

Florida Fossil Horse Newsletter

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Tennessee Tapirs and Rhinos, Too

In July paleontologists from the FLMNH, including Bruce MacFadden, Richard Hulbert, and new zoology graduate student Larisa Grawe participated in excavations at the Gray Fossil Site in eastern Tennessee. As a result of road excavations in 2000, fossil bones were unearthed and these were brought to the attention of paleontologists who determined that they represented the remains of extinct tapirs. These fossils were deposited in organic rich sediments that filled in



Richard Hulbert (left) and Larisa Grawe (right) have exposed a femur of the articulated Teleoceras skeleton. Bruce MacFadden Photo

an ancient sinkhole. Subsequent excavations by paleontologists at Eastern Tennessee State University led by Assistant Professor of Geology Dr. Stephen Wallace have discovered a truly unique extinct fauna including tapirs, the rhinoceros *Teleoceras*, camel, peccary, rodents, short-faced bear, and the surprising discovery of a red panda. Based on the fossil evidence, the age of this site is either late Miocene or early Pliocene (between about 7.5 and 4.5 million years old) and represents ancient mammals that probably lived in a well developed oak-hickory forest. Ninety percent of the larger mammals collected from the Gray site represent tapirs, which today inhabit

forests of Central and South America and Asia. Miocene and Pliocene land mammals are exceedingly rare in eastern North America, with only a handful of other localities known outside of the rich deposits from Florida (e.g., the phosphate mines and shell pits). The Tennessee Department of Transportation has funded the initial outlay of eight million dollars to build a paleontological museum on the Gray site.

During our trip to ETSU and the Gray site, Larisa Grawe collected tooth samples for chemical analyses and Richard Hulbert made the spectacular discovery of a nearly complete *Teleoceras* skeleton. This and the other exciting fossil discoveries at the Gray site will advance our currently limited knowledge of extinct mammals from Tennessee. For more information about the Gray Fossil site, go to: http://www.etsu.edu/grayfossilsite

Bruce J. MacFadden

Welcome Back Bruce Shockey

Bruce Shockey, a UF paleontology graduate and assistant at Thomas Farm during the 1990's recently returned to Gainesville where he is a Visiting Assistant Professor in Zoology. After a Fulbright year in Bolivia, Bruce taught biology at New Jersey City University and then Valdosta State University in Georgia. During his current two-year appointment here at UF, Bruce will teach comparative anatomy, vertebrate zoology, and general biology while continuing his research on



Bruce Shockey studies notoungulates from Bolivia at the FLMNH vertebrate paleontology collection. (Paula Tarrant Photo)

fossil mammals from the highlands of Bolivia and Peru.

We are glad that Bruce has returned to UF and look forward to his continuing participation in the vertebrate paleontology program at the FLMNH.

SW Florida Fossil Club Award to VP student

The SW Florida Fossil Club generously makes an annual award of \$500 to a deserving vertebrate paleontology student in support their research. This year Jonathan Hoffman, a UF Geology Masters student is the recipient of this award for his research on Miocene horses from the Florida panhandle. A native of Arizona, Jonathan received his B. S. degree in Geology in 2003 from Occidental College in Los Angeles, CA. He is currently working under the supervision of Bruce MacFadden. We are most grateful to the SWFFC for their continued support of our students.

Megalodon

Late Tertiary sharks like "megalodon" (Carcharodon megalodon) evolved enormous body size rivaling that of giant whales of today and dinosaurs of the Mesozoic. Studies have estimated that megalodon exceeded 60 feet in length, more than double the length of the modern great white shark. An unanswered question about megalodon is how did it grow to be so large? Relative to its ancestor, which was a "normal-sized" 30-foot long ferocious shark that lived during the Oligocene and Miocene, did megalodon grow faster, or did it grow at the same rate but for a longer time? This question will be answered by Bruce MacFadden and his Ph. D student Joann Labs Hochstein with support from a four-year project recently funded by the National Science Foundation. They will determine the growth rate of megalodon and other related "lamnoid" sharks by studying the incremental growth (like counting tree rings) preserved in the ancient vertebral centra of fossil sharks.

