

## Florida Fossil Horse Newsletter

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### How Can Horses Stand for So Long?

When I was a teenager I worked in a kitchen at a country club outside of New York City where I would work standing up for 10-12 hours each day. At the end of each day my feet and legs were absolutely exhausted. I'm sure others of you who have spent long periods of time standing up can attest to the amount of fatigue that sets in after so many hours, even though you may be relatively sedentary. Why does this happen? Your body has evolved certain structures involving bones and muscles that support your weight while standing, counteracting the force of gravity. This constant activity of holding up your skeleton for long periods of time puts strain on your muscles, which then tire and ache. Now imagine that you had to support a body weight of 500 pounds or more and you stood for more than 20 hours each day. That's what horses do all the time!

About four years ago I was in Ithaca, NY with John Hermanson, an anatomy professor at Cornell. As we passed by an *Equus* skeleton in an anatomy lab John asked if I had ever thought about how horses can stand for such long periods of time. He then went on to tell me that there are anatomical structures that are well known in modern *Equus* (including tendons, muscles, and bony structures) that function together to allow long periods of upright posture; these are called the passive stay apparatus (Fig. 1).

Although muscles and tendons do not fossilize, bony structures do.

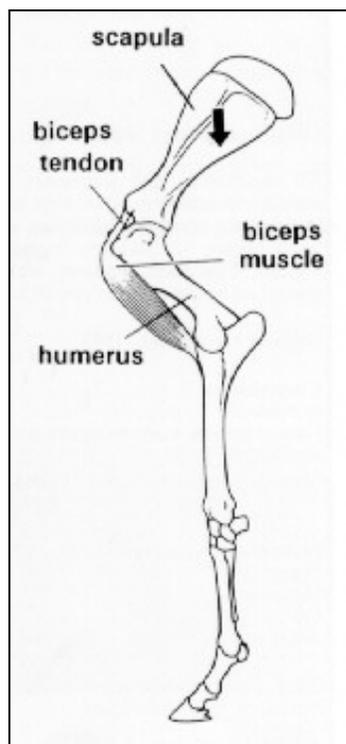
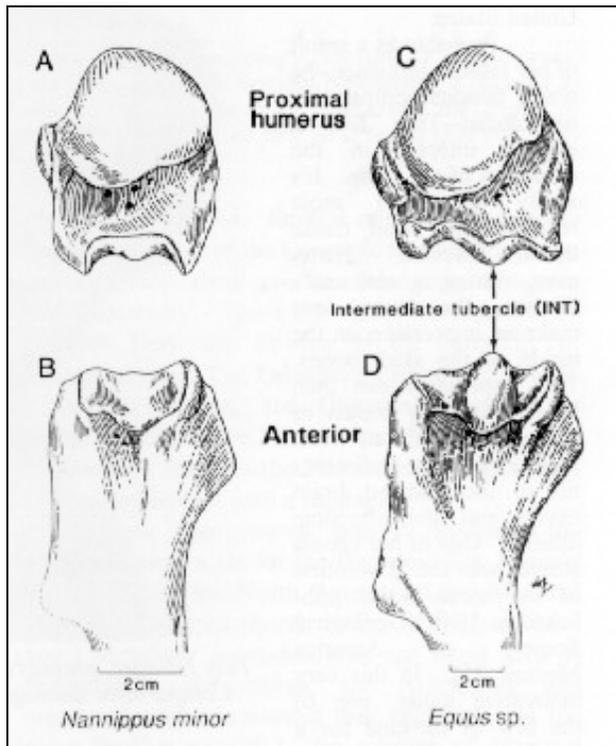


Fig. 1. Forelimb of a modern horse. The force of gravity (dark arrow pointing downward) can cause collapse of the leg. Gravitational forces are counteracted by the functional complex including the biceps muscle and tendon; the tendon fits over the humerus and locks the forelimb forming the passive stay apparatus.

