dried riverbed littered with horse carcasses. Eventually the riverbed refilled with water, either with the arrival of late rains of the season or perhaps with the next season’s rainfall. There was enough of a time lag that carcasses had decomposed sufficiently to scatter loose bones about the riverbed. As the river filled, bones were moved some and then buried, resulting in the deposit seen today. Although only one species of Equus was present at Hagerman three million years ago, by 2.5 million years ago we can recognize multiple species that are descendants.

Shortly after the appearance of Equus simplicidens, the species diversified and evolved. Even though we think of this species as being “extinct,” it is not a true extinction but rather a reflection of its success at adapting to the changing environment by evolving into new species. By the end of the Pliocene, fossil localities from Texas to Idaho have more than one species of Equus. Not only did Equus simplicidens evolve into new species, but its descendants dispersed and moved into new habitats. This took place across the North American continent and also into Asia and Europe. The earliest record of Equus in Asia and Europe is about 2.6 million years old. Equus finally entered Africa about 1.9 million years ago, where it is found in Kenya and Ethiopia. African zebras are descended from these pioneers.

Dispersal of Equus was not limited to Asia, Europe, and Africa; it was also part of the faunal interchange between North
and South America along with llamas, tapirs, and peccaries. About 500,000 years ago, Equus crossed the Isthmus of Panama into South America. Remains of Equus are widespread on the continent and have been found on the pampas of Argentina, in caves in Brazil, and in tar pits in Peru and Ecuador. By the end of the Ice Age, Equus had become extinct there just as its relatives in North America also became extinct. The question of why the horse disappeared in South America after being successful for half a million years is just as much a mystery as its disappearance from North America, the continent of its origin.

An admirable running machine, Equus adapted not only to open country but a variety of environments. Its descendants have occupied all the world's continents except Australia and Antarctica. An efficient grazer, the horse processed vegetation avoided by other herbivores. Social behavior and a close bond between man and horse may have helped the Hagerman lineage survive, yet the rapid spread of humanity also restricts equine habitat.
Horses such as the quagga are now extinct. Grevy's zebra, Przewalski's horse, and the Somalian ass are considered endangered species. The modern threat to equine survival is unprecedented. Industry, agriculture, and other human-induced ecological transformations have accelerated the rate of change beyond the capacity of the animals to adapt. We can only hope that our activities can be modified so that the descendants of the Hagerman Horse will survive to amaze, intrigue, and delight future generations.