Bruce and Joann are grateful to local shark experts Dr. Gordon Hubbel of Gainesville

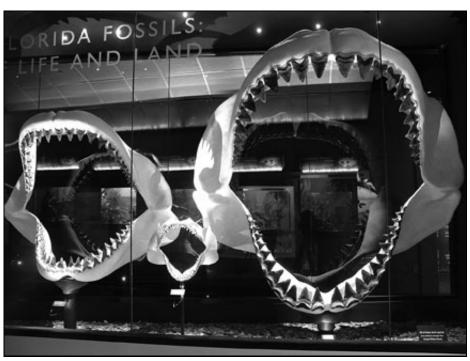


and Dr. Cliff Jeremiah of Jacksonville who have either donated or allowed us to study important specimens from their collections as part of this project.

Bruce J. MacFadden

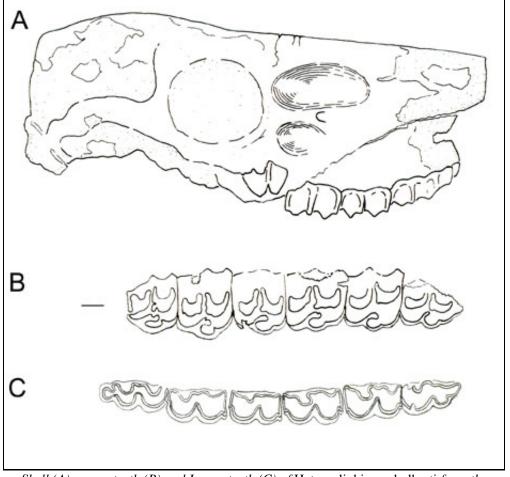
The Last Decade (More or Less) of Equid Paleobiology

In this last issue of The *Pony Express*, the editor and I thought it would be appropriate to summarize recent advances and discoveries in the field of equid paleontology. At first, the last ten years seemed like a good



These two magnificent Charcarodon megalodon jaws gracing the entrance of the new Hall of Florida Fossils, were made by Dr. Clifford Jeremiah. The cartilagenous portion is made of fiberglass and fitted with real Charcharodon teeth. The smaller jaw in the middle is from a smaller species of fossil shark. (Erika Simons Photo)

duration to cover. But, considering that Bruce MacFadden's 1992 book Fossil Horses is the most likely source for "upto-date" information on fossil horses for readers of this publication, I decided to cover the interval from 1993 to the present, slightly more than a decade. The first section, dealing with systematics and taxonomy, will only cover North American taxa, as to include those from other continents would take many more pages than the editor has allotted me. The second section will cover the topics of



Skull (A), upper teeth (B) and Lower teeth (C) of Heteropliohippus hulberti from the Miocene of California. This genus and species was named by Thomas Kelly in 1995, one of nine new fossil horses named since 1993.

evolutionary processes and biogeography, and the third will be on paleoecology.

Systematics and Taxonomy Six new genera and nine new species of fossil horses from North America were named between 1993 and 2004. The genera are: Parapliohippus, Kelly 1995; *Heteropliohippus* Kelly, 1995; Acritohippus Kelly, 1995; Sifrhippus Froehlich, 2002; Minippus Froehlich, 2002; and *Arenahippus* Froehlich, 2002. The species are Acritohippus quinni Kelly, 1995; *Archaeohippus* mannulus O'Sullivan, 2003; *Cormohipparion* quinni Woodburne,

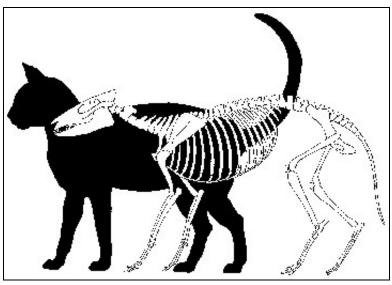
1996; *Equus enormis* Downs and Miller, 1994; *Equus fromanius* Repenning and others, 1995; *Equus pseudaltidens* Hulbert, 1995; *Heteropliohippus hulberti* Kelly, 1995; *Minippus jicarillai* Froehlich, 2002; and *Nannippus morgani* Hulbert, 1993.