Therefore, we can survey various fossil horse taxa to determine when and how the passive stay apparatus evolved. We first looked at the forelimb of horses. In *Equus*, dissections of the upper arm revealed that the biceps tendon travels from the top of the **humerus** (upper arm bone) to attach to the **scapula** (shoulder blade; Fig. 1). In contrast to other mammals, in modern horses this **biceps** tendon is dimpled. When the animal is standing this dimple fits over a unique intertubercular crest (**INT**) in the middle of the top (proximal part) of the humerus (Fig. 2). This locks the forearm from collapse and relieves the strain that otherwise would be felt by the muscles. Next we looked at many fossil horse humeri to see when the INT evolved. Our research indicates that the INT is absent during most of horse evolution. It first appears in *Dinohippus* about 5 million years ago. By the Pliocene, some 3 million years ago, the INT is well developed in all fossil species of *Equus* that we surveyed (Fig. 2). This bony structure and all of its associated muscles and tendons are known from all modern horses, zebras, and their relatives.

Why did the INT evolve in Pliocene and Pleistocene horses? The ability to stand for long periods of time may have been advantageous for individuals on the lookout for predators. It also may have allowed horses to feed on grasses for longer periods of time. And it could have been, at least in part, related to increased body size in *Equus*. This is a unique structure; some other large mammals, for example rhinos, also have a passive stay, but it evolved differently than horses. This illustrates an example in evolutionary theory called **opportunism**, in which there is not only a single way (or morphology) to evolve certain structures--horses did it in one way using the INT and rhinos and other large mammals evolved other structures.

Fig. 2. The intertubercular crest (INT) in the upper forelimb (humerus) of two fossil horses from Florida. In the primitive condition (A, B), the INT is absent in 5-7 million year old *Nannippus minor*. In the advanced condition (C, D), the INT forms as a bony crest in the middle of the top surface of the humerus (anterior and proximal; see vol. 1, No. 2 for anatomical terminology) that articulates with the shoulder blade (scapula) in Pleistocene *Equus* and related horses.



### Famous Horseologists--Tilly Edinger (1897-1967)

Tilly Edinger was born, raised, and educated in Frankfort, Germany early in this century. After completion of her doctoral degree in zoology (with a dissertation on Mesozoic marine reptiles) she was given a curatorial position at the famous Senckenberg Museum in Frankfort. Given her Jewish ancestry, the rise of Hitler and Nazi Germany during the 1930s made her position there increasingly more tenuous. Although the museum director, who was a member of the Nazi party, was sympathetic to Tilly's plight, she nevertheless had to go underground. For example, her nameplate was taken off her door at the museum and she frequently entered and exited work by the back door. In 1938 she was expelled from the museum by Nazi authorities. In the early 1940s she emigrated to the US where she obtained a position at Harvard in the Museum of Comparative Zoology and also taught comparative anatomy for a few years at Wellesley College. Hearing disabilities, however, forced her to leave teaching and concentrate on museum research. She was grateful for her position and the welcome that she found at Harvard; she later became a citizen of the United States.



*Tilly Edinger, photograph courtesy of Museum of Comparative Zoology, Harvard University.*

Probably as a result of her father's influence--he was a famous comparative neurologist--Tilly had a serious interest in the evolution of the brain. It's surely clear to most readers that brain tissue doesn't fossilize. However, during a mammal's lifetime, the brain does make an impression on the inside of the skull bones. This impression can then be fossilized by means of brain

endocasts, i.e., when mud and other sediments fill in the vacated brain cavity and then become lithified. One of her classic studies was the "Evolution of the horse brain" published in 1948 (Geological Society of America Memoir 25). In this very innovative study, one of the few of its kind for a fossil group, she traced the increasing complexity of fossil horse brains from *Hyracotherium* to *Equus* based on study of fossilized sediment endocasts (Fig. 3) While her classic depiction of the straight-line (orthogenetic) progression is highly oversimplified by today's standards, and subsequent workers such as Radinsky have questioned some of her interpretations, her work on fossil horse brains still remains as a classic and innovative study of paleobiology and evolution.