MacFadden's (1992, pp. 90-94) discussion of the oldest horses ("Hyracotherium") relied heavily on work published by Jeremy Hooker of the British Museum in the late 1980s. Subsequent analysis by David Froehlich has significantly changed our understanding of the first horses and how they are related to other perissodactyls. Froehlich's work supports a basal split within the perissodactyls, with those related to tapirs and rhinos forming one branch or clade (the Tapiromorpha), and those more related to horses forming a second clade, the Hippomorpha. The latter not only includes the family of true horses, the Equidae, but also the primarily Old World Palaeotheriidae. Among the many recognized species classically assigned to *Hyracotherium*, Froehlich's analysis places some in the Tapiromorpha, some in the Palaeotheriidae, and some form the base of the Equidae. One point of agreement between the work of Hooker and Froehlich is that the type species of the genus Hyracotherium, Hyracotherium leporinum, is a member of the Palaeotheriidae, so that generic name can not be correctly applied to any member of the Equidae, the true horses. Froehlich's (2002) solution is to recognize seven early Eocene genera of Equidae, one from Europe (*Pliolophus*), and six from North America (Sifrhippus, Minippus, Arenahippus, Xenicohippus, Eohippus, and *Protorohippus*). Among the important results of Froehlich's work are that the oldest rocks to produce fossil horses (ca. 55.6 Ma from Wyoming) contain two species, the very small *Sifrhippus* sandrae and the medium-sized Arenahippus grangeri. Within 2 to 3 million years, known equid diversity in North America was on the order of six to nine species (considering that early Eocene sediments are known from a relatively small percentage of the continent, the true value was almost certainly higher). Froehlich also revived O. C. Marsh's classic but long unused generic name

Eohippus, but applied it to only one species, Eohippus angustidens.

The Miocene browsing horse Anchitherium has made a comeback. In 1992, and again in 1998, MacFadden declared that Anchitherium was never in North America, and referred species usually placed in that genus to *Kalobatippus*. More recently, MacFadden (2001) reversed course after study of specimens from Nebraska, Texas, and Florida (including fossils collected by Pony Express workers at Thomas Farm), and concluded that several species of Anchitherium were indeed present in North America, including Anchitherium clarencei of Florida.

Other recently published works on the systematics and taxonomy of North American horses are those by Kelly (1995, 1998) on Miocene Equini from California, Woodburne (1996, 2003) on *Cormohipparion* and *Merychippus*,



A skeletal reconstruction Sifrhippus sandrae (from the early Eocene of Wyoming) is compared to that of an average house cat. Sifrhippus is the most primitive horse known. From MacFadden (1992) with author's permission.

Hulbert (1993a) on Florida *Nannippus*, MacFadden (2002) on *Dinohippus* from Mexico, and Azzaroli and Voorhies (1993), Downs and Miller (1994), Azzaroli (1995), and Repenning and others (1995) on *Equus*. O'Sullivan's (2003) new species of *Archaeohippus* was featured in the Spring 2004 PE Newsletter. (see *Pony Express* Vol. 13, no.1)

Evolution and Biogeography Hermanson and MacFadden (1996) investigated the ability of horses to stand upright for very long periods of time using a specialized system of limb bones and ligaments with minimal muscle exertion. In a 1992 study, they had shown that such a system evolved in the forelimb about 5 Ma within the Equini. Their 1996 analysis of the hindlimb produced different results. Specialized knee joints for standing showed up in horses as early as 15 Ma, and they are found in both equine and hipparionine horses. No clear explanation was provided for why this feature evolved so much earlier in the hindlimb, or why it was found in a much broader range of horse taxa, but the authors speculated that it might relate to differences in posture and joint angles in the bones of the fore- and hindlimb.