Tilly Edinger passed away in 1967 the day after she was involved in a street accident. Her numerous publications in diverse aspects of paleontology attest to her competence and enthusiasm for her chosen work. Al Romer characterized Tilly as "a charming friend--enthusiastic, warm-hearted, and outgoing ... this emotional warmth erupted in friendship and affection, and won her hosts of friends." Tilly is also remembered for "Tilly bones," bony thickenings along the vertebral column of numerous kinds of fishes. (Next time: Len Radinsky)

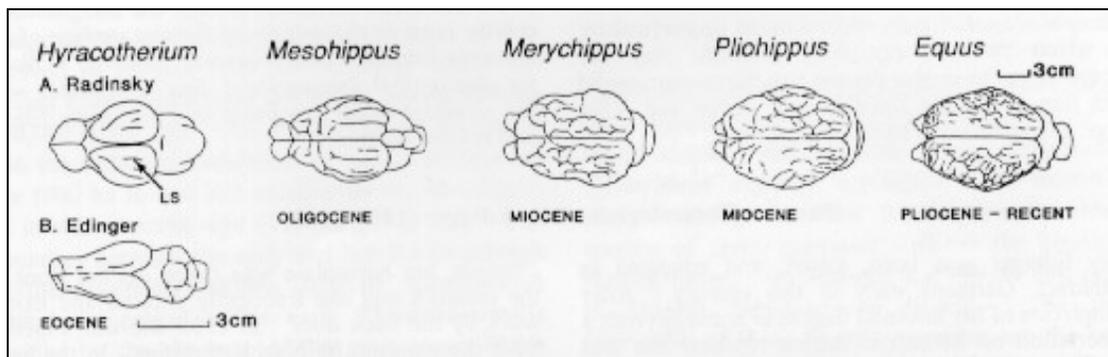


Fig. 3. The evolution of fossil horse brains, modified from Edinger's 1948 monograph. Her interpretation of the relatively simple brain of *Hyracotherium* (B) was reinvestigated by Radinsky (A) who believed that the original work was based on a contemporaneous Eocene condylarth mammal, not *Hyracotherium*. Using other specimens not available to Edinger, Radinsky found that the *Hyracotherium* brain was indeed more complex (including the presence of a lateral sulcus [LS]) than previously believed and had characteristics similar to more advanced horses later in the Cenozoic.

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## What's in a Name, or What Time is it?: Part 1

by Gary Morgan

*editor's note: I had intended to write an article on geological time terminology relevant to fossil horses. After I read Gary's article published recently in the Florida Paleontological Society Newsletter, I decided to reprint it here, with slight modifications, because it does an excellent job of explaining the technical terminology that paleontologists use to describe geological time. This is the first in a series and I hope to also reprint other installments as they become available)*

Some of the questions most frequently asked of paleontologists at the Florida Museum of Natural History relate to various technical "terms of the trade". Whether they are scientific names (*Parahippus leonensis*-a Miocene three-toed horse), anatomical terms (tarsometatarsus-the lower leg bone of a bird), time periods (Hemingfordian-an early Miocene land mammal age), or stratigraphic names (Caloosahatchee Formation-a late Pliocene geologic unit from southern Florida), technical terms often confuse or intimidate avocational paleontologists, many of whom may not have had formal training in zoology and or geology. My intention in this article is to try to make these technical terms more understandable to the general paleontological public.

Most people interested in fossils probably have a general understanding of the basic units of geological time, but for the sake of completeness I will briefly review the geological time scale as it pertains to