Hulbert (1993b) studied the rates at which new species originated and at which species became extinct for North American horses between 18 and 2 Ma. Although the new species described by Kelly and others noted above will modify the results of this study, they will not dramatically effect the overall conclusions. On average, each horse species persisted for 3.2 million years. Periods of higher than average species originations or extinctions were correlated with global or regional changes in climate and vegetation.

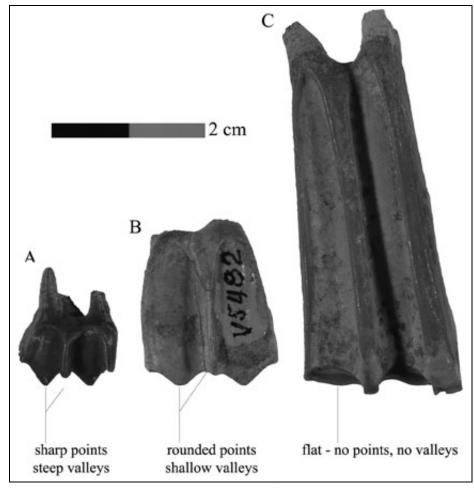
Although this essay is primarily summarizing results of paleontological studies, a recently published paper using DNA from modern *Equus* has implications for interpretation of paleontological data. Oakenfull and others (2000) compared the sequence of two genes from mitochondrial DNA from all living species of *Equus*. The resulting evolutionary tree supported the four main groups based on traditional anatomical characters-the caballines (the domestic horse and it wild progenitor *Equus przewalskii*); the hemionines (the Asiatic onager and kiang); the asses (the African wild ass and the domestic donkey); and the zebras. Their DNA evidence suggests that the caballine group was the first to diverge from other members of *Equus* (paleontologic data suggests instead that the zebras were the first group to diverge). They also failed to find support for uniting the hemionine and ass groups together, as is often the case with anatomical studies.

Alberdi and others (1995) looked at patterns of body size evolution in the equine clade of horses in relation to changes in climate and vegetation. They concluded that smaller body size was favored by warm climate, wooded to partly wooded environments, and hard soils; conversely cold climates, open, treeless habitats, and softer soils favor larger species of horses. These results were used to explain the different trends observed in Pleistocene *Equus* in North America (generally increased in size) and Europe (generally decreased in size).

One of the major biogeographical events in the history of the horse family was the dispersal of three-toed hipparion horses from North America into Eurasia in the Miocene. Two similar studies, by Woodburne and others (1996) and Garcés and others (1997) presented data that this event occurred about 11 Ma, somewhat later than previously thought. Garcés et al. (1997) noted that the dispersal of hipparions into the Old World coincided with a major global cooling event that saw lower sea levels and rearrangement of oceanic currents. The Woodburne et al. (1996) study also concluded that the most primitive European hipparions (i.e., those most similar to their North American ancestor) were populations of *Hippotherium primigenium* from Central Europe. However, Bernor and others (2004) provisionally referred an even more primitive population of hipparions from a ca. 10.5 Ma site in Ethiopia to the North American genus *Cormohipparion*.

Hulbert and Harington (1999) described a Pliocene maxilla of a young foal from Ellesmere Island in Arctic Canada. At 78° 33' N latitude, it is the northernmost record for a fossil horse. The combination of its large size, dental features, and reduced facial fossa suggest greater affinity with Pliocene hipparion horses from Asia than with mid-latitude Pliocene hipparions from North America. So it likely represents the first known dispersal of an hipparion from Asia to North America. Paleoecology MacFadden (1992) has turned out to be very prophetic in its anticipation that stable isotopes of carbon, oxygen, and nitrogen preserved in fossils, especially tooth enamel, would become widely used tools in the field of paleoecology. Indeed, much of Dr. MacFadden's own research and that of his graduate students over the past decade has involved stable isotope analysis. Examples of this can be found in such publications as Wang and others (1994), MacFadden and Cerling (1996), MacFadden and others (1999a, 1999b), and Feranec and MacFadden (2000). Technological improvements to the equipment (mass spectrometer) that determines the relative abundances of the stable isotopes have dramatically decreased the amount of enamel needed for a sample. That means that much less damage is done in the sampling process, and it allows researchers to take multiple samples per tooth.