Florida. In a recent issue of *Papers in Florida Paleontology* (No. 6, May 1992, see review in *Pony Express*, Vol. 1, No. 3), Richard Hulbert provided a detailed summary (Table 1, page 3) of the geological time units of Florida and their ages. All rocks, sediments, and fossils found at the surface in Florida (or near the surface in mines, shell pits, sinkholes, etc.) belong to the Cenozoic Era, the period of time covering the last 65 million years. Million years is sometimes abbreviated Ma for mega-anna (for example 2.5 Ma for 2.5 million years) and thousand years is abbreviated ka for kilo-anna (for example 10 ka for 10,000 years). The **Cenozoic Era** is subdivided into seven **Epochs** (from oldest to youngest with approximate age range in Ma): **Paleocene** (65-57 Ma), **Eocene** (57-35 Ma), **Oligocene** (35-23 Ma), **Miocene** (23-5.2 Ma), **Pliocene** (5.2-1.6 Ma), **Pleistocene** (1.6 Ma-10 ka), and **Holocene** (10 ka-present). No Paleocene rocks occur at the surface of Florida. Our oldest rocks and fossils are middle Eocene in age, approximately 45 million years old. Several other less commonly used subdivisions of the Cenozoic that you may have heard or read about are the Paleogene, Neogene, and Quaternary. These are called **Periods** and fit between Eras and Epochs in the hierarchy of geological time. The **Paleogene Period** includes the Paleocene, Eocene, and Oligocene Epochs; the **Neogene** includes the Miocene and Pliocene; and the **Quaternary** includes the Pleistocene and Holocene (also called Recent with a capital R).

Now that we've briefly reviewed the geological time scale for the Cenozoic Era, I would like to discuss the North American Land Mammal Ages (NALMA for short). Many of you may have heard vertebrate paleontologists use terms such as Irvingtonian, Hemphillian, and Arikarean, and wondered what relationship they might have to the more familiar epochs. The concept of Mammal Ages for North America was first proposed in 1941 in a paper by Horace E. Wood and six other authors entitled "Nomenclature and correlation of the North American continental Tertiary." (*Bulletin of the Geological Society of America*, Vol. 52, p. 1-48). Wood et al. (1941) named most of the NALMA currently in use today, although they did not include the Pleistocene. The two Pleistocene NALMA the Irvingtonian and Rancholabrean, were named later in a paper by Donald Savage (1951. *Late Cenozoic vertebrates of the San Francisco Bay region*. University of California Publications in the Geological Sciences, vol. 28, p. 215-314.).

North American Land Mammal Ages are characterized by a composite fauna of land mammals, usually genera, that coexisted in North America during a particular interval of the Cenozoic Era. The typical mammalian assemblage for each NALMA has been constructed from correlative faunas throughout North America, and contains genera and or species that are either restricted to that Age or have their first or last appearance during that Age. For example, the Hemphillian NALMA, which covers the time period from the late Miocene to the early Pliocene (approximately 9-4.5 Ma), is characterized by the first appearance of ground sloths (*Pliometanastes* and *Thinobadistes*) in North America and the last appearance of North American rhinoceroses (*Aphelops* and *Teleoceras*). All four of these genera are known from sites of Hemphillian age in Florida.

Fossils representing nine North American Land Mammal Ages are known from Florida. In order from oldest to youngest these are (with age ranges in Ma): Whitneyan (29-28 Ma); Arikarean (28-20 Ma); Hemingfordian (20-16.5 Ma); Barstovian (16.5-11.5 Ma); Clarendonian (11.5-9 Ma); Hemphillian (9-4.5 Ma); Blancan (4.5-1.9 Ma); Irvingtonian (1.9-0.3 Ma); Rancholabrean (0.3 Ma-10 ka). These NALMA rather conveniently divide into four groups which I will discuss in separate columns, starting with the youngest and working backward in time to the oldest. The youngest NALMA the Rancholabrean, will be discussed in the remainder of this article. Detailed discussions of the other NALMA represented in Florida will be presented in future articles.

The Rancholabrean Land Mammal Age began approximately 300,000 years ago and lasted until the end of the Pleistocene 10,000 years ago. Savage (1951) named this NALMA for the late Pleistocene fauna from the famous Rancho la Brea tar pits in Los Angeles in southern California. The beginning of the Rancholabrean is defined by the first appearance of *Bison* in North America. *Bison* evolved in Eurasia and then migrated across the Bering Land Bridge into the North America about 300,000 years ago. The Rancholabrean is divided into the early Rancholabrean of middle Pleistocene age (300 ka to 130 ka) and the late Rancholabrean of late Pleistocene age (130 ka to 10 ka). The boundary between the early and late Rancholabrean is the beginning of the last or Sangamonian interglacial period. The early Rancholabrean is typified by the presence of the giant bison, *Bison latifrons*, while the species *Bison antiquus* occurs in later Rancholabrean faunas. The end of the Rancholabrean is characterized by the first arrival of humans in the

New World about 12,000 years ago and the subsequent rapid extinction of almost 30 species of large mammals (often called the Pleistocene megafauna). Proponents of the "Human Overkill Hypothesis" suggest that overhunting by humans caused the extinction of the Pleistocene megafauna in a remarkably short period of time between 12,000 and 10,000 years ago. Other paleontologists attribute these extinctions to climatic and vegetational changes that occurred at the end of the Pleistocene.

Many other species of mammals besides Bison are characteristic of Florida Rancholabrean faunas. Xenarthrans or edentates found in Florida during the Rancholabrean include: the glyptodont *Glyptotherium floridanum*, the giant armadillo *Holmesina septentrionalis*, the beautiful armadillo *Dasypus bellus*, Jefferson's ground sloth *Megalonyx jeffersonii*, and Harlan's ground sloth *Paramylodon harlani*. Among large carnivores, typical Rancholabrean species include: the dire wolf *Canis dirus*, the sabretooth cat *Smilodon fatalis* (also called *Smilodon californicus*, *S. floridanus*, and *S. populator* by various authors), the American lion *Panthera atrox* (some authors consider this to be the same species as the African lion *Panthera leo*), the jaguar *Panthera onca*, and the Florida cave bear *Tremarctos floridanus*. Ungulates found in Florida Rancholabrean faunas include: the Vero tapir *Tapirus veroensis*, the extinct horse *Equus* (the fossil species of *Equus* are currently in a state of chaos), the forest peccary *Mylohyus fossilis*, the flatheaded peccary *Platygonus compressus*, the shortlimbed llama *Palaeolama mirifica*, and the longlimbed llama *Hemiauchenia macrocephala*. The American mastodon *Mammuth americanum* and the Mammuthus columbi typically occur together in Florida Rancholabrean faunas. A third elephant-like species, the gomphothere *Cuvieronius tropicus*, apparently went extinct Columbian mammoth in Florida during the early Rancholabrean. Many species of small mammals such as the opossum, shrews, moles, bats, rodents, and rabbits also occur in Florida Rancholabrean faunas. The most impressive of these "small" mammals are the bear-sized giant beaver *Castoroides ohioensis* and the extinct capybara *Nechoerus pinckneyi*. The latter species is a close relative of the largest living rodent, the South American capybara.

Webb (1974) provided faunal lists of mammals for more than 30 of the best known Rancho-labrean sites from Florida. Kurten and Anderson (1980) discussed many of these same sites. Because of their proximity to the Recent, there are far more Rancholabrean vertebrate faunas known from Florida than those of any other NALMA. More than 100 Rancholabrean faunas are known from Florida, the great majority of which are late Rancholabrean in age. On the other hand, early Rancholabrean faunas are rather rare in the state. The best known Florida early Rancholabrean faunas are the Bradenton Site in Manatee County which produced several beautiful *Bison latifrons* skulls, the Haile 8A Site in Alachua County which yielded a complete skeleton of an adult and a juvenile *Bison latifrons*, and the Daytona Beach Site in Volusia County best known for several skeletons of the giant ground sloth *Eremotherium mirabile*.