Two other techniques have also become more widely used to study the paleoecology of fossil mammals, including horses. Analysis of diets of fossil mammals using the microscopic scratches and pits on enamel from the occlusal surface of teeth (called microwear) has been done for several decades, but recently Solounias and Semprebon (2002) introduced a new, faster method to study microwear that does not use a scanning electron microscope. Among their initial test subjects were are series of fossil horse genera. Their specimens of "Hyracotherium"



Mesowear analysis compares the degree of wear on the occlusal surface of moderately worn molars. Archaeohippus blackbergi (A) shows the sharp points and steep valleys on the lingual side of a browser molar, Merychippus gunteri (B) shows the more rounded points and gentler valleys of a mixed feeder molar and Neohipparion (C) shows the almost flat-worn surface of a grazer molar. Erika Simons photo

(unfortunately not identified to species, so it is not known which genus or genera of horses these are using Froehlich's (2002) classification scheme) had microwear patterns consistent with a diet of fruit, seeds, and leaves. The microwear patterns of Mesohippus, Parahippus, and Merychippus, were overall similar to each other and to that of the modern elk. Solounias and Semprebon (2002) suggested a mixed diet of browse and fresh grass for these horses, with *Mesohippus* consuming the least grass and *Merychippus* the most.

Another new technique for interpreting diets of fossil mammals is mesowear analysis (Fortelius and Solounias, 2000; Kaiser, 2003; Kaiser and Fortelius, 2003; Kaiser and Solounias, 2003; Kaiser et al., 2003). Mesowear analysis compares several easy to observe features on the occlusal surface of moderately worn molars, so

unlike the other methods discussed here, many individuals can be sampled to allow for intraspecific variation. The studies of Kaiser and others have focused on populations of the late Miocene species *Hippotherium primigenium*, the first hipparion horse in Europe. Mesowear analysis suggests the diet of this species varied according to the availability of local vegetation, with populations varying from browsing to grass-dominated mixed-feeding. Both mesowear and microwear suggest a mixed-feeding diet (leaves and grasses) for a 10.5 Ma hipparion from Ethiopia (Bernor et al., 2004). A much younger and more advanced hipparion from South Africa was classified by mesowear analysis as a pure grazer (Franz-Odendaal et al., 2003).

With the added tools of stable isotopes, mesowear, and microwear analyses to interpret paleodiet, combined with traditional anatomical indicators such as metapodial dimensions, crown height, tooth enamel morphology, incisor orientation, and muzzle width, paleontologists are beginning to unravel the paleoecologic history of the Equidae to a much finer degree than ever before possible. Its is now very clear that the simplistic picture of all horses falling into only two dietary categories, browsing or grazing, which was famously shown in both Simpson's (1951, p. 114; reprinted on p. 42 of MacFadden, 1992) and MacFadden's (1992, p. 99) evolutionary trees of the Equidae (and later reproduced in numerous biology and geology textbooks) is wrong. Many mid-Tertiary species were mixed-feeders, eating various proportions of leaves and grasses.

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Richard Hulbert

An Update on the Fossil Birds from the Thomas Farm Site

I am continuing to study the fossil birds from Thomas Farm. This research is part of a larger project called Early Bird that is funded by the National Science Foundation's "Assembling the Tree of Life" Program. The goal of the project is to develop a much better understanding of the relationships among all living orders and families of birds. The other seven scientists involved in Early Bird are studying DNA. The paleontological data that I generate helps to calibrate their molecular data, with a goal of putting together a comprehensive phylogeny of birds that has a chronology based on both fossils and DNA.