In the limited space available, it will only be possible to mention several of Florida's best known late Rancholabrean faunas. Three of the earliest sites of this age discovered in Florida were the Vero Beach Site in Indian River County, the Melbourne Golf Course locality in Brevard County, and Seminole Field in Pinellas County. These sites were all found early in this century by paleontologists from the American Museum of Natural History, Smithsonian Institution, and Harvard University. Dry caves, sinkholes, and fissures have produced large samples of Rancholabrean vertebrate fossils, particularly from northern Florida. Cave and fissure sites often have extremely rich samples of microvertebrates such as snakes, birds, bats, and rodents. Well-known localities of this type include Arredondo and Haile in Alachua County, Reddick in Marion County, and Sabertooth Cave in Citrus County.

Many rivers in Florida, particularly in the northern half of the state, have long been known to produce well-preserved fossils of large mammals. In fact, almost all of the species of Pleistocene megafauna mentioned above have been recovered from one or more of Florida's rivers. Some (but certainly not all) of the rivers known to produce rich samples of Rancholabrean fossils are: Chipola, Aucilla, Steinhatchee, Santa Fe, Ichetucknee, Waccasassa, Oklawaha, Rainbow, Withlacoochee (southern), and Peace. Several deep underwater sinkholes and springs in Florida have also produced rich late Rancholabrean faunas. Best known among these are Wakulla Springs in Wakulla County, Devils Den in Levy County, Hornsby Springs in Alachua County, and Little Salt Springs and Warm Mineral Springs both of which are in Sarasota County. Little Salt Springs and Warm Mineral Springs are especially important because both sites document the association of paleoindians and extinct Pleistocene megafauna, including *Smilodon fatalis*, *Megalonyx jeffersonii*, and the giant land tortoise *Geochelone crassiscutata*.

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## Members Profile--Claire and Dylan Cerling

Claire and Dylan live in Salt Lake City UT. They originally became interested in fossil horses when their parents took them on camping trips to places such as to the Big Horn Basin of Wyoming where they collected 50 million-year old *Hyracotherium*. Claire and Dylan have also participated in other fossil digs, such as collecting Miocene fossil mammals in -Turkey. Claire, 12, has worked in the geochemistry laboratory at the University of Utah where she has learned to prepare fossil mammal teeth (including many fossil horses) for chemical analyses to find out what they ate. Dylan, 9, maintains a collection of fossils, minerals, and other natural history specimens at his home.



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## Book Review

*Megaherbivores., The Influence of Very Large Body Size on Ecology*, 1988 (Paperback 1992), by R. N. Owen-Smith, Cambridge University Press, 369 pages, ISBN 0 521 42637, retail \$34.95 (paperback).

The mega- in the title stands for large, meaning mammals with body sizes of ca. 450 pounds or greater. Owen-Smith, an expert on mammal ecology, writes a treatise on varied aspects of the biology of modern large herbivorous mammals and how they have impacted terrestrial ecosystems. He draws extensively from his own field research and observations on the rich mammalian herbivore assemblages from modern Africa, which include such large beasts as elephants, hippos, rhinos, and giraffes. One interesting part of this book deals with fossil megaherbivores during the later Cenozoic, and, in particular, the factors that affected the Pleistocene megafauna (e.g., mammoths, mastodons, ground sloths) including some smaller forms like *Equus*. This part has relevance to the fossil sequence and extinctions in Florida.

This is a rather specialized book but is written in such a way that it can appeal to the person with a general interest in large mammals, both living and extinct. Originally issued as a hardcover version, the price of the recently published paperback version puts it within potential reach of a larger readership. It is a wellwritten and very interesting book--I kept finding myself reading the accounts of modern herbivorous mammals and wondering how their behavior and ecology relate to their extinct relatives.

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## *Pony Express*

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## **Direct all Correspondence to:**

***Pony Express*** Department of Natural Sciences  
Florida Museum of Natural History  
P.O. Box 117800  
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The purpose of this newsletter is to communicate news and information and disseminate knowledge about fossil horses, particularly in Florida, and to develop a state-wide constituency that will support and enhance the research, exhibition, and educational programs offered at the FLMNH that pertain to fossil horses. Contributions to the Fossil Horse Fund are deposited into an account at the University of Florida Foundation, Inc., a tax-exempt entity, and will be used for the purposes stated here.

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