Because of their delicate bones and lack of teeth, birds are preserved as fossils much less frequently than mammals, at least in continental situations. Nevertheless, the fossil birdlife from Thomas Farm is exceedingly rich. In fact it includes more species than in any other early Miocene site in North America. For those of us who have spent so many hours screen-washing sediment at Thomas Farm, it is gratifying that the tiny bones ("microfauna") we discover have quite a story to tell. With cooperation and blessings from Bruce MacFadden, Art Poyer, and Richard Hulbert, my assistants (Tabitha Cale, Sharyn O'Day, Matthew Reetz) and I now have washed, picked, and sorted all bones from the 75 bags of sediment that we brought to the museum from the two *Pony Express* Digs in April 2004. The number of identifiable fossils of birds from Thomas Farm now exceeds 400. Bone by bone, they are providing a wealth of new evidence about Florida's birdlife 18 million years ago.

Just as with the reptiles and mammals, all of the species of birds from Thomas Farm are extinct. Only seven of the 25+ species that I have recognized thus far even have names. These are an anhinga, three hawks, a chachalaca, a small turkey-like gamebird, and a dove. Called *Columbina prattae*, this dove is by far the most common species of bird at Thomas Farm. It is a little larger than the Common Ground Dove (*Columbina passerina*) that lives in Florida today. Awaiting further study is a heron, ibis, two rails, a pigeon, cuckoo, owl, various songbirds, and others. Many of the birds from Thomas Farm represent families that live today only in the tropics. These would include a roller (today in Africa and Asia), a motmot and puffbird (today in Mexico, Central America, and South America), and barbets (today in both the New World and Old World tropics). The tropical affinities of the birds matches what Gary Morgan and Nick Czaplewski have discovered with the bats from Thomas Farm, which include representatives of families that now are confined to tropical regions.

Additional screen-washing of sediments from Thomas Farm, which is planned for the 2005 field season (see below), is sure to produce more new species of birds, and thus help us to understand avian evolution and biogeography in Florida and throughout North America. A valuable by-product of this effort is a large accumulation of fossils from other small vertebrates such as frogs, toads, salamanders, lizards, snakes, bats, and rodents.

David Steadman (FLMNH Curator of Ornithology)

Thomas Farm Digs - Spring 2005 - The Hummingbird Challenge!

Please join Dave Steadman and Erika Simons at the Thomas Farm site in Gilchrist County on one of two long weekends in April 2005 (See page 8



Long-time Pony Express participant, Bill Lee is pictured screen-washing Thomas Farm matrix and looking for microfossils. Bruce MacFadden photo

for the dates). After 13 years of running the annual *Pony Express* Thomas Farm Fossil Dig, Bruce MacFadden has passed the trowel to Dave Steadman. While we will excavate and save the larger species just as before (alligators, tortoises, horses, rhinos, camels, bear-dogs, etc.), in 2005 we will have a special focus on the microfossils, which represent the small species that actually far outnumber the large ones. (See the article by Erika Simons in

Pony Express Vol. 12, no. 2). During the 2004 *Pony Express* Thomas Farm Fossil Dig, veteran excavator Bill Lee produced two buckets of sand that were extremely rich in microfauna, setting a high standard for anyone working at Thomas Farm. In 2005, we will do some screen-washing on site, although most of it will take place under more controlled conditions at the museum after the field work is completed.

Dave's research on the birds from Thomas Farm (see accompanying article above) is behind our new focus on the microfauna. We call this year's dig The Hummingbird Challenge for two reasons. The first is that it calls attention to the small species of vertebrates that rarely are recovered (or at least rarely are studied) in pre-Pleistocene deposits. The second is that a fossil hummingbird has been discovered recently in the late Oligocene of Germany, whereas in the Americas (where hummingbirds are confined today), there is not a single fossil of these tiny,

colorful, nectar-feeders before the late Pleistocene. Finding a hummingbird fossil at Thomas Farm would be a major discovery. Even if hummingbirds elude us, the rich microfauna sample that we generate almost certainly will include new species for the Thomas Farm fauna. David Steadman



Farewell to a Museum Tradition



Many, many thanks to the staff and volunteers who have served at Pony Express Thomas Farm Digs. The order and size of the pictures is totally arbitrary and based on availability and fit with exception of Bruce MacFadden, Program Director. Left to right, Top To bottom: Art Poyer and Gary Morgan, Dennis Ruez, Jr., Mark Swan, Richard Hulbert, David Bunger, Bill Bishop, Penny Higgins, Tabitha Cale, Joann Labs-Hochstein and Bob Simons, Bruce MacFadden, Russell McCarty, Erika Simons, Julie Meachen, Bruce Shockey, Matt Smith, Suzan and Stephen Hutchens, David Whiddon, Helen Evans, Jay O'Sullivan, Barry Albright, Tabitha Cale (shown twice because her face was covered in previous picture), Amanda Barrett, Brian Beatty, Dan Cordier (no picture available). Erika Simons composite

things must come to an end, and so it goes with the annual Thomas Farm field camp. I recall the very first one back in 1982 or '83 when we all were young. Like a pack of meercats on speed, you all dug one hell of a big hole out the re at Thomas Farm. And what a bunch of unforgettable characters you are. I remember the first few years when we camped out at the old, deserted Thomas family farmhouse about an eighth of a mile from the fossil site. It was there where we cooked, showered (hosed off, more like it), ate our meals, told jokes and ghost stories at night, and generally acted like a bunch of adolescents at summer camp for a week. In addition to the real science we accomplished at the fossil site, there was much fun and a lasting sense of camaraderie among the veterans of the Thomas Farm digs, memories of a lifetime. Thanks to your efforts, the Thomas Farm fossil fauna has grown into one of the most important collections the museum holds in trust for its citizens. In the later years we had the annual workshops at the museum where many of you had a chance to work on the specimens you found. Although, the *Pony Express* Digs have ended, there is continuity to your endeavors. Dr. David Steadman, our resident Curator of Birds, has taken up the banner. Thanks to the fossil specimens you have found at Thomas Farm Dr. Steadman is now devoting his efforts to recover and document the little known bird fauna of Thomas Farm. Great job, Everyone!

Russ McCarty, Preparator VP

Calendar of Events 2004 - 2005

Thomas Farm Spring Digs at Thomas Farm led by Dr. David Steadman

Session 1 - March 31 - April 3, 2005

Session 2 - April 7 - April 10, 2005

Limit: 14 persons per Dig.

Price: \$275 per person. The price includes everything that was provided in previous Pony Express Digs:

• All meals from dinner on Thursday through lunch on Sunday and full access to the facilities • Evening lectures by fossil experts on Friday and Saturday nights • Great company and a very good time excavating at one of Florida's most famous and productive fossil sites. **Please direct inquiries**

David Steadman: dws@flmnh.ufl.edu telephone: 352-392-1721 x 464 or 465

Newberry Rhino Dig: November 16 - December 18, 2004

The Division of Vertebrate Paleontology of the Florida Museum of Natural History will conduct a major fossil excavation near Newberry, Florida. We seek interested individuals who would like to volunteer to assist and work side-by-side with museum staff and students excavating 8-million-year old fossils of rhinoceroses, elephants, horses, camels, and many other extinct animals. No experience necessary--just a willingness to work hard. **Please direct inquiries to:** Dr. Richard Hulbert, Vertebrate Paleontology Collection Manager: e-mail: rhulbert@flmnh.ufl.edu. For more information and registration forms: http://www.flmnh.ufl.edu/vertpaleo/2004_dig.htm.

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Editorial Staff:

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- Erika H. Simons, Editor and Program Coordinator

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Please make checks out to **UF Foundation** and send your request to: *Pony Express*Bruce MacFadden
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